Peatland carbon balance and climate change: from the past to the future

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Abstract

Storage of atmospheric carbon in northern peatlands imparts a cooling effect upon global climate. Climate change may alter peatland carbon cycling, accelerating both decomposition and plant productivity, potentially driving positive or negative climate feedbacks. Experimental and palaeoecological methods are commonly used to investigate peatland responses to climate change, but results are often in disagreement. Whether positive or negative climate feedbacks will dominate in the future is uncertain. This thesis links experimental and palaeoecological approaches on a raised bog in Wales (Cors Fochno), testing the effects of ten-years of warming and increased drought frequency upon ecosystem functioning, and comparing climate responses with those that have occurred in the bog during the past ~1500 years.

In the experimental plots, warming reduced both carbon accumulation and methane emissions, and when combined with drought caused the bog to become a net carbon emitter. Shrub abundance increased with warming, which was also seen in the palaeoecological record. *Sphagnum* abundance did not respond to experimental manipulations. During the past ~1500 years, changes in carbon accumulation corresponded with vegetational succession. Sustained water table drawdown and wildfires resulted in more decay-resilient plant communities. Climate manipulation altered the stabilisation of organic matter with depth. Temperature increases similar to those in the past millennium did not affect decay rates in the plots. Decay during the last ~1500 years resulted from vegetation changes, rather than from temperature changes.

Climate change may cause positive feedbacks to dominate in the short term, but long-term shifts towards more decay resistant plant species may offset emissions and contribute to climate cooling. The climatic sensitivity of peatland palaeoecological proxies should be tested in modern settings before they are used to test climate models. As a result of anthropogenic disturbance, palaeoecological records are no longer a good analogue for contemporary and future peatland functioning.

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Declaration

I declare that this thesis is a presentation of original work and that I am the sole author. This work has not previously been presented for an award at this, or any other university. All sources are acknowledged as references. The co-authors of the papers presented in this thesis can affirm that they are substantively the work of the PhD candidate, L. Andrews.

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L. Andrews was invited to submit a paper reviewing the usefulness of testate amoebae in pollen slides as indicators of palaeohydrological change, for a special issue about non-pollen palynomorphs published by the Geological Society of London. This was submitted on the 20th Feb 2020 and was published on the 8th Mar 2021, and is included in the appendices (Appendix IV). The full reference is:

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Chapter 1: Introduction

1.1. Motivation

In 2015, global average atmospheric carbon dioxide concentrations exceeded 400 ppm for the first time in recorded history. As of 2021, average rates exceed 415ppm and are increasing (NOAA, 2021). The past six years have seen record breaking global temperatures, with 2020 and 2016 the warmest years since records began (Voosen, 2021).

Most of the world's ecosystems are affected by anthropogenic climate change (Nolan *et al.,* 2018). These impacts may affect ecosystem functions such as carbon cycling in terrestrial ecosystems, potentially impacting feedback mechanisms that may ameliorate or intensify climate warming (Field *et al.,* 2007). One such ecosystem is peatlands, which store around 600 billion tonnes of carbon in their soils (Yu, 2011). This has accumulated throughout the past c. 10,000 years due to an imbalance between productivity and decay (Gorham, 1991; MacDonald *et al.,* 2006). Peat initiation mainly occurs in cooler, wetter ecosystems such as those that occur in higher latitudes (Limpens *et al.,* 2008; Xu *et al.,* 2018). While rropical and Southern Hemispheric peatlands also represent globally significant carbon stores and are also responsive to the effects of climate change (Leng *et al.*, 2019), the focus of this thesis is on Northern Hemispheric peatlands. In the Northern Hemisphere, the biggest future changes in temperatures and precipitation are projected to occur due to climate change (Lee *et al.,* 2021). These changes may disrupt the carbon balance of peatlands (Belyea, 2009; Frolking *et al.,* 2011).

Peatland ecosystems are complex and climate change may impact on a number of autogenic and allogenic processes that moderate a sites' response to climate change stressors (Frolking *et al.,* 2009; Waddington *et al.,* 2015). Peatlands influence climate primarily through exchanges of two important greenhouse gases with the atmosphere: carbon dioxide (CO_2) and methane (CH_4) (Blodau, 2002; Bridgham *et al.,* 2006). The former is more abundant, but the latter has a more potent effect upon radiative forcing (Forster *et al.,* 2021). CO_2 is mainly produced in aerobic conditions whereas CH_4 production occurs under anaerobic conditions beneath the water table, and peatlands absorb CO_2 by photosynthesis of plants and microbes living on their surface (Bubier *et al.,* 1995; Wu and Roulet, 2014). Currently, pristine peatlands are considered to be net carbon sinks, cooling global climate (Korhola*,* 1995; Frolking and Roulet, 2007). However, the effects of climate change are likely to affect the proportion in which these gases are emitted to the atmosphere from peatlands: warming may increase plant productivity, increasing CO_2 uptake, but may also increase the rate of decay resulting in increased CO_2 production (Fenner and Freeman, 2001; Loisel and Yu, 2013). Likewise, CH_4 emissions may increase with rising temperatures but soil drying may reduce CH_4 production (Couwenburg, 2009; Huang *et al.,* 2021). Climate change is also likely to influence plant community composition in peatlands, which are fundamental for peat growth and ecosystem functioning (Walker *et al.,* 2016; Dieleman *et al.,* 2015). Changes in peatland vegetation may influence carbon accumulation, decomposition rates and CH_4 emissions (Ward *et al.,* 2013; 2015; Bell *et al.,* 2018). Peat soils are mainly composed from the remains of dead vegetation. The character of the overlying plant community therefore directly influence rates of carbon accumulation and decomposition (Dieleman *et al.,* 2015; Walker *et al*., 2016).*Sphagnum* mosses are an important peat forming moss which function as ecosystem engineers, maintaining peatland ecosystem functioning (van Breemen, 1995). Changes in *Sphagnum* cover and replacement by other vegetation types (e.g., vascular plants such as shrubs or sedges) may drive substantial changes in soil biogeochemistry, hydrology, plant productivity and decomposition (Ward *et al.,* 2013; Norby *et al.,* 2019), resulting in changes in carbon cycling. In UK peatlands, a particularly abundant shrub species is *Calluna vulgaris* (Walker *et al*., 2015). This species forms associations with ericoid mycorrhizal fungi in the soil, allowing them to acquire additional resources from the nutrient-sparse peat (Read *et al*., 2004). While shrubs such as C*alluna vulgaris* are able to grow rapidly, sequestering relatively large amounts of carbon relative to slower growing *Sphagnum* mosses (Walker *et al*., 2015), they also produce root exudates which may prime decomposition of belowground peat, enhancing CO_2 emissions (Walker *et al*., 2016). Sedges are another type of vegetation that commonly inhabit peatlands. In northern peatlands, the most widespread sedges are those of the genus *Carex* and the species *Eriophorum vaginatum* (Robroek *et al.,* 2017). Sedges exhibit both high productivity rates and rapid biomass turnover, meaning that they may contribute little to carbon accumulation, but like shrubs they can stimulate peat decay by increasing the supply of readily decomposed plant litter and root exudates into the sub-soil (Marinier *et al.,* 2004). Furthermore, sedges can increase emissions of CH_4, owing to some species possessing specialised cells in their roots called aerenchyma that can facilitate methane transport from deep peat (Greenup *et al.,* 2000; Strack *et al*., 2006a).

It is currently unclear how peatlands will respond to projected climate changes in the future. Two different approaches are generally used to investigate this issue:

Experimental and palaeoecological studies. Experimental studies manipulate changes in environmental conditions (e.g., temperature, precipitation) in laboratory or field settings and monitor how peatland ecosystem functions and processes respond to these changes (e.g., Ward *et al.,* 2013, Dieleman *et al.,* 2015; Jassey *et al.,* 2015; Wilson *et al.,* 2016; Li *et al.,* 2021). Palaeoenvironmental studies investigate how long-term accumulation of carbon by peatlands, inferred from peat cores, changes in response to climate over both space and time (Mauquoy *et al.,* 2002; Gallego-Sala *et al.,* 2018). Both approaches have specific advantages and limitations: Experimental studies can be highly detailed and allow for control of climate variables, but are typically small scale, short lived and are subject to experimental artefacts (Updegraff *et al.,* 2001; Johnson *et al.,* 2013). Palaeoecological studies allow for consideration of peatland responses to real climate change events over time-periods far longer than are possible with experimental studies (multi-decadal to millennial), but do not allow for mechanisms of change to be explored at the same level of detail as is possible with experimental studies (Mauquoy and Yeloff, 2008). Additionally, carbon accumulation rates derived from peat cores are subject to artefacts relating to differences in the degree of decomposition that has taken place through time, as well as by removal of peat, which may occur as a result of wildfire, loss via hydrological pathways, erosion, or peat extraction (Holden, 2005; Ratcliffe *et al.,* 2018). Core-derived carbon accumulation rates cannot quantify carbon losses from the system (Young *et al.,* 2019; 2020). Both methods are complimentary and could be applied together for the same site. This may allow for a better understanding of the results of experimental studies in the context of a sites' long-term history and to better understand the mechanisms that influence both short- and long-term processes (e.g., carbon accumulation) in peatlands (Lamentowicz *et al.,* 2016).

However, these approaches are rarely applied together. The results of both approaches are often very different. For example, experimental research in peatlands suggests that climate warming may result in the rapid loss of ancient, deep carbon, enhancing climate warming (Dorrepaal *et al.,* 2009; Walker *et al.,* 2016). By contrast, much of the palaeoecological research suggests the opposite: peatlands accumulate greater quantities of carbon under warmer climatic conditions (Mauquoy *et al.,* 2002; Charman *et al.,* 2013; Gallego-Sala *et al.,* 2018).

The aim of this thesis is to understand how climate change (warming and drought) may affect northern peatlands in an interdisciplinary study, combining experimental and palaeoecological approaches to identify which result is closest to reality.

1.2. Aims, objectives and hypotheses

The objectives of this thesis are addressed using a long-term climate manipulation experiment that integrates passive experimental warming with simulated periods of episodic, seasonal water table drawdown to determine the effects of climate warming and drought upon ecosystem functions in northern ombrotrophic peatlands. Droughts, as defined in this study, refer to reduced precipitation resulting in low streamflow in rivers and low water levels in lakes and groundwater (van Loon, 2015). Palaeoecological reconstructions are generated using a peat core taken from the same peatland, adjacent to the experimental site. The overarching aim of this thesis is to integrate palaeoecological and experimental studies to better understand peatland ecosystem function and climate feedback responses to climate warming and increased drought severity.

This thesis tests the following primary hypothesis: *Peatlands will impart a net positive climate feedback in response to projected warming and increased drought frequency due to anthropogenic climate change.* This will be accomplished by addressing four general objectives:

1. Calculate modern carbon budgets for the experimental treatments

This study will measure CO_2 and CH_4 fluxes and porewater DOC concentrations from experimentally manipulated plots on an ombrotrophic peat bog and assess how each carbon flux differs in response to experimental warming, drought and combined warming and drought. Functional relationships will be calculated between measured carbon fluxes and environmental variables, and models used to estimate multi-year annual carbon budgets for all measured carbon fluxes within each plot, using logged environmental conditions for each experimental treatment. These multi- year carbon budgets will then be assessed to test the effects of each climate manipulations upon annual carbon accumulation rates.

2. Relate the long-term context of carbon accumulation to the modern carbon budgets

This study will create a record of Late Holocene peat accumulation for the site where the experiment is located, as well as long-term (Holocene) average apparent rates of carbon accumulation. Average apparent carbon accumulation rates (derived from a peat core) will be calculated for known periods of climate change during the Late Holocene. These results will be compared with the modern multi-year carbon budgets for each experimental treatment, to assess where the carbon budgets for the different manipulations fall within the late Holocene envelope. Finally, possible reasons for the general disagreement between core-derived carbon accumulation rates and estimated net ecosystem carbon budgets will be explored.

3. Test the sensitivity and effectiveness of palaeoenvironmental proxies to simulated warming and drought

This study will assess how organic matter decomposition rates and commonly used palaeoecological proxies for decomposition are affected by warming, drought and combined warming and drought within the experimental site. The climatic sensitivity of each palaeoenvironmental proxy to changes in temperature within the experimental plots will be tested. The changes in temperature imparted by the experimental warming are comparable to those that have occurred during the Late Holocene. The magnitude and direction of changes observed within the experiment will be compared with changes in each proxy, reconstructed from the Late Holocene record, in order to see how faithfully these proxies reflect climate change effects seen in the experiment.

4. Compare responses in the experiment with responses to real climatic change in the past

This study will compare peatland responses to warming and drought seen in the experiment with responses to real climate change that the site has experienced during the Late Holocene. By correlating Late Holocene carbon accumulation rates at Cors Fochno with long-term (> 350 year) instrumental measurements of environmental conditions for central England, and reconstructed average temperature anomalies for the Northern Hemisphere, relationships between long-term drivers of carbon accumulation may be explored. The drivers of long-term carbon accumulation will be compared with those governing contemporary carbon fluxes in the experimental plots. Furthermore, changes in vegetation community composition and carbon accumulation rates between known periods of climate change: the Medieval Climate Anomaly (MCA; c. 950 – 1250 CE) and the Little Ice Age (LIA; c. 1350 – 1850 CE) (Mann *et al.,* 2009) will be compared with the annual carbon budgets from the experimental plots, to determine whether the experiment realistically reflects the magnitude and direction of change seen following climatic changes in the past.

Together, these objectives meet the overarching aim of uncovering the reasons underlying the apparent disparity between the results of experimental and palaeoecological studies and will reduce uncertainty as to how peatlands may respond to future anthropogenic climate change, determining their future role in the global climate system.

1.3. Thesis structure

This thesis is presented as a sequence of three standalone papers, applying a novel suite of interdisciplinary methods to address the above set of objectives. The first chapter provides a general introduction, setting the motivation, aims and objectives of the thesis. This is followed by a literature review summarising the background and rationale behind the project. The second chapter provides a comprehensive methodology for the thesis, detailing how the objectives will be met using a multi-disciplinary framework, applying a suite of field, laboratory, and statistical methods. The third chapter assesses whether changes in vegetation community seen in the experimental treatments are represented by the long-term palaeo-vegetation record during past periods of warming and water table drawdown.

In this thesis, the following hypotheses are tested:

1. The experimental site at Cors Fochno imparts a significant treatment effect upon air temperature and water table depth comparable to future projected climate changes for the region.
2. Ten years of experimental warming, drought and combined warming and drought drives significant changes in plant community composition in our experimental site.
3. The effects of experimental warming and drought upon plant community composition are amplified in the plots where these treatments are applied in combination.
4. Changes in plant community composition seen in the experimental plots resemble those that occurred in the long-term vegetation record within the same site over the past c. 1500 years in response to past warming and drought.

In chapter four, measured carbon fluxes and multi-year annual carbon budgets are compared with core-derived long-term carbon accumulation rates from the same site, and reasons for the apparent disparity between palaeo and experimental studies are explored. This chapter tests the following hypotheses:

1. Experimental warming, drought and combined warming and drought cause a net reduction in carbon accumulation rates within the experimental plots.
2. Experimental warming, drought and combined warming and drought increase the rate of net carbon dioxide emissions from the experimental plots.
3. Experimental warming, drought and combined warming and drought reduce the productivity rate of vegetation within the experimental plots.
4. Experimental warming, drought and combined warming and drought increases the rate of methane emissions within the experimental plots.
5. Experimental warming, drought and combined warming and drought increase the production rate of dissolved organic carbon within the experimental plots.
6. Experimental warming, drought and combined warming and drought cause the peatland to switch from a net sink to a net source of carbon.
7. The effects of warming and drought upon each component of the carbon cycle are amplified within the combined treatment plots.
8. The main environmental drivers governing carbon accumulation rates in the experimental plots resemble those that have controlled long-term carbon accumulation rates for the same site.
9. Long-term carbon accumulation rates derived from peat cores are comparable to carbon budgets estimated for the experimental plots.
10. Changes in carbon accumulation rates seen in the experimentally manipulated plots resemble those seen during warmer and/or drier periods in the palaeoecological record of the same site.

Finally, the effects of experimental warming and drought upon organic matter decomposition and stabilisation and the sensitivity of three palaeoecological decomposition proxies are tested in chapter five. This chapter tests the following hypotheses:

1. Increased temperatures and drought frequency increase the rate of decomposition for below and above-ground litter.
2. These changes are driven by differences in environmental conditions, such as temperature, water table depth and vegetation community composition, within the experimental plots.
3. Changes in decomposition and litter stabilisation rates are reflected by changes in the palaeoecological proxies.
4. The changes seen in the palaeoecological proxies in response to experimentally simulated warming and drought reflect those seen in the palaeoecological record in terms of magnitude and direction in response to past climate warming and/or drying.

Chapter six synthesises the results of these three chapters and discusses their overall implications, fitting them into the context of the existing literature and discussing the implications of these findings for peatlands in the UK and for northern peatlands as a whole. A final concluding chapter describes how, when taken together, the chapters meet the aims and objectives of this thesis and whether we can accept the primary hypothesis.

1.4. Literature review

1.4.1. Climate change

The term ‘climate change’ describes long and short-term changes in local, regional, or global temperature and weather patterns. Throughout Earth’s history, atmospheric greenhouse gas concentrations have influenced global climate (MacDonald *et al.,* 2006; Haywood *et al.,* 2011). For example, the transition between the generally warmer Medieval Climate Anomaly (MCA; c. 950 – 1250 CE) to the cooler Little Ice Age (LIA; c. 1350 – 1850 CE) was associated with reduced atmospheric CO_2 concentrations of between 7 – 10 ppmv (Lamb, 1965; Mann *et al.,* 2008; 2009).

The global carbon cycle describes the movement of carbon between the ocean, atmosphere, and terrestrial biosphere (IPCC, 2021; Figure 1.1.). The carbon-based greenhouse gases CO_2 and CH_4 are important components of this cycle (Friedlingstein *et al.,* 2020). Since 1750, atmospheric concentrations of CO_2 and CH_4 have risen by 47 % and 156 % respectively, mainly as a consequence of anthropogenic activities such as fossil fuel combustion and land use changes (IPCC, 2021). This has warmed global mean surface temperatures, such that 2001 – 2020 was the warmest 20-year period in recorded history, with temperatures higher by c. 1°C relative to 1850 – 1900 baselines (IPCC, 2021). Projections of future climate change indicate that global mean temperatures will continue to increase throughout the 21st century (Lowe *et al.,* 2018; IPCC 2021). Even the most optimistic projections indicate that global temperatures will increase by at least 1.5 °C by 2100 (IPCC, 2021). Climate warming is projected to affect global weather patterns, change regional precipitation rates, and may increase the frequency and intensity of droughts in some regions (Lee *et al.,* 2021).

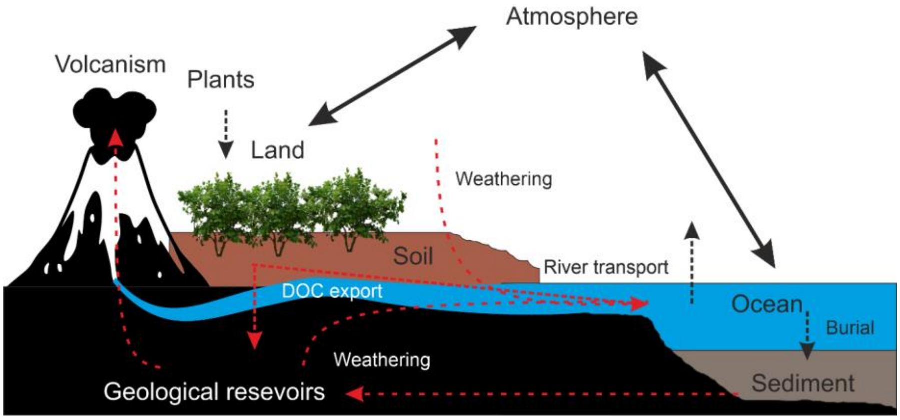


Figure 1.1. Simple model of the global carbon cycle showing its main components. Figure adapted from IPCC, 2021.

Terrestrial ecosystems such as peatlands are important contributors to the biological carbon cycle, exchanging CO_2 and CH_4 with the atmosphere and storing vast quantities of organic carbon in their soils (Gorham, 1991; Clymo *et al.,* 1998; Davidson and Jassens, 2006; Nichols and Peteet, 2019). Their ability to sequester and store carbon depends upon prevalent climatic conditions that govern the balance between carbon uptake and microbial decay (Harenda *et al.,* 2018). Future climate change threatens to disrupt this balance, potentially releasing ancient, stored carbon into the atmosphere (Chapin *et al.,* 2006; Dorrepaal *et al.,* 2009). This potential for climate feedback means that understanding how peatlands will respond to future climate changes is an important research priority (Wilson *et al.,* 2016; Hopple *et al.,* 2020).

1.4.2. What are peatlands?

Peatlands are terrestrial wetland ecosystems characterised by their anoxic, waterlogged soils, which are composed mostly of organic material (>60 %) (Joosten and Clarke, 2002; Chambers and Charman, 2004). Peatlands differ from other terrestrial wetlands due to their shallow water table and anoxic biogeochemistry that facilitates their highly efficient carbon store function (Charman, 2002). They are important habitats for many specialised species of plants and animals and provide a wealth of ecosystem services that are of importance to society, such as drinking water provision, flood mitigation and carbon sequestration (Gorham, 1991; Gao *et al.,* 2016; Fenner *et al.,* 2021).

Peatlands cover approximately 4.2 million km^2 of terrestrial land, roughly equivalent to the area covered by all EU member states (Xu *et al.,* 2018). They develop where climatic and topographic conditions allow for organic matter to accumulate more quickly than it can decay (Clymo *et al.,* 1998). These conditions are most prevalent in the Northern Hemisphere (between 45 – 75 °N), where c. 80 % of all peatlands reside, with the largest concentrations found in Russia, Canada, and the United States of America (Limpens *et al.,* 2008; Xu *et al.,* 2018). In these regions, a large proportion of peatlands are underlain by permafrost (Hugelius *et al.,* 2020).

1.4.3. Peatland formation, classification, and development

Modern peatland initiation in the Northern Hemisphere began following the end of the last Glacial Period. The oldest sites developed in ice-free portions of North America and Asia c. 16 – 14 kyr BP (thousand years before present: 1950 CE) followed by more widespread initiation as glacial ice receded, with the highest rates of peat initiation occurring between 12 and 8 kyr BP (MacDonald *et al.,* 2006). Peat initiation occurs by three pathways: 1. terrestrialisation, where organic matter fills a lake or depression until peatland vegetation establishes; 2. primary peat formation on exposed mineral soils, where peat develops without an aquatic phase (Noble *et al.,* 1984; van Breemen, 1995) and 3. paludification, where peat expands laterally from its site of initiation (Korhola *et al.,* 1996; Anderson *et al.,* 2003).

Methods for the classification of peatlands differ regionally and between disciplines (Lindsay, 2016). Peatlands are mostly described in terms of their hydrology. For example, ombrotrophic (rain-fed) bogs depend upon precipitation for their hydrological and mineral inputs, whereas minerotrophic fens are fed by ground or surface water and thus their soils are relatively enriched by nutrients and minerals (Wheeler and Proctor, 2000; Bridgham *et al.,* 2008). Fens can be further classified by the relative richness of their mineralogical supply, ranging from relatively nutrient poor (oligotrophic) to heavily enriched (eutrophic) sites (Lindsay, 2016). Fens may also be differentiated by their water source: some are fed primarily by ground water (topogenous) while others by overland water flow (soligenous) (Wheeler, 1984).

Following initiation, peatlands undergo gradual vegetational successions resulting in ecological transition in response to changes in their hydrology and nutrient supply over time (Granath *et al.,* 2010). For example, a fen may transition into a relatively nutrient deficient ‘poor fen’ or become an ombrotrophic ‘bog’ as vertical peat accumulation separates the surface peat from its groundwater supply (Ingram, 1982; Belyea, 2009). Transitions into ombrotrophic bogs only occur in areas where precipitation rates exceed those of evapotranspiration and run-off, allowing a positive water balance to be maintained (Lindsay, 2016). Ombrotrophic bogs often differ from one-another in terms of their continental setting; oceanic bogs receive increased supplies of nutrients and ions from seawater than continental sites and thus often exhibit differing vegetation and ecosystem functions (Sparling *et al.,* 1967). Large differences in pore water chemistry, litter quality, trace gas fluxes, carbon accumulation rates and water table levels can occur between sites of differing trophic status (Bridgham *et al.,* 1996; 1998; 2008; Chapin *et al.,* 2004). Differences in nutrient supply often mean peatlands exhibit large variation in plant community composition, with fens typically having more abundant sedges and limited shrub cover, while ombrotrophic bogs are mostly dominated by mosses (Lindsay, 2016). These differences in vegetation may explain the variation in ecosystem functioning between fens and bogs, since plant community composition in peatlands are key drivers behind many ecosystem functions (Ward *et al.,* 2013; Kuiper *et al.,* 2014; Robroek *et al.,* 2015; 2017).

The waterlogged, acidic, and nutrient deficient conditions characteristic of peatland soils are hostile to many types of vegetation, thus northern peatlands are botanically simple ecosystems (Rodwell, 1991). Northern peatlands are typically dominated by bryophytes, particularly in the case of ombrotrophic bogs (Rydin and Jeglum., 2006). Mosses of the family Sphagnaceae are characteristic of northern peatlands and are widely considered to be the most important peat-forming vegetation in the world (van Breemen, 1995). *Sphagnum* mosses grow vertically from their terminal apex (the capitulum). They feature multiple branches that radiate from a central stem, covered by single celled leaves, featuring two distinctive cell types. One type of cell is enlarged, porous and thickened, facilitating water storage and vertical transport to the growing parts of the plant (hyaline cells). The other cell type is smaller and enclosed, facilitating photosynthesis (chlorophyllose cells) (Clymo and Hayward, 1982). *Sphagnum* mosses are fundamental to the stability and resilience of northern peatlands (Turetsky *et al.,* 2012), producing decay-resistant litter (Dorrepaal *et al.,* 2005; Ward *et al.,* 2009), antimicrobial compounds that inhibit decomposition (van Breemen, 1995; Opelt *et al.,* 2007) and contributing to the water-holding capacity of peat, whilst simultaneously creating their own ecological niche at the expense of other vegetation (van Breemen, 1995).

Despite the adverse growing conditions created by *Sphagnum* mosses, other vegetation also frequently co-occur in peatlands (Dorrepaal *et al.,* 2005; Kuiper *et al.,* 2014). These include vascular plants such as sedges, forbs, grasses, shrubs, and trees. The latter two often occur as stunted, dwarfed forms due to the nutrient deficient and waterlogged conditions in which they grow (van Breemen, 1995). The distribution of peatland vegetation varies within sites across ecological gradients, relating to spatial variation in nutrient availability and hydrology (Andersen *et al.,* 2011). This spatial differentiation results in the development of an undulating microtopography across peatland surfaces. Within this heterogenous landscape, the distribution of competing species depends upon their ecological preferences (Andersen *et al.,* 2011). Dry-tolerant species may form raised hummocks while others occupy hollows or lawns which are closer to the water table (Clymo and Pearce, 1995; Anderson *et al.,* 2011).

1.4.4. Peat accumulation, carbon cycling and storage

Peat grows over thousands of years as vegetative material accumulates vertically over time. Decomposition is inhibited by the anaerobic and cool conditions in the sub-soil (Yavitt *et al.,* 1997; Billet *et al.,* 2010). Organic carbon stored within this buried organic matter may be stored for thousands of years under these conditions (Davidson and Jassens, 2006; Belyea, 2009). The steady accumulation of peat over thousands of years has resulted in northern peatlands storing more carbon than any other terrestrial ecosystem, estimated at around 612 billion tonnes of carbon (Gt C) (Yu 2011), despite their relatively small extent (c. 3 % of terrestrial land cover) (Gorham, 1991; Xu *et al.,* 2018). This constitutes around one third of all terrestrial soil stocks (Gorham, 1991; Waddington *et al.,* 2015), while some estimates suggest that the peatland carbon store is higher than 1000 Gt C (Nichols and Peteet, 2020). The continuous sequestration and storage of atmospheric carbon by peatlands since their initiation is estimated to have cooled global temperatures by 1.5-2.0°C throughout the Holocene (Korhola *et al.,* 1995; Frolking and Roulet, 2007). Peatlands do not always have a cooling effect upon global climate (MacDonald *et al.,* 2006). Peat soils can also be sources of greenhouse gases, emitted in the form of CO_2 and CH_4, which are produced as end products of decay processes in the peat (Blodau, 2002; Bridgham *et al.,* 2006).

A simplified version of the peatland carbon cycle is shown by Figure 1.2. Peatland carbon balances are governed by different processes occuring within two separate stratigraphic zones, differentiated by aerated (oxic) and permanently waterlogged (anoxic) conditions (Frolking *et al.,* 2009). The uppermost zone, representing recently accumulated peat above the water table is termed the acrotelm (Ingram, 1978). This zone is typically between 20 – 30 cm thick and is characterised by fluctuating soil moisture levels, living vascular plant roots and a large supply of labile (readily decomposed) organic material (Lindsay, 1996; Limpens *et al.,* 2008). In the acrotelm, peat is relatively uncompacted, allowing for water to flow both laterally and vertically (Reeve *et al.,* 2000; Jennings *et* *al.,* 2020). Here, atmospheric CO_2 is sequestered by autotrophs (vegetation and photosynthetic microbes) in the uppermost surface (Jassey *et al.,* 2015). Northern peatlands typically sequester CO_2 at a rate of between 20 to 60 g CO_2 – C m^{-2} y^{-1} (Wu and Roulet, 2014), with productivity rates governed by the availability of light, temperature, soil moisture and the composition of the overlying vegetation community (Frolking *et al.,* 1998; Bubier *et al.,* 1999; Dinsmore *et al.,* 2013; Peichl *et al.,* 2018). Within this zone, aerobic conditions allow heterotrophic microbes to use oxygen in their metabolic processes, producing mainly CO_2 as a by-product of the decay of organic matter (Clymo and Hayward, 1982). The high abundance of labile (readily decayed) organic material in the acrotelm means that c. 90 % of all the carbon stored in this zone is promptly returned to the atmosphere (Gorham, 1995).

Decay rates decline as temperatures fall and recalcitrant (decay resistant) organic matter concentrations increase with depth throughout the peat profile (Gorham, 1995; Moore, 2002). Remaining buried organic material eventually enters the zone of peat permanently beneath the water table, termed the catotelm (Ingram, 1978). This zone is characterised by reduced hydraulic conductivity, lower soil temperatures and the presence of methanogens; organisms of the kingdom Euryarchaeota (Domain Archaea). These methanogens produce CH_4 as the final product in the decay of organic material. In the catotelm, the rate of decay is greatly reduced and organic carbon entering this zone may be stored for timescales from centuries to millennia (Wilson *et al.,* 2016). Radiocarbon analysis of CH_4 and CO_2 emissions from peat suggests that most trace gas emissions derive from recently deposited material rather than older carbon (Charman *et* al., 1999; Chasar *et al*., 2000; Wilson *et al.,* 2016). This suggests that most CH_4

production is not entirely derived from the older accumulation of peat buried at depth (Chasar *et al.,* 2000). Therefore, although decay processes do continue at depth, carbon stored within the catotelm is more-or-less stable.

Because the depth of each zone is defined by the height of the water table, hydrological changes determine the volume of substrate available for aerobic and anaerobic decay to occur (Rowson *et al.,* 2013). Lowered water tables, resulting from drought or anthropogenic disturbance, increase the depth of the acrotelm, generally facilitating increased CO_2 emissions and reducing CH_4 emissions (Turetsky *et al.,* 2008; Frolking *et al.,* 2011). Such changes can cause individual peatlands to switch from being net carbon sinks to sources (Moore and Roulet, 1993; Alm *et al.,* 1999).

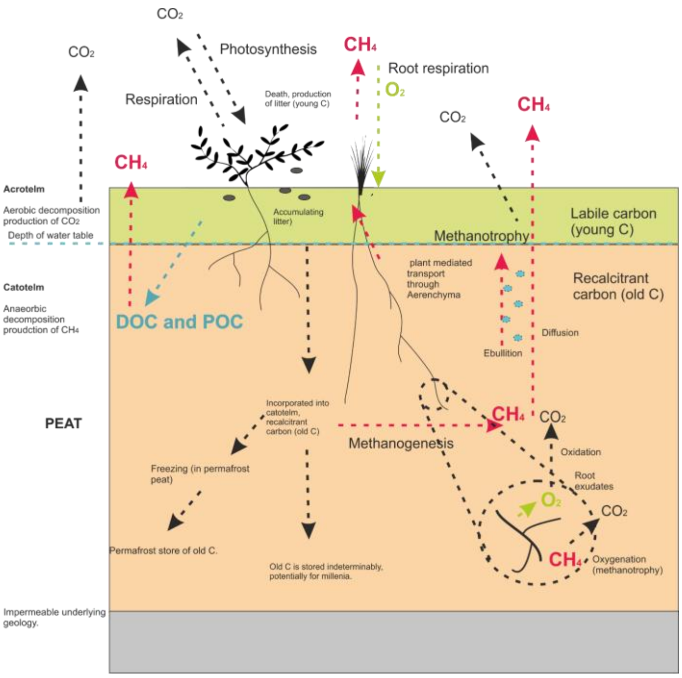
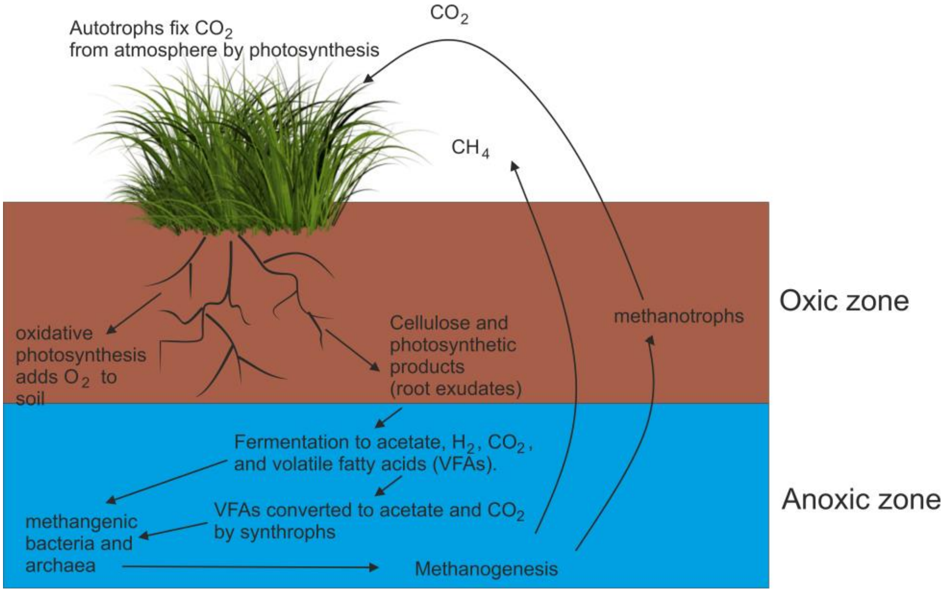


Figure 1.2. Simple model of the peatland carbon cycle.

1.4.5. Methane production, emission, and oxidation

CH_4 production (methanogenesis) occurs under anaerobic conditions and is mainly driven by soil moisture and water table depth (Moore and Roulet, 1993; Bubier *et al.,* 1995). Other important controls also include plant community composition, temperature, the character of the microbial community, and the chemical properties of the soil (Turetsky *et al.,* 2008; Ward *et al.,* 2013). Due to the number of factors that can influence methanogenesis, the rate of CH_4 production can show great spatial and temporal variation (Moore *et al*., 1990). In peatlands, acetoclastic methanogenesis and CO_2 reduction are the most common pathways for CH_4 generation (Conrad, 1999, Figure 1.3). In fens with a high abundance of *Carex* sedges, the supply of high-quality root exudates has been shown to favour CH_4 promotion by acetate fermentation (Galand *et al.,* 2005; Keller and Bridgham 2007; Noyce *et al.,* 2014) whereas in *Sphagnum* dominated peat bogs, more methane is produced by the reduction of dissolved CO_2 (Kelly *et al.,* 1992).

Figure 1.3. Diagram illustrating methane production pathways in peatlands (Based upon Kotsyurbenko *et al*., 2019).



In general, CH_4 production rates increase along with increasing temperatures and fall with increased water table depth (Turetsky *et al.,* 2008; Frolking *et al.,* 2011). Methane production rates are also influenced by the abundance of other microorganisms that compete with archaea for metabolic substrates (Kotsyurbenko *et al.,* 2019) such as sulphate or iron reducing bacteria and acetogens (Hunger *et al.,* 2015). A large portion of the CH_4 produced by peatlands is oxidised into CO_2 by methanotrophic organisms in the oxic layer above the water table (Smemo and Yavitt, 2011; Gupta *et al.,* 2012; Boon *et al.,* 2014). The balance between CH_4 production (methanogenesis) and oxidation (methanotrophy) determines the rate at which CH_4 is emitted from peatlands into the atmosphere (Couwenburg, 2009). Some methanotrophs are symbiotic with *Sphagnum*, meaning that the presence of *Sphagnum* may limit the amount of CH_4 released from peatlands (Hornibrook *et al.,* 2009; Kip *et al.,* 2010; Nichols *et al*., 2014).

CH_4 is transported through the peat into the atmosphere by three pathways: diffusion through the soil, ebullition (bubbling) and via plant mediated transport, channelled through gas conduits termed aerenchyma, present in the roots of vascular plant species, mostly sedge-type vegetation (Bubier and Moore, 1994; Joabsson *et al.,* 1999; Couwenburg, 2009; Greenup *et al.,* 2000). Aerenchyma are an adaptation that allow species possessing them to survive in waterlogged soils by providing a route for oxygen to reach their growing roots (Kelker and Chanton, 1997). Transport of CH_4 either through aerenchyma or by ebullition means CH_4 can bypass the methanotrophic layer at the peat surface, and thus high sedge abundance can lead to large CH_4 emissions (Segers, 1998; Bridgham *et al.,* 2013; Couwenberg, 2009). Because sedges often develop roots that can be tens of centimetres deep, the presence of these vegetation may greatly enhance CH_4 production and transport, greatly increasing CH_4 emissions (Lai, 2009).

Ebullition is another major pathway for methane emissions from peatlands (Ramirez *et al.,* 2015). Ebullition is the process whereby CH_4 is emitted to the atmosphere as bubbles, which form when pore waters become super-saturated with CH_4 (Chanton and Whiting, 1995). These bubbles accumulate within the pore-spaces in the peat and travel through the peat column as more CH_4 is produced (Ramirez *et al.,* 2015). If these bubbles are emitted slowly, much of this CH_4 may be consumed by methanotrophs, however abrupt emissions can occur if this gas is suddenly released all at once, either the result of a gas pressure threshold being crossed, or following disturbance (Lai, 2009; Ramirez *et al.,* 2015).

Greenhouse gases have differing radiation absorption efficiency and atmospheric residency times, therefore their effect upon climate is often disproportionate to their total emissions. Peatlands are one of the biggest natural sources of atmospheric CH_4, emitting almost as much CH_4 annually as is produced by human activity (Mikaloff-Fletcher *et al.,* 2004; Frolking *et al.,* 2011). CH_4 is an important greenhouse gas, contributing c. 20% of all radiative forcing related to greenhouse gasses and contributes the most to climate change after CO_2, despite constituting only a minute fraction (c. 1 % on a mol/mol basis) of total atmospheric carbon (Abdalla *et al.,* 2016). The relative contributions of greenhouse gases are often compared using an index known as Global Warming Potential (GWP). This index accounts for differences in the radiative properties and atmospheric lifetimes of different greenhouse gases relative to CO_2 (Stoker *et al.,* 2013). Most studies follow the Kyoto Protocol for estimating GWP, which uses a 100-year time horizon and only considers direct radiative effects of greenhouse gas pulse emissions (Grubb *et al.,* 1999; Roulet, 2000). The IPCC considers CH_4 to have a GWP c. 27.2 times higher than CO_2 over a 100-year horizon (Forster *et al.,* 2021). By this protocol, the combined contributions of CO_2 and CH_4 from peatlands are frequently considered to act as net sources of atmospheric greenhouse gases, and thus contribute towards climate warming over short timescales (Whiting and Chanton, 2001; Frolking and Roulet, 2007). However, over 100 years, the warming effect of CH_4, which has an atmospheric half-life of c. 8.6 years, diminishes (Muller and Muller, 2017). By this time the warming effect of the remaining CH_4 is overcome by the net sequestration of CO_2 by peatlands, and they are considered net greenhouse gas sinks, imparting a net cooling effect upon global climate (Frolking *et al.,* 2006; Whiting and Chanton 2001; Frolking and Roulet, 2007). However, GWP estimates are highly uncertain due to their reliance on several doubtful assumptions, e.g., that atmospheric concentrations of greenhouse gases, are unchanging over time (Roulet, 2000; Lashof, 2000) They may be misleading, because these estimates are based upon single pulse emissions and do not consider the cumulative effects of changes in CH_4 emissions over time (Allen *et* al., 2018; Lynch *et al*., 2020).

1.4.6. Hydrological carbon fluxes from peatlands

Another important yet often overlooked component of peatland soil carbon fluxes are those lost via hydrological pathways, in the form of particulate and dissolved organic carbon (POC and DOC) as well as dissolved inorganic carbon (DIC). (Freeman *et al.,* 2004a; Dawson *et al.,* 2004; Strack *et al.,* 2008; Dinsmore *et al.,* 2013). DOC includes organic carbon smaller than 0.45µm (Thurman, 1985) and is comprised of a mixture of simple organic acids and complex molecules such as humic and fulvic acids, principally derived from plant exudates and soil organic matter (Moore and Dalva, 2001; Wiłkomirski and Malawska, 2011). Studies of aquatic carbon fluxes from peatlands tend to focus on DOC, because the other fluxes typically represent a relatively insignificant portion of peatland carbon losses, particularly in pristine sites where peat erosion is minimal (Lindsay, 2010; Dinsmore *et al.,* 2013), although a certain amount of DIC can be added in the form of dilute carbonic acid in rainfall and as dissolved CO_2 (Lindsay, 2010).

Fluxes of both POC and DIC are generally considered to be low from acidic peat soils, although both have the potential to represent important carbon fluxes from peatland systems (Davidson and Janssens, 1997). These fluxes are commonly ignored in peatland carbon budgeting studies (Ryder *et al*., 2014), with the exception of a few studies for upland peat catchments in the UK (e.g., Worrall *et al.,* 2003; 2007).

DOC can be quantified both in terms of its *in-situ* production and export from a site (Strack *et al.,* 2008). Pore-water DOC concentrations vary widely between sites, with values ranging from 3 to 400 mg l^{-1}, although values typically average around 30 mg l^{-1} (Strack *et al.,* 2008). DOC production has been linked to several physical and hydrological factors, including soil properties and vascular plant productivity, with increased root exudate supply promoting DOC production (Moore and Dalva, 2001; Freeman *et al.,* 2004a; Dinsmore *et al.,* 2013). Reduced soil moisture has been shown to increase pore-water DOC production by enhancing the rate of peat erosion (Holden, 2005). Other factors include changes in atmospheric CO_2 concentration, higher air and soil temperatures, changes in microbial and enzyme activity and soil chemistry (Worrall and Burt, 2008; Freeman *et al.,* 2001a; 2004a; Monteith *et al.,* 2007; Oulehle *et al.,* 2013; Kang *et al.,* 2018). DOC concentrations in waterways have increased in peatland dominated catchments throughout the past few decades (Schlunz and Schneider, 2000; Freeman *et al.,* 2001; Worrall *et al.,* 2003; Evans *et al.,* 2012).

While future changes in water table depth, vegetation, and droughts due to climate change may enhance DOC production (Freeman *et al.,* 2004a; Tang *et al.,* 2013), the increased DOC production seen in recent years has been attributed to changing DOC solubility following recovery after acidification (Kang *et al.,* 2018). The export of peat DOC is controlled by hydrology and is greater in peatlands with higher discharge rates (Pastor *et al.,* 2003; Freeman *et al.,* 2001). Large hydrological carbon fluxes can occur following extreme flow events such as storms (Hinton *et al.,* 1997; Austnes *et al.,* 2010), especially following periods of prolonged drought, as biogeochemical and physical changes promote decomposition and erosion of peat (Freeman *et al.,* 2001; Worrall and Burt, 2004; Worrall *et al.,* 2006; Ryder *et al*., 2014). DOC fluxes following storm events tend to be highest during the summer and autumn relative to those occurring during the winter and spring, due to the rapid flushing of DOC produced during the warmer months following the first heavy rainfall event (Kohler *et al*., 2009; Jennings *et al*., 2020).

Rates of DOC efflux from intact peatlands typically range between 10 – 20 g C m^{-2} yr^{-1} (Frolking *et al.,* 2009) but can be as high as 25 – 40 g C m^{-2} yr^{-1} from degraded sites (Billett *et al.,* 2004; Dinsmore *et al.,* 2010; Strack and Zuback, 2013). Therefore, DOC can represent an important carbon flux, sufficiently large to cause a peatland to switch from being a net sink to a net source when considered in annual carbon budgets.

1.4.7. Nitrous oxide

In addition to CO_2 and CH_4, peatlands contribute the greenhouse gas N_2O to the atmosphere. N_2O has a GWP 273 times greater than CO_2 over a 100-year time-period (Forster *et al.,* 2021). However, fluxes of this gas are negligible from intact peatlands, which contribute less than 0.2% of total N_2O emissions from natural sources (Frolking *et al.,* 2011). Although these relatively small emissions have the potential to impart a significant climate forcing affect considering their GWP, N_2O is not a component of the carbon cycle of peatlands. For these reasons, we do not consider N_2O emissions in this study.

1.4.8. Effects of anthropogenic disturbance on peatland carbon cycling

Although natural peatlands are considered overall net sinks and stores of carbon, these ecosystem functions have been negatively impacted by anthropogenic disturbance in recent centuries (Turetsky and St. Louis, 2006). Approximately 15 % of all peatlands have been degraded by human activities such as drainage, land conversion for agriculture, grazing, burning and deposition of atmospheric pollutants such as nitrogen and sulphur (Turetsky and St. Louis, 2006; Payne, 2014; Meyer *et al.,* 2015; Joosten, 2016). In Europe, this disturbance has disrupted peatland hydrology over the past c. 300 years, such that only c. 50% of the estimated c. 600,000 km^2 of existing peatlands are still actively accumulating peat (Tannenberger *et al.,* 2017; Swindles *et al.,* 2019). These changes have caused many degraded peatlands to become net carbon sources (Turetsky *et al.,* 2002), despite a net reduction in CH_4 emissions following water table drawdown (Drosler *et al.,* 2008; Swindles *et al.,* 2019; Frolking and Roulet, 2007; Turetsky *et al.,* 2012). Even in relatively pristine or restored sites, peatland functioning may be affected by past disturbances or atmospheric pollution (Talbot *et al.,* 2014; Swindles *et al.,* 2016). Anthropogenic disturbance can also alter the vegetation composition in peatlands. This may be gradual, in response to changes in environmental conditions (Page *et al.,* 2016), or abrupt, resulting from chance events such as wildfire (Shiller *et al.,* 2014). Anthropogenic pollution, such as increased inputs of atmospheric nutrients, also drives local or regional extinction of key species, such as the case for *Sphagnum austinii*, which was a formerly common species in northern peatlands prior to its widespread decline over the past c. 2000 years (Swindles *et al.,* 2015; Schillereff *et al.,* 2021). Changes in peatland vegetation composition have been shown to influence carbon accumulation rates and greenhouse gas emissions (Malmer and Wallén, 2004; Ward *et al.,* 2013; Gatis *et al.,* 2016; Swindles *et al.,* 2019). Changes in the stoichiometry of phosphorous and nitrogen in peat soils due to human activities can also influence decomposition rates and carbon accumulation rates, which may initially stimulate peat accumulation, but also higher rates of decay once certain ecological thresholds are crossed (Schillereff *et al.,* 2021). Peatlands are, therefore, susceptible to become carbon sources as a direct result of human activities.

1.4.9. The role of peatlands in the future climate system

In recent years, there has been growing awareness of the potential vulnerability of the peatland carbon balance and store to anthropogenic climate change impacts (Millar *et* *al.,* 2018). Processes that increase the rate of carbon emissions to the atmosphere could amplify climate warming (Belyea, 2009; Frolking *et al.,* 2011). Climate change is expected to transform the ecology and ecosystem functioning of peatlands, modifying decomposition rates, hydrology, and vegetation communities (Bu *et al.,* 2011). Climate change driven increases in land surface temperatures and changes in precipitation rates are projected be greatest in the northern latitudes where most peatlands reside (Xu *et al.,* 2018; Lee *et al.,* 2021) (Figure 1.4). The stability of the vast carbon pool stored by northern peatlands may be vulnerable to such changes, which threaten to disrupt the hydroclimatic balance favouring peat accumulation above decay. Such concern is based on several studies where warmer and drier conditions lead to enhanced decay rates from peatlands (Ise *et al.,* 2008; Dorrepaal *et al.,* 2009; Fenner and Freeman, 2011). Drier conditions may promote CO_2 production in peatlands but also suppress CH_4 emissions (Huang *et al.,* 2021). These two competing responses confound attempts to determine the magnitude and direction of future climate feedbacks from peatlands in response to warming (Losiel *et al.,* 2021; Huang *et al.,* 2021).

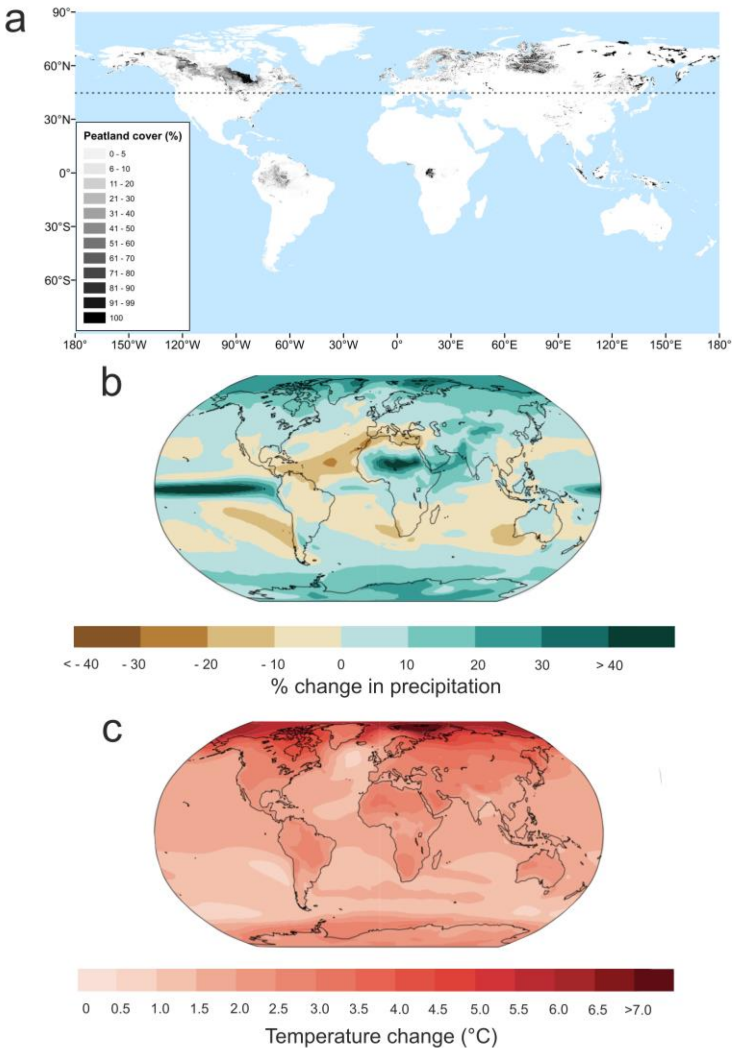


Figure 1.4. Figure illustrating how mid-range climate projections will affect areas with existing peatland climate change. a. PEATMAP, showing global distribution of peatlands. The horizontal dashed line reflects the position of the 45° parallel. All peatlands north of this line are northern peatlands. Figure from Xu *et al.* (2018). b. Projected annual mean temperature changes for the period 2081-2100 relative to 1850-1900 baselines at 2°C global warming. c. annual mean changes in precipitation for the period 2081-2100 relative to 1850 – 1900 baselines. Panels b and c are adapted from IPCC, (2021).

On one hand, warmer temperatures are likely to enhance decay rates and promote CO_2 emissions sufficient to alter the carbon sink capacity of many peatlands (Ise *et al.,* 2008; Bridgham *et al.,* 2008; Dorrepaal *et al.,* 2009; Huang *et al.,* 2021). Such a change may lead to substantial losses of deep, ancient peat (Dorrepaal *et al.,* 2009). Changes in soil moisture and thermal regimes may expose formerly waterlogged peat to oxygen, increasing rates of aerobic decay (Blodau *et al.,* 2004; Roulet *et al.,* 2007; Bridgham *et* *al.,* 2008; Walker *et al.,* 2016). Increased peatland carbon emissions may be triggered by the 'enzymic latch' mechanism (Fenner and Freeman, 2001; Freeman *et al.,* 2004b). Waterlogged conditions inhibit phenol oxidase activity, an enzyme that degrades phenolic compounds that limit organic matter decomposition in peat. Increased phenol oxidase activity may occur as peat is oxygenated following drought or increased evapotranspiration (Fenner and Freeman, 2001). This may increase CO_2 and CH_4 emissions and promote the production of DOC by removing the constraints that usually inhibit decay (Fenner and Freeman, 2011; Freeman *et al.,* 2004b; Huang *et al.,* 2021). Warming in northern regions is also likely to promote permafrost thaw, resulting in increased decomposition and greenhouse gas emissions from affected sites, driving positive feedbacks upon global climate (Christensen *et al.,* 2004; Heimann and Reichstein, 2008). Permafrost thaw may also expose formerly frozen labile organic material to aerobic conditions whilst simultaneously changing the structure and hydrological conductivity of peat, facilitating lower water tables and increased soil aeration. This may accelerate CO_2 production further, enhancing positive climate feedbacks (Frolking *et al.,* 2011; Wisser *et al.,* 2011). Future climate projections also indicate that some regions will experience an increase in the rate, duration, and severity of droughts (Stocker *et al.,* 2013; IPCC, 2021). Seasonal drought can shift peatlands from functioning as carbon sinks to becoming significant sources (Freeman *et al.,* 2001), although the severity of this depends upon many factors including the water-holding capacity of the soil, the sensitivity of overlying vegetation to drought, the duration and severity of the drought and the time of year in which the drought occurs (Heimann and Reichstein, 2008; Lund *et al.,* 2012; Goodrich *et al.,* 2017). While the effects of single drought events and sustained water table drawdown have been relatively well studied in recent years (e.g., Rinne *et al.,* 2020), few studies have examined the long-term effects that may occur due to increased drought occurrence. In addition to drought, increased shrub-abundance and drier conditions may promote the frequency and severity of wildfires. These indirect climate change impacts may further exacerbate carbon losses from peatlands in affected regions (Hogg *et al.,* 1992; Turetsky *et al.,* 2011a; 2011b; Bourgeau-Chavez *et al.,* 2020).

On the other hand, peatland carbon accumulation may benefit from increased temperatures, longer growing seasons and increased atmospheric CO_2 concentrations (Lund *et al.,* 2010; Charman *et al.,* 2013). Warmer conditions may promote plant productivity in areas where moisture levels are unchanged or enhanced by runoff from permafrost thaw, increased snowmelt, or changes in precipitation (Davidson and Janssens, 2006; Strack and Waddington, 2007; Mauquoy *et al.,* 2002; 2008; Yu *et al.,* 2011; Loisel and Yu, 2013; Charman *et al.,* 2013). This increased productivity may compensate for increases in decomposition. The notion that carbon accumulation may increase in northernmost regions is supported by evidence from peat cores, where carbon accumulation rates have accelerated throughout the last century across boreal regions (Hinzman *et al.,* 2005; Klein *et al.,* 2013; Loisel and Yu, 2013). Warmer temperatures may also permit peatlands to expand beyond their current climatic range (Clymo *et al.,* 1998; Limpens *et al.,* 2008; Yu *et al.,* 2011; Frolking *et al.,* 2011; Dieleman *et al.,* 2015). However, there may be topographical limits to this expansion (Anderson *et al.,* 2003) as well as temperature thresholds that limit the amount of warming that can be withstood by peatland vegetation (Gallego-Sala *et al.,* 2018). Reduced soil moisture due to enhanced evapotranspiration and changing precipitation may reduce CH_4

emission rates, as drier conditions inhibit CH_4 production, compensating for increased CO_2 emissions in the short-term (Strack *et al.,* 2004; Huang *et al.,* 2021).

Peatlands exhibit a number of autogenic (internal) feedbacks that are mainly governed by the position of the water table (Waddington *et al*., 2015). These feedbacks are complex and interact over a range of spatial and temporal scales, making integrating peatlands into global climate models challenging (Frolking *et al*., 2009). The response of the carbon cycle to these feedbacks can be both positive and negative (Waddington *et al*., 2015). Autogenic feedbacks regulate peatland responses to external influences and may in some cases confer to them some resistance against changes in climate (Heimann and Reichstein, 2008; Dise, 2009; Belyea, 2009; Waddington *et al.,* 2015). For example, peatland surfaces are able to adjust in response to changing soil moisture, rising and falling along with fluctuations in the water table. This feedback helps peatlands to maintain a relatively constant water level, reducing the effects of changes in water table depth upon water availability for *Sphagnum* (Dise, 2009, Waddington *et al.,* 2015). Accelerated peat growth may result in the accumulation of loose, poorly decomposed peat, enhancing its water holding capacity (Dise, 2009; Ise *et al.,* 2008). This allows the water table to rise along with the growing peat surface, promoting further growth (Waddington *et al.,* 2015). Conversely, this may also increase the rate at which water flows laterally through the surface peat, potentially increasing water losses that drive increases in peat humification. Increased peat decay can reduce hydrological conductivity, allowing more water to be retained (Price *et al.,* 2008). Encroachment of vascular plants in response to a lowering of the water table may increase transpiration and interception rates, causing additional increases in water table depth whilst promoting further encroachment by vascular plants (Weltzin *et al*., 2015, Waddington *et al.,* 2015). However, increased vascular plant cover increases the amount of shading, which may reduce evapotranspiration rates (Ketteridge *et al.,* 2013). When dessicated, *Sphagnum* capitula become lighter in colour (Waddington *et al.,* 2015). This bleaching causes evapotranspiration rates to decline as water is no longer drawn up by *Sphagnum* from the water table to the peatland surface (Thompson and Waddington, 2008). This bleaching may increase surface albedo, reflecting heat and maintaining cool conditions beneath the surface (Ketteridge and Baird, 2008).

Within autogenic systems, negative feedbacks typically outweigh positive feedbacks; however, the strengths of these feedbacks vary by site depending on environmental and site-specific conditions such as climatic setting and trophic status, with bogs and poor fens in continental areas showing a greater propensity towards positive feedbacks than fens or bogs and poor fens in coastal areas (Waddington *et al.,* 2015). Therefore, autogenic feedbacks alone cannot be relied upon to prevent ecosystem changes following changes in climate or environmental conditions.

1.4.10. Vegetation change and associated feedbacks

An important additional feedback mechanism relates to changes in peatland vegetation resulting from changes in climate. Although peatland plant communities are generally stable through time and are resilient to changes in climate (Backéus, 1972; Belyea, 2009; Churchill *et al.,* 2015), abrupt changes may occur, often in response to relatively small changes in hydrology or temperature (Belyea and Malmer, 2004; Yu, 2006; Belyea 2009; Mauquoy *et al.,* 2002; Magnan *et al.,* 2019). Such abrupt shifts are frequently seen in peatland palaeoecological records, where rapid changes in vegetation can occur in response to relatively gradual changes in climate (Klein *et al.,* 2013; Magnan *et al.,* 2019). Vegetation composition is fundamental to peatland carbon cycling and carbon storage (Ward *et al.,* 2013; 2015); therefore, the response of peatlands to climate change is intrinsically linked to the response of their overlying vegetation communities (Vitt, 2006; Ward *et al.,* 2013; 2015; Walker *et al.,* 2016; Dieleman *et al.,* 2015). Vegetation responses to climate change stressors can differ between species, making future changes difficult to predict (Weltzin *et al.,* 2000) and studies linking vegetation responses to greenhouse gas fluxes and carbon accumulation rates are limited, and often of short duration (e.g., Ward *et al.,* 2013).

Of all peatland vegetation, *Sphagnum* is the most vital for maintaining the stability and resilience of peatlands to environmental change and upholds key ecosystem functioning including carbon sequestration and storage (Turetsky *et al.,* 2012; van Breemen, 1995; Kuiper *et al.,* 2014). *Sphagnum* productivity is sensitive to changes in soil moisture (Gunnarsson, 2005; Robroek *et al.,* 2007a; 2007b), as these mosses conduct water to their growing parts (capitula) via capillary action (Thompson and Waddington., 2008). How *Sphagnum* mosses will respond to warming is less clear. In some cases, *Sphagnum* productivity has been shown to increase alongside rising temperature (Pakarinen, 1978; Johansson and Linder, 1980; Lindholm and Vasander, 1990; Gerdol *et al.,* 1998; Dorrepaal *et al.,* 2004; Robroek *et al.,* 2007b), while in other cases warming either has no effect (Weltzin *et al.,* 2000; 2003; Walker *et al.,* 2006) or reduces productivity (Dorrepaal *et al.,* 2004; Breeuwer *et al.,* 2008). A critical temperature for *Sphagnum* decline appears to exist, with productivity falling when *Sphagnum* is exposed to temperature increases c. 5°C above ambient conditions (Dieleman *et al.,* 2015; Bragazza *et al.,* 2016; Norby *et al.,* 2019).

Changes in peatland plant community composition that reduce *Sphagnum* cover in favour of other vascular plants may significantly alter peatland carbon cycling (Dieleman *et al.,* 2015; 2016; Norby *et al.,* 2019). Increased temperatures, water table depths and elevated atmospheric CO_2 concentrations have been shown to favour vascular plant expansion at the expense of *Sphagnum,* since vascular plants are often better adapted to cope with drier conditions (Weltzin *et al.,* 2000, Strack *et al.,* 2006a; Gallego-Sala and Prentice, 2012; Pearson *et al.,* 2013; Dieleman *et al.,* 2015). This has been seen in permafrost areas, where increased thermokarst lake development and peat subsidence has facilitated plant succession, resulting in a shift towards non-peat forming communities (Christensen *et al.,* 2004; Swindles *et al.,* 2015). Warming has been shown to drive increases in the abundance of ericaceous shrubs (Weltzin *et al.,* 2003; Buttler *et al.,* 2015; Malhotra *et al.,* 2020), which can increase soil respiration rates (Ward *et al.,* 2013). Increased vascular plant expansion and *Sphagnum* decline may stimulate microbial activity, as increased supply of readily decomposed (high quality) litter and root exudates coincide with a reduced supply of inhibitory polyphenol compounds from *Sphagnum* (Crow and Wieder, 2005; Fenner and Freeman, 2011; Bragazza *et al.,* 2013; Bell *et al.,* 2018). Taller vegetation may also shade out low-lying vegetation and drive a reduction in soil moisture, negatively impacting *Sphagnum* productivity (Norby *et al.,* 2019). *Sphagnum* decline is not unanimously reported with warming (e.g., Dorrepaal *et al.,* 2004), and in areas where warming increases *Sphagnum* productivity, *Sphagnum* mosses may be able to maintain their competitive advantage over other plants, stabilising peatland vegetation against change (Keuper *et al.,* 2011). Increased graminoid cover due to climate change (e.g., Dieleman *et al.,* 2015) may drive increases in both CO_2 and CH_4 emissions, as aerenchyma present in the roots of these plants facilitates the transport of oxygen into previously anoxic peats, while simultaneously providing a conduit for CH_4 emissions to travel un-impeded through the peat (Greenup *et al.,* 2000; Strack *et al.,* 2006b; Hardie *et al.,* 2009). Increased graminoid cover may also increase evapotranspiration rates, leading to reduced soil moisture and accelerating CO_2 production (Admiral and Lafleur, 2007a; 2007b) although this effect may also inhibit CH_4 production (Abdalla *et al.,* 2016).

Increased vascular plant cover does not always negatively impact carbon accumulation rates. *Calluna vulgaris* litter (a commonly occurring shrub type species) has been shown to suppress microbial activity where it falls, lowering soil respiration rates (Read *et al.,* 2004; Ward *et al.,* 2009; 2015). Vascular plant expansion can also increase primary productivity rates in some cases, as these plant types are typically faster growing than *Sphagnum* (Pearson *et al.,* 2013).

1.4.11. Addressing this problem using palaeoecological and experimental approaches

It is important to determine whether positive or negative feedback mechanisms will dominate when assessing the future role of peatlands in the global climate system (Limpens *et al.,* 2008). It is considered that terrestrial ecosystems will provide mostly positive feedbacks under climate warming (Charman *et al.,* 2013; Heimann and Reichstein, 2008) and expert assessment suggests that peatlands will undergo net losses in their carbon stores (Loisel *et al.,* 2021), with recent developments suggesting that projected drier conditions will cause a net increase in CO_2 and reduction of CH_4 emissions from peatlands, causing a net warming effect on future climate (Huang *et al.,* 2021; Evans *et al.,* 2021). However, confidence in these projections is low (Loisel *et al.,* 2021). Because of these uncertainties, and the complexity and variation of peatland responses to climate change, peatlands are rarely included in global terrestrial models (IPCC, 2021) and have yet to be incorporated into any Earth system models (Loisel *et al.,* 2021). This is despite their proven role in driving changes in global climate throughout the Holocene (MacDonald *et al.,* 2006) and the potential for large positive feedbacks should their carbon store be compromised (Limpens *et al.,* 2008).

Two approaches are in common usage to address the issue of whether peatlands will intensify or ameliorate future climate change: experimental climate manipulation and palaeoecological methods. Climate manipulation studies, which can be either field based or undertaken *in vitro* using peat mesocosms simulate climatic, chemical, and hydrological changes in peatlands to measure ecosystem responses to changing environmental conditions (e.g., Bridgham *et al.,* 2008; Dorrepaal *et al.,* 2009; Ward *et al.,* 2013, Dieleman *et al.,* 2015; Jassey *et al.,* 2015; Wilson *et al.,* 2016; Li *et al.,* 2021). Over the past c. 20 years, such studies have been increasingly used to probe the responses of carbon cycling (Dorrepaal *et al.,* 2009; Zhang *et al.,* 2021), decomposition (Bell *et al.,* 2018; Górecki *et al.,* 2021), and vegetation communities (Keuper *et al.,* 2011; Ward *et al.,* 2013; Walker *et al.,* 2016; Malhotra *et al.,* 2020) to changes in temperature, water table depths and a number of other environmental stressors in peatlands (Updegraff *et al.,* 2001; Strack and Waddington, 2007; Chivers *et al.,* 2009). Climate manipulation studies generally report increased greenhouse gas emissions occur with warming (e.g., Turetsky *et al.,* 2008; Sampson *et al.,* 2018) and increased CO_2 emissions but reduced CH_4 emissions occur following water table drawdown (Deng *et al.,* 2015). However, studies also report varying effects of warming and water table drawdown upon plant productivity and net carbon accumulation rates, which are sometimes influenced by the methods used to achieve warming (Eriksson *et al.,* 2010a; Pearson *et al.,* 2015; Gong *et al.,* 2020). In some cases, certain studies produce results that are in stark contrast with those of other studies, promoting further uncertainty (Laiho*,* 2006; Eriksson *et al.,* 2010a; 2010b). To resolve the often-contrasting results of these studies, Gong *et al.* (2020) analysed the results of multiple field climate manipulation experiments in northern peatlands in a meta-analysis. They found that most studies indicate that warming significantly increased CO_2 emissions, productivity and CH_4 emissions from peat, overall resulting in reduced carbon accumulation rates. However, these results were based on a limited number of studies (20). Huang *et al.* (2021) were able to compile a much larger data set (96 publications) to test the effects of water table drawdown upon greenhouse gas fluxes. They projected these findings onto estimated future water table conditions for global peatlands under high-range climate change emission scenarios, finding that water table drawdown due to climate change and human activities will increase CO_2 emissions by approximately 1.1 Gt yr^{-1}, whereas CH_4 CO_2-equivalent emissions will decrease by 0.26 Gt yr^{-1}. Thus, experimental studies indicate that future projected changes in climate are likely to increase net carbon emissions and exert a positive climate feedback.

Climate manipulation studies are frequently short-lived, rarely exceeding five growing seasons (Updegraff *et al.,* 2001; Lafleur *et al.,* 2005, see Table 1.1). Therefore, these studies are of limited use for probing long-term responses to sustained climate change, as these can occur over longer time periods (Belyea, 2009). Gong *et al.* (2020) report that CO_2 and CH_4 emission rates are higher where warming has been sustained for longer periods, although only two long-term studies were used to draw these conclusions. Experimental studies can also be affected by experimental artefacts due to disturbance during establishment or by taking repeated measurements. Potential drying by infra-red lamps, and substantial differences between the results of laboratory and field experiments can also artificially influence results (Kennedy, 1995; Kreyling and Beier, 2013; Johnson *et al.,* 2013; Frei *et al.,* 2020; Gong et al, 2020). Experimental manipulation studies are also biased towards the study of fen-type ecosystems, with ombrotrophic sites relatively underrepresented in the literature (Gong *et al.,* 2020, see Table 1.1). Additionally, many regions are poorly represented by global datasets. In particular, there is a lack of data from Russian peatlands, despite this region containing > 30 % of global peatlands within the higher latitudes where the greatest changes in temperature and precipitation are projected to occur (Xu *et al.,* 2018; Fewster *et al*., 2022). These issues limit the usefulness and reliability of such studies for capturing the long-term responses of peatlands to future projected climate change (Dorrepaal *et al.,* 2009).

Peatlands record a sensitive archive of environmental and climatic change within their stratigraphic profiles, tracing environmental change over decadal to millennial timescales (Barber, 1993; Chambers and Charman, 2004). Palaeoenvironmental conditions can be inferred from biological, chemical, or physical proxies throughout a peat core using methods such as testate amoebae (Mitchell *et al.,* 2008) and peat humification analysis (Payne and Blackford, 2008), allowing for detailed reconstructions of palaeoenvironmental change through time. Peat profiles can be dated using a suite of methods, allowing for a high level of chronological control, often within sub-decadal resolution (Turetsky *et al.,* 2004; Piotrowska *et al.,* 2011; Swindles, 2010; Swindles *et al.,* 2010). These studies allow for the examination of long-term peatland responses to climatic and environmental change, for example, changes in carbon accumulation rates can be derived from peat cores and related to changes or spatial differences in environmental conditions (Beilman *et al.,* 2009; Charman *et al.,* 2013; 2015; Holmquist *et al.,* 2014; 2016; Gallego-Sala *et al.,* 2018; Magnan *et al.,* 2019). Records covering the past millennium are particularly useful for assessing peatland contributions to global carbon cycling, since climatic conditions during this relatively recent time-period are well-known for many regions (Gallego-Sala *et al.,* 2016).

Palaeoecological studies are limited by the difficulty of discerning climatic effects from anthropogenic impacts in some instances (Turner *et al.,* 2014), as well as by issues relating to dating uncertainties and taphonomic effects influencing the preservation of biological proxies throughout a core (Mauquoy and Yeloff, 2008). These factors reduce the precision with which mechanisms of change can be probed using these methods (Kuhry and Turunen, 2006, Mauquoy and Yeloff, 2008; Swindles *et al.,* 2020). Past changes in climate may be poor analogies for future climate changes due to anthropogenic emissions, since most projected increases in temperature due to climate change exceed the variation seen throughout the Holocene (Mauquoy and Yeloff, 2008). In addition, many commonly used proxies are qualitative and have not been tested experimentally. While reconstructions based upon biological proxies (most commonly testate amoebae in ombrotrophic peatlands) have been validated and refined by experimental and comparative studies (e.g., Charman *et al.,* 2009; Payne *et al.,* 2011; Swindles *et al.,* 2015; 2020), several commonly used qualitative climate proxies measuring changes in decomposition rates through time (e.g., peat humification, C/N ratios) have rarely been tested experimentally (Zaccone *et al.,* 2018). The validity of these methods for faithfully reconstructing paleoclimatic signals has been criticised (Yeloff and Mauquoy, 2006; Payne and Blackford, 2008); however, they remain frequently used in recent peat-based palaeoenvironmental reconstructions (e.g., Zhang *et al.,* 2021; Tsyganov et al, 2021; Babeshko *et al.,* 2021).

Our understanding of peatland responses to future climate change across short and long timescales could be improved by incorporating both climate manipulation studies and centennial or millennial-scale proxy records (Rull 2010; Seddon *et al.,* 2014; Lamentowicz *et al.,* 2016). Both methods are complementary, and could be applied together for the same site, permitting comparison between short-term (experimental) changes with long-term changes in response to warmer and/or drier conditions, and comparison between short and long-term drivers of change (Rull, 2010; Seddon *et al.,* 2014; Lamentowicz *et al.,* 2016). The use of palaeoecology alongside experimental studies may also allow for present-day responses to be considered in the context of its long-term history (Willis *et al.,* 2010; Lamentowicz *et al.,* 2016).

Palaeoecological and experimental studies are rarely applied together (Frolking *et al.,* 2014; Lamentowicz *et al.,* 2016). Both methods often produce contrasting results. For instance, while there is a great deal of variation in the results of experimental studies examining the effects of warming and drought upon peatlands (Table 1.1), they generally indicate that climate warming will lead to rapid loss of older, formerly stored carbon, resulting in positive feedbacks to climate change (Ise *et al.,* 2008; Bridgham *et al.,* 2008; Dorrepaal *et al.,* 2009; Walker *et al.,* 2016; Huang *et al.,* 2021). In contrast, many palaeoecological studies suggest that peatlands have accumulated more carbon in the past under warmer climatic conditions (van Bellen *et al.,* 2011; Charman *et al.,* 2013; Turner *et al.,* 2014; van der Linden *et al.,* 2014). For example, van Bellen *et al*. (2020) took cores from seven sites around Northern Alberta in Canada, finding that the highest rates of carbon accumulation occurred around c. 1100 CE and the lowest rates were around c. 1750 CE, during the MCA and LIA respectively. Other studies have found similar results. Malmer and Wallén (2004) analysed carbon accumulation rates and environmental conditions from Swedish peatlands, finding that southern sites accumulated more carbon during the MCA, and both southern and northern sites accumulated less carbon during the LIA. Large global compilations of peat accumulation rates have been related to spatial variation in environmental and climatic conditions (Charman *et al.,* 2013; Gallego-Sala *et al.,* 2018). Charman *et al*. (2013) found evidence to support the notion that warmer climatic conditions will enhance carbon accumulation rates. Gallego-Sala *et al*. (2018) found that the length of the growing season was the dominant factor governing carbon accumulation in northern peatlands and that, while rising temperatures may drive increased carbon accumulation, a temperature threshold may be met by 2100 CE that could reverse this trend, causing peatlands to switch from exerting a negative climate feedback to a positive one. Both studies suggest that climatic variables governing productivity rates are the dominant controls influencing long-term carbon accumulation rates over hydrological conditions that govern decay (Charman *et al.,* 2013; Gallego-Sala *et al.,* 2018). However, studies of carbon accumulation rates based upon individual cores frequently show a relationship between carbon accumulation rates and the botanical composition of the peat (Malmer and Wallén, 2004; Mauquoy *et al.,* 2002; Loisel and Garneau, 2010). Anthropogenic disturbances such as wildfires and nitrogen pollution have also had great impacts upon apparent carbon accumulation rates in peatlands in recent years, even in relatively pristine sites (Shiller *et al.,* 2014; Lamentowicz *et al.,* 2016).

Another factor that complicates the integration of experimental and palaeoecological methods is that carbon accumulation rates derived from contemporary greenhouse gas measurements from peatland ecosystems often fail to converge with long term carbon accumulation rates derived from peat cores (Frolking *et al.,* 2014; Ratcliffe *et al.,* 2018). This has been related to a known artefact that affects palaeoecological estimates of carbon accumulation. Losses of carbon through time cannot be quantified by these methods and negative values are impossible, resulting in an apparent reduction of carbon accumulation rates during periods of carbon loss (Clymo, 1984; Yu, 2011; Frolking *et al.,* 2014; Young *et al.,* 2019; 2021). In addition, carbon accumulation rates derived from recently accumulated peat are often higher than in the deeper peats, due to the incomplete decomposition of labile organic material at the peat surface (Young *et al.,* 2019; 2021). These artefacts mean that carbon accumulation rates derived from a peat core do not accurately reflect the amount of carbon accumulated at the time of deposition, but instead reflect the amount of carbon retained after initial capture. Some studies have related changes in recently accumulated carbon rates to land management practices (Heinemeyer *et al.*, 2018; Marrs *et al.*, 2019), however these rates are not directly comparable to those from deeper peat (Young *et al*., 2019).

Despite these issues, studies that link palaeo and experimental approaches may improve our understanding of how future climate change will affect peatland ecosystem functioning over different timescales (Lamentowicz *et al.,* 2016). Interdisciplinary studies that link both approaches and research communities are necessary to work towards generating a common understanding of peatland carbon dynamics and drivers.

Table 1.1. Table of peatland climate manipulation experiments and their results. Experimental treatment effects are given as reported in the cited paper where available. Site names are given except when they are not reported, instead state names or nearby locations are given. Increases in temperature and water table depths are indicated by a plus sign. The study by Rowson *et al*. (2012) indicated by an asterisk, relates to this study, reporting on the early results of the experimental climate manipulation experiment used in this thesis. This is not a comprehensive list of all climate manipulation experiments that have been conducted in peatlands.

Source	Years	Dates	Experiment type	Location	Peatland type	Measured fluxes	Experimental treatments	Results
Ballantyne *et al.*, 2014	2	2009-2010	Field	Seney National Wildlife Refuge peatland, Michigan USA	Fen	CO_2, CH_4	Long-term (>80 years) water table drawdown of + 15 cm and inundation by 10 cm	Inundation decreased CO_2 respiration and productivity, but increased CH_4 emissions. Reduced water tables increased CO_2 respiration and productivity but decreased CH_4 emissions.
Bragazza *et al.*, 2016	3	2011 – 2013	Transplantation (climate gradient)	Hoscrajen and Lormoos bogs, Switzerland	Bog	CO_2	Warming (+5°C) and reduced precipitation (-60 %)	Soil respiration increased and peat accumulation fell by 30 % in transplanted mesocosms.
Bridgham *et al.*, 2008	7	1994 – 2002	Mesocosm	Alborn, Minnesota, USA	Fen and Bog	Soil carbon balance (changes in mean surface height)	Warming by infrared lamps between 1.6 – 4.1°C and increased water table depth (+3, +16, +25 cm)	Bog: Initial increase in carbon accumulation, greatest with higher water tables, but levels off after 3 years. Fen: losses in carbon or no change, with the greatest losses occurring in the drier and warmer mesocosms.
Chivers *et al.* 2009	2	2005 - 2006	Field	Alaska Peatland Experiment (APEX), Alaska, USA	Fen	CO_2	Warming (0.7 °C) by OTCs and increased (+5 – +8 cm) and reduced (-9 – -11 cm) water table depths.	Lowered water tables reduced productivity, weakening, or reversing the carbon sink function. Flooded plots were greater CO_2 sinks due to increased productivity. Warming increased both CO_2 emissions and

								productivity, and thus did not affect carbon balances.
Deng *et al.,* 2015	3	2004 – 2006	Field	Alaska Peatland Experiment (APEX), Alaska, USA	Fen	CO_2, CH_4	Warming (+0.7°C, 0.9°C and 0.6°C by OTCs, and increased (+8.1cm) and decreased (-20 cm) water table depths.	CO_2 uptake was reduced in both very cold or very warm conditions and increased with increased soil moisture. CH_4 emissions increased with increasing temperatures and higher water tables.
Dorrepaal *et al.,* 2009	8	2000 – 2007	Field	Abisko, north Sweden	Blanket bog	CO_4	Warming (OTC) c. +1° C	CO_2 emissions increased due to warming, with the emissions traced isotopically as being from deep, ancient peat.
Eriksson *et al.,* 2010b	2	2005 – 2006	Field	Degerö Stormyr, Sweden	Mixed mire	CH_4	Warming (OTC) +1.5°C	CH_4 emissions were reduced by warming by 30 % on average
Eriksson *et al.,* 2010a	12	1996 – 2007	Mesocosm	Degerö Stormyr, Sweden	Mixed mire	CH_4	Warming (OTCs +~3.6°C	Warming decreased CH_4 production by 34%.
Hanson *et al.,* 2020	3	2016 – 2018	Whole ecosystem	S1 Bog, Minnesota, USA	Bog	CO_2, CH_4	Warming (+ 2.3°C, + 4.5°C, + 6.8°C, + > 9°C) by propane fired furnaces and increased atmospheric CO_2 (+ 800 – 900 ppmv)	Increased CO_2 and CH_4 emissions with increased warming, accelerating carbon losses by 4.5 to 18 times relative to historical accumulation rates. No effect of increased atmospheric CO_2 concentrations.
Hopple *et al.,* 2020	5	2015 – 2018	Whole ecosystem	S1 Bog, Minnesota, USA	Bog	CO_2, CH_4	Warming (+2.3°C, + 4.5°C, + 6.8°C, + > 9°C) by propane fired furnaces and increased atmospheric CO_2 (+ 500 ppmv) for last 3 years	Warming increases CH_4 and CO_2 emissions, while increased atmospheric CO_2 has no discernible effect on gas fluxes.
Johnson *et al.,* 2013	2	2009 - 2010	Field	Site in Michigan, USA	Fen	CO_2, CH_4	Warming by OTCs (no significant warming effect) and Infrared heat lamps of +1.4 – 1.9°C	Warming with infra-red lamps increased productivity, while OTCs had no effect on CO_2 fluxes. Warming from both OTCs and

								Infra-red lamps increased CH_4 emissions however.
Juszczak *et al.*, 2016	1	2015	Field	Rzecin peatland, Poland	Fen	CO_2	Reduced precipitation (35 %) and warming of air temperatures (0.4°C) using heat lamps	Warming increased CO_2 emissions and productivity, drought reduced productivity and for combined warming and drought CO_2 emissions were reduced.
Laine *et al.*, 2019	3	2011 – 2013	Field	Sites near Siikajoki, Finland	Fens	CO_2, CH_4	Warming by OTCs and land use differences resulting in water table differences of ~ + 20 cm.	Warming increased productivity rates for all land use types. Reduced water table depth and temperature increases increased CH_4 only slightly since these sites were already dry.
Li *et al.*, 2021	2	2018-2020	Mesocosm	La Guette peatland, France	Fen	CO_2, CH_4	Warming of air temperature (0.9°C) using OTCs	Increased CO_2 uptake with warming. Respiration, carbon balances and CH_4 not effected.
Munir and Strack, 2014	3	2011 – 2013	Field	Wandering River, Canada	Bog	CH_4	Warming by OTCs + ~1°C) and increased water table depth (+ 38, + 74 and + 120 cm)	Water table drawdown reduced CH_4 emissions differently depending on the age of drainage (emissions were higher in areas that had been drained for longer). Warming increased CH_4 flux, which also increased with water table drawdown. In hummocks, the opposite happened. CH_4 emissions were reduced by warming and declined further with as water table depths fell. Combined warming and drought effects on CH_4 were overall negative but not significant.
Munir *et al.*, 2014	3	2011 - 2013	Field	Wandering River, Canada	Bog	CO_2	Warming (~1°C) by OTCs and increased water table	CO_2 accumulation increased with warming, showing an interaction

							depth (+ 38, + 74 and + 120 cm) over long and short terms.	with water level. Net carbon uptake was enhanced by warming and long-term drainage, while short term drainage accelerated carbon losses.
Olefeldt *et al.*, 2017	9	2005 – 2013	Field	Alaska Peatland Experiment (APEX), Alaska, USA	Fen	CO_2, CH_4	Warming by OTCs (0.7°C, 0.9°C and 0.6°C for control), and increased and lowered water table depth (+ 8.1, -20 cm)	Water table drawdown reduced productivity, carbon accumulation and CH_4 emissions.
Pearson *et al.*, 2015	3	2008 – 2010	Field	Lakkasuo, Narhinneva and Lompolojankka, sites in Finland.	Fens	CO_2, CH_4	Warming by OTCs between +0.2 – 2.0°C) and long-term water table drawdown (+5 - 10 cm and +10 - 30 cm)	Warming effects were negligible for CO_2 emissions. Water level drawdown overrode any temperature effect except at the northernmost Lompolojankka site. CH_4 emissions fell with long-term drainage at all sites and fell slightly with warming.
Rowson *et al.*, 2012*	3	2010 – 2012	Field	Cors Fochno, Wales	Bog	CO_2	Warming by OTCs + 0.7°C and episodic, seasonal drought (average + 10 cm increase in water table depth during summer)	Warming and drought reduced net ecosystem exchange of CO_2. Combined warming and drought have a cumulative effect and these plots effectively became carbon neutral or weak sources.
Strack *et al.*, 2004	3	2001 – 2003	Mesocosm	St. Charles-de-Bellachasse, Quebec, Canada	Fen	CH_4	Water table drawdown c + 20 cm	CH_4 emissions were reduced by up to 97 % following water table drawdown.
Strack *et al.*, 2006a	2	2001 – 2002	Field	St. Charles-de-Bellachasse, Quebec, Canada	Fen	CO_2	Water table drawdown c +20 cm	CO_2 emissions were higher in the drained sites, while productivity was reduced in hummocks but increased at drained lawns and hollows.

Strozecki *et al.*, 2020	3	2015 – 2017	Field	Rzecin peatland, Poland	Fen	CH_4	Warming of air (+ 0.4°C) by heat lamps. Reduced precipitation by 24 % and 38 % for 2016 to 2017.	Warming and reduced precipitation increased CH_4 emissions except during a wet and warm year (2017).
Turetsky *et al.*, 2008	2	2005-2006	Field	Alaska Peatland Experiment (APEX), Alaska, USA	Fen	CH_2	Warming (+0.7°C, 0.9°C and 0.6°C by OTCs, and increased (+ 8.1 cm) and decreased (-20 cm) water table depths.	Warming increased CH_4 emissions while raised water tables increased CH_4 emissions.
Updegraff *et al.*, 2001	3	1995 – 1997	Mesocosm	Toivola bog, Alborn fen, Michigan, USA.	Bog, Fen	CO_2, CH_4	Warming by Infrared lamps (+ 3°C). and manipulated water table depths (-1, +10 and +20 cm)	CO_2 emissions increased at a similar rate for fen and bogs due to temperature increases, while not responding to changes in water table depth. CH_4 emissions were three times higher in the bog and increased along with temperature and reduced water table depth. CH_4 emissions became progressively stronger each year.
Ward *et al.*, 2013	2	2009 – 2010	Field	Moorhouse nature reserve, England	Blanket bog	CO_2, CH_4	Warming by OTCs ~1°C	Warming increased soil respiration, but the effect of warming on carbon accumulation and CH_4 emissions were governed by vegetation communities.
White *et al.*, 2008	6	1994 – 1999	Mesocosm	Sites in northeast Minnesota, USA	Bog, Fen	CH_4	Warming by infrared lamps + 1.6 – 4.1°C. Water table depth manipulations, increased and decreased	CH_4 emissions mostly increased with rising water tables, but are indirectly influenced by DOC and plant productivity, that increase with higher temperature.

1.5. Summary

Northern peatlands contain a vast store of carbon and are important components of the global carbon cycle. Anthropogenic climate change threatens to disrupt the ecosystem functioning of peatlands and may cause this carbon to be returned to the atmosphere, potentially imparting large positive feedbacks, amplifying climate warming. However, the future response of peatlands to climate change is unclear, and they are not currently included in Earth System Models, despite their significance in the global climate system. An important impediment in resolving this uncertainty is the disconnect between different approaches used by experimental ecologists and palaeoecologists. By combining both palaeoecological and experimental approaches using an inter-disciplinary approach, this project aims to make substantive progress towards reducing this uncertainty.

1.6. References

Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, Ü. and Smith, P., (2016). Emissions of methane from northern peatlands: a review of management impacts and implications for future management options. *Ecology and Evolution*, *6*(19), 7080-7102.

Admiral, S.W. and Lafleur, P.M., (2007a). Partitioning of latent heat flux at a northern peatland. *Aquatic Botany*, *86*(2), 107-116.

Admiral, S.W. and Lafleur, P.M., (2007b). Modelling of latent heat partitioning at a bog peatland. *Agricultural and Forest Meteorology*, *144*(3-4), 213-229.

Allen, M. R., Shine, K. P., Fuglestvedt, J. S., Millar, R. J., Cain, M., Frame, D. J., and Macey, A. H. (2018). A solution to the misrepresentations of CO2-equivalent emissions of short-lived climate pollutants under ambitious mitigation. *Npj Climate and Atmospheric Science*, *1*(1), 1-8.

Alm, J., Saarnio, S., Nykänen, H., Silvola, J. and Martikainen, P., (1999). Winter CO 2, CH 4, and N 2 O fluxes on some natural and drained boreal peatlands. *Biogeochemistry*, *44*(2), 163-186.

Andersen, R., Poulin, M., Borcard, D., Laiho, R., Laine, J., Vasander, H. and Tuittila, E.T., (2011). Environmental control and spatial structures in peatland vegetation. *Journal of Vegetation Science*, *22*(5), 878-890.

Anderson, R.L., Foster, D.R. and Motzkin, G., (2003). Integrating lateral expansion into models of peatland development in temperate New England. *Journal of Ecology*, *91*(1), 68-76.

Austnes, K., Evans, C. D., Eliot-Laize, C., Naden, P. S., and Old, G. H. (2010). Effects of storm events on mobilisation and in-stream processing of dissolved organic matter (DOM) in a Welsh peatland catchment. *Biogeochemistry*, *99*(1), 157-173.

Babeshko, K.V., Shkurko, A., Tsyganov, A.N., Severova, E.E., Gałka, M., Payne, R.J., Mauquoy, D., Mazei, N.G., Fatynina, Y.A., Krasnova, E.D. and Saldaev, D.A., (2021). A multi-proxy reconstruction of peatland development and regional vegetation changes in subarctic NE Fennoscandia (the Republic of Karelia, Russia) during the Holocene. *The Holocene*, *31*(3), 421-432.

Backéus, I., (1972). Bog vegetation re-mapped after sixty years, studies on Skagershultamossen, central Sweden. *Oikos*, 384-393.

Ballantyne, D.M., Hribljan, J.A., Pypker, T.G. and Chimner, R.A., (2014). Long-term water table manipulations alter peatland gaseous carbon fluxes in Northern Michigan. *Wetlands Ecology and Management*, *22*(1), 35-47.

Barber, K.E., (1993). Peatlands as scientific archives of past biodiversity. *Biodiversity and Conservation*, *2*(5), 474-489.

Basiliko, N., Stewart, H., Roulet, N.T. and Moore, T.R., (2012). Do root exudates enhance peat decomposition? *Geomicrobiology Journal*, *29*(4), 374-378.

Beilman, D.W., MacDonald, G.M., Smith, L.C., and Reimer, P.J., (2009). Carbon accumulation in peatlands of West Siberia over the last 2000 years. *Global Biogeochemical Cycles*, *23*(1).

Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J., Freeman, C., and Clark, J.M., (2018). Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma*, *331*, 29-37.

Belyea, L. R., and Malmer, N. (2004). Carbon sequestration in peatland: patterns and mechanisms of response to climate change. Global Change Biology, 10(7), 1043-1052.

Belyea, L.R. and Baird, A.J., (2006). Beyond “the limits to peat bog growth”: Cross-scale feedback in peatland development. *Ecological Monographs*, *76*(3), 299-322.

Belyea, L.R., (2009). Nonlinear dynamics of peatlands and potential feedbacks on the climate system. *Carbon cycling in northern peatlands*, American Geophysical Union. *184*, 5-18.

Berghuis, B. A., Yu, F. B., Schulz, F., Blainey, P. C., Woyke, T., and Quake, S. R. (2019). Hydrogenotrophic methanogenesis in archaeal phylum Verstraetearchaeota reveals the shared ancestry of all methanogens. *Proceedings of the National Academy of Sciences*, *116*(11), 5037-5044.

Billett, M.F., Charman, D.J., Clark, J.M., Evans, C.D., Evans, M.G., Ostle, N.J., Worrall, F., Burden, A., Dinsmore, K.J., Jones, T., and McNamara, N.P., (2010). Carbon balance of UK peatlands: current state of knowledge and future research challenges. *Climate Research*, *45*, 13-29.

Billett, M.F., Palmer, S.M., Hope, D., Deacon, C., Storeton-West, R., Hargreaves, K.J., Flechard, C. and Fowler, D., (2004). Linking land-atmosphere-stream carbon fluxes in a lowland peatland system. *Global Biogeochemical Cycles*, *18*(1).

Blodau, C., (2002). Carbon cycling in peatlands A review of processes and controls. *Environmental Reviews*, *10*(2), 111-134.

Blodau, C., Basiliko, N. and Moore, T.R., (2004). Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*, *67*(3), 331-351.

Boon, A., Robinson, J.S., Chadwick, D.R. and Cardenas, L.M., (2014). Effect of cattle urine addition on the surface emissions and subsurface concentrations of greenhouse gases in a UK peat grassland. *Agriculture, Ecosystems and Environment*, *186*, 23-32.

Bourgeau-Chavez, L.L., Grelik, S.L., Billmire, M., Jenkins, L.K., Kasischke, E.S. and Turetsky, M.R., (2020). Assessing boreal peat fire severity and vulnerability of peatlands to early season wildland fire. *Frontiers in Forests and Global Change*, *3*, p.20.

Bragazza, L., Parisod, J., Buttler, A. and Bardgett, R.D., (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, *3*(3), 273-277.

Bragazza, L., Bardgett, R.D., Mitchell, E.A. and Buttler, A., (2015). Linking soil microbial communities to vascular plant abundance along a climate gradient. *New Phytologist*, *205*(3), 1175-1182.

Bragazza, L., Buttler, A., Robroek, B.J., Albrecht, R., Zaccone, C., Jassey, V.E. and Signarbieux, C., (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, *22*(12), 4114-4123.

Bragazza, L., Parisod, J., Buttler, A. and Bardgett, R.D., (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, *3*(3), 273-277.

Breeuwer, A., Heijmans, M.M., Robroek, B.J. and Berendse, F., (2008). The effect of temperature on growth and competition between Sphagnum species. *Oecologia*, *156*(1), 155-167.

Bridgham, S.D., Cadillo-Quiroz, H., Keller, J.K. and Zhuang, Q., (2013). Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Global Change Biology*, *19*(5), 1325-1346.

Bridgham, S.D., Megonigal, J.P., Keller, J.K., Bliss, N.B. and Trettin, C., (2006). The carbon balance of North American wetlands. *Wetlands*, *26*(4), 889-916.

Bridgham, S.D., Pastor, J., Dewey, B., Weltzin, J.F. and Updegraff, K., (2008). Rapid carbon response of peatlands to climate change. *Ecology*, *89*(11), 3041-3048.

Bridgham, S.D., Pastor, J., Janssens, J.A., Chapin, C. and Malterer, T.J., (1996). Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands*, *16*(1), 45-65.

Bridgham, S.D., Updegraff, K. and Pastor, J., (1998). Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology*, *79*(5), 1545-1561.

Bu, Z., Hans, J., Li, H., Zhao, G., Zheng, X., Ma, J. and Zeng, J., (2011). The response of peatlands to climate warming: A review. *Acta Ecologica Sinica*, *31*(3), 157-162.

Bubier, J.L. and Moore, T.R., (1994). An ecological perspective on methane emissions from northern wetlands. *Trends in Ecology and Evolution*, *9*(12), 460-464.

Bubier, J.L., Frolking, S., Crill, P.M. and Linder, E., (1999). Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research: Atmospheres*, *104*(D22), 27683-27692.

Bubier, J.L., Moore, T.R., Bellisario, L., Comer, N.T. and Crill, P.M., (1995). Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles*, *9*(4), 455-470.

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A. and Bragazza, L., (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science*, *26*(5), 964-974.

Chambers, F.M. and Charman, D.J., (2004). Holocene environmental change: contributions from the peatland archive. *The Holocene*, *14*(1), 1-6.

Chanton, J. P., and Whiting, G. J. (1995). Trace gas exchange in freshwater and coastal marine environments: ebullition and transport by plants. *Biogenic trace gases: measuring emissions from soil and water*, 98-125.

Chapin, C.T., Bridgham, S.D. and Pastor, J., (2004). pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen. *Wetlands*, *24*(1), 186-201.

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R. and Wirth, C., (2006). Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, *9*(7), 1041-1050.

Charman, D. J., Aravena, R., Bryant, C. L., and Harkness, D. D. (1999). Carbon isotopes in peat, DOC, CO2, and CH4 in a Holocene peatland on Dartmoor, southwest England. *Geology*, *27*(6), 539-542.

Charman, D., (2002). *Peatlands and environmental change*. John Wiley and Sons Ltd.

Charman, D.J., Amesbury, M.J., Hinchliffe, W., Hughes, P.D., Mallon, G., Blake, W.H., Daley, T.J., Gallego-Sala, A.V. and Mauquoy, D., (2015). Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America. *Quaternary Science Reviews*, *121*, 110-119.

Charman, D.J., Barber, K.E., Blaauw, M., Langdon, P.G., Mauquoy, D., Daley, T.J., Hughes, P.D. and Karofeld, E., (2009). Climate drivers for peatland palaeoclimate records. *Quaternary Science Reviews*, *28*(19-20), 1811-1819.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D. and Jackson, S.T., (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, *10*(2), 929-944.

Chasar, L. S., Chanton, J. P., Glaser, P. H., Siegel, D. I., and Rivers, J. S. (2000). Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH4 in a northern Minnesota peatland. *Global Biogeochemical Cycles*, *14*(4), 1095-1108.

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W. and McGuire, A.D., (2009). Effects of experimental water table and temperature manipulations on ecosystem CO 2 fluxes in an Alaskan rich fen. *Ecosystems*, *12*(8), 1329-1342.

Christensen, T.R., Johansson, T., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P. and Svensson, B.H., (2004). Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophysical Research Letters*, *31*(4).

Churchill, A.C., Turetsky, M.R., McGuire, A.D., and Hollingsworth, T.N., (2015). Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen. *Canadian Journal of Forest Research*, *45*(2), 185-193.

Clymo, R.S. and Hayward, P.M., (1982). The ecology of Sphagnum. In: *Bryophyte ecology* (229-289). Springer, Dordrecht.

Clymo, R.S. and Pearce, D.M.E., (1995). Methane and carbon dioxide production in, transport through, and efflux from a peatland. *Philosophical Transactions of the Royal Society of London. Series A: Physical and Engineering Sciences*, *351*(1696), 249-259.

Clymo, R.S., (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *303*(1117), 605-654.

Clymo, R.S., Turunen, J. and Tolonen, K., (1998). Carbon accumulation in peatland. *Oikos*, 368-388.

Conrad, R. (1999). Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. *FEMS microbiology Ecology*, *28*(3), 193-202.

Couwenberg, J., (2009). Methane emissions from peat soils (organic soils, histosols): facts, MRV-ability, emission factors. *Methane emissions from peat soils* (*organic soils, histosols): facts, MRV-ability, emission factors.*

Crow, S.E., and Wieder, R.K., (2005). Sources of CO2 emission from a northern peatland: root respiration, exudation, and decomposition. *Ecology*, *86*(7), 1825-1834.

Davidson, E.A. and Janssens, I.A., (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, *440*(7081), 165-173.

Dawson, J.J., Billett, M.F., Hope, D., Palmer, S.M. and Deacon, C.M., (2004). Sources and sinks of aquatic carbon in a peatland stream continuum. *Biogeochemistry*, *70*(1), 71-92.

Deng, J., Li, C. and Frolking, S., (2015). Modeling impacts of changes in temperature and water table on C gas fluxes in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*, *120*(7), 1279-1295.

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W. and Lindo, Z., (2016). Enhanced carbon release under future climate conditions in a peatland mesocosm experiment: the role of phenolic compounds. *Plant and Soil*, *400*(1), 81-91.

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W. and Lindo, Z., (2015). Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability. *Global Change Biology*, *21*(1), 388-395.

Dinsmore, K.J., Billett, M.F. and Dyson, K.E., (2013). Temperature and precipitation drive temporal variability in aquatic carbon and GHG concentrations and fluxes in a peatland catchment. *Global Change Biology*, *19*(7), 2133-2148.

Dinsmore, K.J., Billett, M.F., Skiba, U.M., Rees, R.M., Drewer, J. and Helfter, C., (2010). Role of the aquatic pathway in the carbon and greenhouse gas budgets of a peatland catchment. *Global Change Biology*, *16*(10), 2750-2762.

Dise, N.B., (2009). Peatland response to global change. *Science*, *326*(5954), 810-811.

Dorrepaal, E., Aerts, R., Cornelissen, J.H., Callaghan, T.V. and van Logtestijn, R.S., (2004). Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure, and production in a sub-arctic bog. *Global Change Biology*, *10*(1), 93-104.

Dorrepaal, E., Cornelissen, J.H., Aerts, R., Wallen, B.O. and van Logtestijn, R.S., (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, *93*(4), 817-828.

Dorrepaal, E., Toet, S., van Logtestijn, R.S., Swart, E., van De Weg, M.J., Callaghan, T.V. and Aerts, R., (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, *460*(7255), 616-619.

Drösler, M., Freibauer, A., Christensen, T.R. and Friborg, T., (2008). Observations and status of peatland greenhouse gas emissions in Europe. In: *The continental-scale greenhouse gas balance of Europe* (243-261). Springer, New York, NY.

Eriksson, T., Öquist, M.G. and Nilsson, M.B., (2010a). Effects of decadal deposition of nitrogen and sulphur, and increased temperature, on methane emissions from a boreal peatland. *Journal of Geophysical Research: Biogeosciences*, *115*(G4).

Eriksson, T., Öquist, M.G. and Nilsson, M.B., (2010b). Production and oxidation of methane in a boreal mire after a decade of increased temperature and nitrogen and sulfur deposition. *Global Change Biology*, *16*(7), 2130-2144.

Evans, C.D., Jones, T.G., Burden, A., Ostle, N., Zieliński, P., Cooper, M.D., Peacock, M., Clark, J.M., Oulehle, F., Cooper, D. and Freeman, C., (2012). Acidity controls on dissolved organic carbon mobility in organic soils. *Global Change Biology*, *18*(11), 3317-3331.

Evans, C.D., Peacock, M., Baird, A.J., Artz, R.R.E., Burden, A., Callaghan, N., Chapman, P.J., Cooper, H.M., Coyle, M., Craig, E. and Cumming, A., (2021). Overriding water table control on managed peatland greenhouse gas emissions. *Nature, 593*(7860), 548-552.

Fenner, N. and Freeman, C., (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, *4*(12), 895-900.

Fenner, N., Meadham, J., Jones, T., Hayes, F. and Freeman, C., (2021). Effects of climate change on peatland reservoirs: a DOC perspective. *Global Biogeochemical Cycles*, *35*(7), p.e2021GB006992.

Fewster, R. E., Morris, P. J., Ivanovic, R. F., Swindles, G. T., Peregon, A. M., and Smith, C. J. (2022). Imminent loss of climate space for permafrost peatlands in Europe and Western Siberia. *Nature Climate Change*, *12*(4), 373-379.

Field, C.B., Lobell, D.B., Peters, H.A. and Chiariello, N.R., (2007). Feedbacks of terrestrial ecosystems to climate change. *Annu. Rev. Environ. Resour.*, *32*, 1-29.

Forster, P., T. Storelvmo, K. Armour, W. Collins, J. L. Dufresne, D. Frame, D. J. Lunt, T. Mauritsen, M. D. Palmer, M. Watanabe, M. Wild, H. Zhang, (2021), The Earth's Energy Budget, Climate Feedbacks, and Climate Sensitivity. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B. and Fenner, N., (2001). Export of organic carbon from peat soils. *Nature*, *412*(6849), 785-785.

Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S. and Hudson, J., (2004a). Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. *Nature*, *430*(6996), 195-198.

Freeman, C., Ostle, N.J., Fenner, N. and Kang, H., (2004b). A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biology and Biochemistry*, *36*(10), 1663-1667.

Frei, E.R., Schnell, L., Vitasse, Y., Wohlgemuth, T. and Moser, B., (2020). Assessing the effectiveness of in-situ active warming combined with open top chambers to study plant responses to climate change. *Frontiers in Plant Science*, *11*.

Friedlingstein, P., O'sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Sitch, S. and Le Quéré, C., (2020). Global carbon budget 2020. *Earth System Science Data*, *12*(4), 3269-3340.

Frolking, S. and Roulet, N.T., (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, *13*(5), 1079-1088.

Frolking, S., Roulet, N. and Fuglestvedt, J., (2006). How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research: Biogeosciences*, *111*(G1).

Frolking, S., Roulet, N. and Lawrence, D., (2009). Issues Related to Incorporating Northern Peatlands Into Global Climate Models. *Geophysical Monographs*, 184, 19-35.

Frolking, S., Talbot, J., and Subin, Z.M., (2014). Exploring the relationship between peatland net carbon balance and apparent carbon accumulation rate at century to millennial time scales. *The Holocene*, *24*(9), 1167-1173.

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S. and Roulet, N., (2011). Peatlands in the Earth’s 21st century climate system. *Environmental Reviews*, *19*(NA), 371-396.

Frolking, S.E., Bubier, J.L., Moore, T.R., Ball, T., Bellisario, L.M., Bhardwaj, A., Carroll, P., Crill, P.M., Lafleur, P.M., McCaughey, J.H. and Roulet, N.T., (1998). Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Global Biogeochemical Cycles*, *12*(1), 115-126.

Galand, P. E., Fritze, H., Conrad, R., and Yrjala, K. (2005). Pathways for methanogenesis and diversity of methanogenic archaea in three boreal peatland ecosystems. *Applied and Environmental Microbiology*, *71*(4), 2195-2198.

Gallego-Sala, A., Charman, D. and Brewer, S., (2016), April. Peatlands and the C cycle during the last millennium. In *EGU General Assembly Conference Abstracts* (EPSC2016-7889).

Gallego-Sala, A.V. and Prentice, I.C., (2013). Blanket peat biome endangered by climate change. *Nature Climate Change*, *3*(2), 152-155.

Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S. and Blyakharchuk, T., (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature Climate Change*, *8*(10), 907-913.

Gao, J., Holden, J. and Kirkby, M., (2016). The impact of land-cover change on flood peaks in peatland basins. *Water Resources Research*, *52*(5), 3477-3492.

Gatis, N., Luscombe, D.J., Grand-Clement, E., Hartley, I.P., Anderson, K., Smith, D., and Brazier, R.E., (2016). The effect of drainage ditches on vegetation diversity and CO2 fluxes in a Molinia caerulea-dominated peatland. *Ecohydrology*, *9*(3), 407-420.

Gerdol, R., Bonora, A., Marchesini, R., Gualandri, R. and Pancaldi, S., (1998). Growth response of Sphagnum capillifolium to nighttime temperature and nutrient level:

mechanisms and implications for global change. *Arctic and Alpine Research*, *30*(4), 388-395.

Gong, Y., Wu, J., Vogt, J. and Ma, W., (2020). Greenhouse gas emissions from peatlands under manipulated warming, nitrogen addition, and vegetation composition change: a review and data synthesis. *Environmental Reviews*, *28*(4), 428-437.

Goodrich, J.P., Campbell, D.I. and Schipper, L.A., (2017). Southern Hemisphere bog persists as a strong carbon sink during droughts. *Biogeosciences*, *14*(20), 4563-4576.

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łuców, D., Kayzer, D. and Juszczak, R., (2021). Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate Sphagnum-peatland. *Science of The Total Environment*, *771*, 145452.

Gorham, E., (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, *1*(2), 182-195.

Gorham, E., (1995). The biogeochemistry of northern peatlands and its possible responses to global warming. In: *Biotic feedbacks in the global climatic system: will the warming feed the warming*, Oxford University Press 169-187.

Granath, G., Strengbom, J. and Rydin, H., (2010). Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology*, *91*(10), 3047-3056.

Greenup, A.L., Bradford, M.A., McNamara, N.P., Ineson, P. and Lee, J.A., (2000). The role of Eriophorum vaginatum in CH4 flux from an ombrotrophic peatland. *Plant and Soil*, *227*(1), 265-272.

Grubb, M., Vrolijk, C., and Brack, D., (2018). *Kyoto Protocol* (*1999): A Guide and Assessment.* Routledge.

Gunnarsson, U., (2005). Global patterns of Sphagnum productivity. *Journal of Bryology*, *27*(3), 269-279.

Gupta, V., Smemo, K.A., Yavitt, J.B. and Basiliko, N., (2012). Active methanotrophs in two contrasting North American peatland ecosystems revealed using DNA-SIP. *Microbial ecology*, *63*(2), 438-445.

Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Ostle, N.J. and Rowland, A.P., (2009). Bomb-14C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon. *Geoderma*, *153*(3-4), 393-401.

Harenda, K.M., Lamentowicz, M., Samson, M., and Chojnicki, B.H., (2018). The role of peatlands and their carbon storage function in the context of climate change. In *Interdisciplinary approaches for sustainable development goals* (169-187). Springer, Cham.

Haywood, A.M., Ridgwell, A., Lunt, D.J., Hill, D.J., Pound, M.J., Dowsett, H.J., Dolan, A.M., Francis, J.E. and Williams, M., (2011). Are there pre-Quaternary geological analogues for a future greenhouse warming? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *369*(1938), 933-956.

Heimann, M. and Reichstein, M., (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, *451*(7176), 289-292.

Heinemeyer, A., Asena, Q., Burn, W. L., and Jones, A. L. (2018). Peatland carbon stocks and burn history: Blanket bog peat core evidence highlights charcoal impacts on peat physical properties and long-term carbon storage. *Geo: Geography and Environment*, *5*(2), e00063.

Hinton, M.J., Schiff, S.L. and English, M.C., (1997). The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. *Biogeochemistry*, *36*(1), 67-88.

Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R.D., Hope, A., Huntington, H.P. and Jensen, A.M., (2005). Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, *72*(3), 251-298.

Hogg, E.H., Lieffers, V.J. and Wein, R.W., (1992). Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. *Ecological Applications*, *2*(3), 298-306.

Holden, J., (2005). Peatland hydrology and carbon release: why small-scale process matters. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *363*(1837), 2891-2913.

Holmquist, J.R., Finkelstein, S.A., Garneau, M., Massa, C., Yu, Z., and MacDonald, G.M., (2016). A comparison of radiocarbon ages derived from bulk peat and selected plant macrofossils in basal peat cores from circum-arctic peatlands. *Quaternary Geochronology*, *31*, 53-61.

Holmquist, J.R., MacDonald, G.M. and Gallego-Sala, A., (2014). Peatland initiation, carbon accumulation, and 2 ka depth in the James Bay Lowland and adjacent regions. *Arctic, Antarctic, and Alpine Research*, *46*(1), 19-39.

Hopple, A.M., Wilson, R.M., Kolton, M., Zalman, C.A., Chanton, J.P., Kostka, J., Hanson, P.J., Keller, J.K. and Bridgham, S.D., (2020). Massive peatland carbon banks vulnerable to rising temperatures. *Nature Communications*, *11*(1), 1-7.

Hornibrook, E. R. C., Bowes, H. L., Culbert, A., and Gallego-Sala, A. V. (2009). Methanotrophy potential versus methane supply by pore water diffusion in peatlands. *Biogeosciences*, *6*(8), 1491-1504.

Huang, Y., Ciais, P., Luo, Y., Zhu, D., Wang, Y., Qiu, C., Goll, D.S., Guenet, B., Makowski, D., De Graaf, I. and Leifeld, J., (2021). Tradeoff of CO2 and CH4 emissions from global peatlands under water table drawdown. *Nature Climate Change*, 1-5.

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B. and Treat, C., (2020). Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proceedings of the National Academy of Sciences*, *117*(34), 20438-20446.

Ingram, H.A.P., (1978). Soil layers in mires: function and terminology. *Journal of Soil Science*, *29*(2), 224-227.

Ingram, H.A.P., (1982). Size and shape in raised mire ecosystems: a geophysical model. *Nature*, *297*(5864), 300-303.

IPCC, (2021). Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Ise, T., Dunn, A.L., Wofsy, S.C. and Moorcroft, P.R., (2008). High sensitivity of peat decomposition to climate change through water table feedback. *Nature Geoscience*, *1*(11), 763-766.

Jansen, E., Overpeck, J., Otto-Bleisner, W., Peltier, R., Rahmstorf, S., Ramesh, R., Raynaud, D., Rind, D.H., Mosley-Thompson, L.T. and Zachos, J., (2005). Paleoclimate. *Notes*, *18*.

Jassey, V.E., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B., Gilbert, D., Laggoun-Défarge, F., Lara, E., and Mills, R.T., (2015). An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. *Scientific reports*, *5*(1), 1-10.

Jennings, E., de Eyto, E., Moore, T., Dillane, M., Ryder, E., Allott, N., Nic Aonghusa, C., Rouen, M., Poole, R. and Pierson, D.C., (2020). From highs to lows: Changes in dissolved organic carbon in a peatland catchment and lake following extreme flow events. *Water*, *12*(10), p.2843.

Joabsson, A., Christensen, T.R. and Wallén, B., (1999). Influence of vascular plant photosynthetic rate on CH4 emission from peat monoliths from southern boreal Sweden. *Polar Research*, *18*(2), 215-220.

Johansson, L.G. and Linder, S., (1980). Photosynthesis of Sphagnum in different microhabitats on a subarctic mire. *Ecological Bulletins*, 181-190.

Johnson, C.P., Pypker, T.G., Hribljan, J.A. and Chimner, R.A., (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO 2/CH 4 dynamics in a northern Michigan peatland. *Ecosystems*, *16*(5), 736-748.

Joosten, H. and Clarke, D., (2002). Wise use of mires and peatlands. *International Mire Conservation Group and International Peat Society*, *304*.

Joosten, H., (2016). Peatlands across the globe. In *Peatland restoration and ecosystem services: Science, Policy, and Practice*, 19-43. Cambridge: Cambridge University Press.

Juszczak, R., Chojnicki, B., Urbaniak, M., Leśny, J., Silvennoinen, H., Lamentowicz, M., Basińska, A., Gąbka, M., Stróżecki, M., Samson, M. and Łuców, D., (2016) Short term response of a peatland to warming and drought–climate manipulation experiment in W Poland. In *Geophysical Research Abstracts* (Vol. 18).

Kang, H., Kwon, M.J., Kim, S., Lee, S., Jones, T.G., Johncock, A.C., Haraguchi, A. and Freeman, C., (2018). Biologically driven DOC release from peatlands during recovery from acidification. *Nature Communications*, *9*(1), 1-7.

Kelker, D. and Chanton, J., (1997). The effect of clipping on methane emissions from Carex. *Biogeochemistry*, *39*(1), 37-44.

Keller, J.K. and Bridgham, S.D., (2007). Pathways of anaerobic carbon cycling across an ombrotrophic-minerotrophic peatland gradient. *Limnology and Oceanography*, *52*(1), 96-107.

Kelly, C. A., Dise, N. B., and Martens, C. S. (1992). Temporal variations in the stable carbon isotopic composition of methane emitted from Minnesota peatlands. *Global Biogeochemical Cycles*, *6*(3), 263-269.

Kennedy, A.D., (1995). Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. *Functional Ecology*, 340-350.

Kettridge, N., and Baird, A. (2008). Modelling soil temperatures in northern peatlands. *European Journal of Soil Science*, *59*(2), 327-338.

Kettridge, N., Thompson, D. K., Bombonato, L., Turetsky, M. R., Benscoter, B. W., and Waddington, J. M. (2013). The ecohydrology of forested peatlands: Simulating the effects of tree shading on moss evaporation and species composition. *Journal of Geophysical Research: Biogeosciences*, *118*(2), 422-435.

Keuper, F., Dorrepaal, E., van Bodegom, P.M., Aerts, R., van Logtestijn, R.S., Callaghan, T.V. and Cornelissen, J.H., (2011). A Race for Space? How Sphagnum fuscum stabilizes vegetation composition during long-term climate manipulations. *Global Change Biology*, *17*(6), 2162-2171.

Kip, N., Van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.J., Smolders, A.J., Jetten, M.S., Damsté, J.S.S. and Op den Camp, H.J., (2010). Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nature Geoscience*, *3*(9), 617-621.

Klein, E.S., Yu, Z., and Booth, R.K., (2013). Recent increase in peatland carbon accumulation in a thermokarst lake basin in Southwestern Alaska. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *392*, 186-195.

Köhler, S. J., Buffam, I., Seibert, J., Bishop, K. H., and Laudon, H. (2009). Dynamics of stream water TOC concentrations in a boreal headwater catchment: Controlling factors and implications for climate scenarios. *Journal of Hydrology*, *373*(1-2), 44-56.

Korhola, A., (1995). Holocene climatic variations in southern Finland reconstructed from peat-initiation data. *The Holocene*, *5*(1), 43-57.

Kotsyurbenko, O. R., Glagolev, M. V., Merkel, A. Y., Sabrekov, A. F., and Terentieva, I. E. (2019). Methanogenesis in soils, wetlands, and peat. *Handbook of hydrocarbon and lipid microbiology Series. Biogenesis of hydrocarbons/AJM Stams and Diana Z. Sousa (Eds.) Springer-Verlag. Berlin Heidelberg. https://doi. org/10.1007/978-3-319-53114-4_9-1*.

Kreyling, J. and Beier, C., (2013). Complexity in climate change manipulation experiments. *Bioscience*, *63*(9), 763-767.

Kuhry, P. and Turunen, J., (2006). The postglacial development of boreal and subarctic peatlands. In: *Boreal Peatland Ecosystems* (25-46). Springer, Berlin, Heidelberg.

Kuiper, J.J., Mooij, W.M., Bragazza, L. and Robroek, B.J., (2014). Plant functional types define magnitude of drought response in peatland CO2 exchange. *Ecology*, *95*(1), 123-131.

Kuiper, J.J., Mooij, W.M., Bragazza, L. and Robroek, B.J., (2014). Plant functional types define magnitude of drought response in peatland CO2 exchange. *Ecology*, *95*(1), 123-131.

Lafleur, P.M., Moore, T.R., Roulet, N.T. and Frolking, S., (2005). Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, *8*(6), 619-629.

Lai, D.Y.F., (2009). Methane dynamics in northern peatlands: a review. *Pedosphere*, *19*(4), 409-421.

Laiho, R., (2006). Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry*, *38*(8), 2011-2024.

Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H. and Tuittila, E.S., (2019). Warming impacts on boreal fen CO2 exchange under wet and dry conditions. *Global Change Biology*, *25*(6), 1995-2008.

Lamb, H.H., (1965). The early medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *1*, 13-37.

Lamentowicz, M., Słowińska, S., Słowiński, M., Jassey, V., Chojnicki, B., Reczuga, M., Zielińska, M., Marcisz, K., Barabach, J., Samson, M. and Kołaczek, P., (2016).

Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of Sphagnum peatlands to drought, fire and warming. *Mires and Peat*, *18*, 20.

Lashof, D.A., (2000). The use of global warming potentials in the Kyoto Protocol. *Climatic Change*, *44*(4), p.423.

Lee, J. Y., J. Marotzke, G. Bala, L. Cao, S. Corti, J. P. Dunne, F. Engelbrecht, E. Fischer, J. C. Fyfe, C. Jones, A. Maycock, J. Mutemi, O. Ndiaye, S. Panickal, T. Zhou, (2021). Future Global Climate: Scenario Based Projections and Near-Term Information. In: *Climate Change 2021: The Physical Science Basis.* [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Leng, L. Y., Ahmed, O. H., and Jalloh, M. B. (2019). Brief review on climate change and tropical peatlands. *Geoscience Frontiers*, *10*(2), 373-380.

Li, Q., Leroy, F., Zocatelli, R., Gogo, S., Jacotot, A., Guimbaud, C. and Laggoun-Défarge, F., (2021). Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change. *Soil Biology and Biochemistry*, *153*, p.108077.

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H. and Schaepman-Strub, G., (2008). Peatlands and the carbon cycle: from local processes to global implications–a synthesis. *Biogeosciences*, *5*(5), 1475-1491.

Lindholm, T. and Vasander, H., (1990), January. Production of eight species of Sphagnum at Suurisuo mire, southern Finland. In *Annales Botanici Fennici* (145-157). The Finnish Botanical Publishing Board.

Lindsay, R. (2010). *Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change*. University of East London, Environmental Research Group.

Lindsay, R., (2016). *Peatland* (*mire types): based on origin and behavior of water, peat genesis, landscape position, and climate*. Springer Netherlands.

Loisel, J. and Garneau, M., (2010). Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*(3-4), 493-533.

Loisel, J. and Yu, Z., (2013). Surface vegetation patterning controls carbon accumulation in peatlands. *Geophysical Research Letters*, *40*(20), 5508-5513.

Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W., Benavides, J.C., Blewett, J., Camill, P., Charman, D.J. and Chawchai, S., (2021). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*(1), 70-77.

Lowe, J.A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G. and Fung, F., (2018). UKCP18 science overview report. *Met Office Hadley Centre: Exeter, UK*.

Lund, M., Christensen, T.R., Lindroth, A. and Schubert, P., (2012). Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. *Environmental Research Letters*, *7*(4), p.045704.

Lund, M., Lafleur, P.M., Roulet, N.T., Lindroth, A., Christensen, T.R., Aurela, M., Chojnicki, B.H., Flanagan, L.B., Humphreys, E.R., Laurila, T. and Oechel, W.C., (2010). Variability in exchange of CO2 across 12 northern peatland and tundra sites. *Global Change Biology*, *16*(9), 2436-2448.

Lynch, J., Cain, M., Pierrehumbert, R., and Allen, M. (2020). Demonstrating GWP*: a means of reporting warming-equivalent emissions that captures the contrasting impacts of short-and long-lived climate pollutants. *Environmental Research Letters*, *15*(4), 044023.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., and Velichko, A.A., (2006). Rapid early development of circumarctic peatlands and atmospheric CH4 and CO2 variations. *Science*, *314*(5797), 285-288.

Magnan, G., Le Stum-Boivin, É., Garneau, M., Grondin, P., Fenton, N. and Bergeron, Y., (2019). Holocene vegetation dynamics and hydrological variability in forested peatlands of the Clay Belt, eastern Canada, reconstructed using a palaeoecological approach. *Boreas*, *48*(1), 131-146.

Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Vander Stel, H., Feron, S.C., Hanson, P.J. and Iversen, C.M., (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences*, *117*(30), 17627-17634.

Malmer, N. and Wallén, B., (2004). Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. *The Holocene*, *14*(1), 111-117.

Mann, M.E., Zhang, Z., Hughes, M.K., Bradley, R.S., Miller, S.K., Rutherford, S. and Ni, F., (2008). Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. *Proceedings of the National Academy of Sciences*, *105*(36), 13252-13257.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. and Ni, F., (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, *326*(5957), 1256-1260.

Marinier, M., Glatzel, S., and Moore, T. R. (2004). The role of cotton-grass (Eriophorum vaginatum) in the exchange of CO2 and CH4 at two restored peatlands, eastern Canada. *Ecoscience*, *11*(2), 141-149.

Marrs, R.H., Marsland, E.L., Lingard, R., Appleby, P.G., Piliposyan, G.T., Rose, R.J., O'Reilly, J., Milligan, G., Allen, K.A., Alday, J.G. and Santana, V., (2019). Experimental evidence for sustained carbon sequestration in fire-managed, peat moorlands. *Nature Geoscience*, *12*(2), 108-112.

Mauquoy, D. and Yeloff, D., (2008). Raised peat bog development and possible responses to environmental changes during the mid-to late-Holocene. Can the palaeoecological record be used to predict the nature and response of raised peat bogs to future climate change? *Biodiversity and Conservation*, *17*(9), 2139-2151.

Mauquoy, D., van Geel, B., Blaauw, M. and van der Plicht, J., (2002). Evidence from northwest European bogs shows 'Little Ice Age' climatic changes driven by variations in solar activity. *The Holocene*, *12*(1), 1-6.

Mauquoy, D., Yeloff, D., van Geel, B., Charman, D.J. and Blundell, A., (2008). Two decadally resolved records from north-west European peat bogs show rapid climate changes associated with solar variability during the mid–late

Holocene. *Journal of Quaternary Science: Published for the Quaternary Research Association*, *23*(8), 745-763.

Meyer, C., Diaz-de-Quijano, M., Monna, F., Franchi, M., Toussaint, M. L., Gilbert, D., and Bernard, N. (2015). Characterisation and distribution of deposited trace elements transported over long and intermediate distances in north-eastern France using Sphagnum peatlands as a sentinel ecosystem. *Atmospheric Environment*, *101*, 286-293.

Mikaloff Fletcher, S.E., Tans, P.P., Bruhwiler, L.M., Miller, J.B. and Heimann, M., (2004). CH4 sources estimated from atmospheric observations of CH4 and its 13C/12C isotopic ratios: 1. Inverse modeling of source processes. *Global Biogeochemical Cycles*, *18*(4).

Millar, D.J., Cooper, D.J. and Ronayne, M.J., (2018). Groundwater dynamics in mountain peatlands with contrasting climate, vegetation, and hydrogeological setting. *Journal of Hydrology*, *561*, 908-917.

Mitchell, E.A., Charman, D.J. and Warner, B.G., (2008). Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present, and future. *Biodiversity and Conservation*, *17*(9), 2115-2137.

Monteith, D.T., Stoddard, J.L., Evans, C.D., De Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J. and Keller, B., (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, *450*(7169), 537-540.

Moore, T. R., and Knowles, R. (1990). Methane emissions from fen, bog, and swamp peatlands in Quebec. *Biogeochemistry*, *11*(1), 45-61.

Moore, P.D., (2002). The future of cool temperate bogs. *Environmental Conservation*, *29*(1), 3-20.

Moore, T.R. and Dalva, M., (2001). Some controls on the release of dissolved organic carbon by plant tissues and soils. *Soil Science*, *166*(1), 38-47.

Moore, T.R. and Roulet, N.T., (1993). Methane flux: water table relations in northern wetlands. *Geophysical Research Letters*, *20*(7), 587-590.

Muller, R., and Muller, E. (2017). Fugitive methane and the role of atmospheric half-life. *Geoinformatics and Geostatistics: An Overview*, *5*(1).

Munir, T.M. and Strack, M., (2014). Methane flux influenced by experimental water table drawdown and soil warming in a dry boreal continental bog. *Ecosystems*, *17*(7), 1271-1285.

Munir, T.M., Perkins, M., Kaing, E. and Strack, M., (2014). Carbon dioxide flux and net primary production of a boreal treed bog: responses to warming and water table manipulations. *Biogeosciences Discussions*, *11*(9).

National Oceanic and Atmospheric Administration (NOAA), (2021). [online] Trends in Atmospheric Carbon Dioxide. [online source] Available at: <https://gml.noaa.gov/ccgg/trends/gl_trend.html> [Accessed 02/12/2021].

Nichols, J.E. and Peteet, D.M., (2019). Rapid expansion of northern peatlands and doubled estimate of carbon storage. *Nature Geoscience*, *12*(11), 917-921.

Nichols, J. E., Isles, P. D., and Peteet, D. M. (2014). A novel framework for quantifying past methane recycling by Sphagnum-methanotroph symbiosis using carbon and hydrogen isotope ratios of leaf wax biomarkers. *Geochemistry, Geophysics, Geosystems*, *15*(5), 1827-1836.

Noble, M.G., Lawrence, D.B. and Streveler, G.P., (1984). Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. *Bryologist*, 119-127.

Nolan, C., Overpeck, J.T., Allen, J.R., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R. and Djamali, M., (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, *361*(6405), 920-923.

Norby, R.J., Childs, J., Hanson, P.J. and Warren, J.M., (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, *9*(22), 12571-12585.

Noyce, G. L., Varner, R. K., Bubier, J. L., and Frolking, S. (2014). Effect of Carex rostrata on seasonal and interannual variability in peatland methane emissions. *Journal of Geophysical Research: Biogeosciences*, *119*(1), 24-34.

Olefeldt, D., Euskirchen, E.S., Harden, J., Kane, E., McGuire, A.D., Waldrop, M.P. and Turetsky, M.R., (2017). A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability. *Global Change Biology*, *23*(6), 2428-2440.

Opelt, K., Chobot, V., Hadacek, F., Schönmann, S., Eberl, L. and Berg, G., (2007). Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. *Environmental Microbiology*, *9*(11), 2795-2809.

Oulehle, F., Jones, T.G., Burden, A., Cooper, M.D.A., Lebron, I., Zieliński, P. and Evans, C.D., (2013). Soil–solution partitioning of DOC in acid organic soils: results from a UK field acidification and alkalization experiment. *European Journal of Soil Science*, *64*(6), 787-796.

Page, S.E., and Baird, A.J., (2016). Peatlands and global change: response and resilience. *Annual Review of Environment and Resources*, 41, 35-57.

Pakarinen, P., (1978). Production and nutrient ecology of three Sphagnum species in southern Finnish raised bogs. In: *Annales Botanici Fennici* (15-26). Finnish Botanical Publishing Board.

Pastor, J., Solin, J., Bridgham, S.D., Updegraff, K., Harth, C., Weishampel, P. and Dewey, B., (2003). Global warming and the export of dissolved organic carbon from boreal peatlands. *Oikos*, *100*(2), 380-386.

Payne, R. J. (2014). The exposure of British peatlands to nitrogen deposition, 1900–2030. *Mires and Peat*, *14*(04), 1-9.

Payne, R.J., and Blackford, J.J., (2008). Peat humification and climate change: a multi-site comparison from mires in south-east Alaska. *Mires and peat*, 1-11.

Payne, R.J., Lamentowicz, M. and Mitchell, E.A., (2011). The perils of taxonomic inconsistency in quantitative palaeoecology: experiments with testate amoeba data. *Boreas*, *40*(1), 15-27.

Pearson, M., Penttilä, T., Harjunpää, L., Laiho, R., Laine, J., Sarjala, T., Silvan, K. and Silvan, N., (2015). Effects of temperature rise and water table-level drawdown on greenhouse gas fluxes of boreal sedge fens. *Boreal Environment Research,* 20(4).

Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S., Damoulas, T., Knight, S.J. and Goetz, S.J., (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), 673-677.

Peichl, M., Gažovič, M., Vermeij, I., De Goede, E., Sonnentag, O., Limpens, J. and Nilsson, M.B., (2018). Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production. *Scientific reports*, *8*(1), 1-11.

Piotrowska, N., Blaauw, M., Mauquoy, D. and Chambers, F.M., (2011). Constructing deposition chronologies for peat deposits using radiocarbon dating. *Mires and Peat*, *7*(10), 1-14.

Price, J. S., Whittington, P. N., Elrick, D. E., Strack, M., Brunet, N., and Faux, E. (2008). A method to determine unsaturated hydraulic conductivity in living and undecomposed Sphagnum moss. *Soil Science Society of America Journal*, *72*(2), 487-491.

Ramirez, J. A., Baird, A. J., Coulthard, T. J., and Waddington, J. M. (2015). Ebullition of methane from peatlands: Does peat act as a signal shredder?. *Geophysical Research Letters*, *42*(9), 3371-3379.

Ratcliffe, J., Andersen, R., Anderson, R., Newton, A., Campbell, D., Mauquoy, D. and Payne, R., (2018). Contemporary carbon fluxes do not reflect the long-term carbon balance for an Atlantic blanket bog. *The Holocene*, *28*(1), 140-149.

Read, D.J., Leake, J.R. and Perez-Moreno, J., (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243-1263.

Reeve, A.S., Siegel, D.I. and Glaser, P.H., (2000). Simulating vertical flow in large peatlands. *Journal of hydrology*, *227*(1-4), 207-217.

Rinne, J., Tuovinen, J.P., Klemedtsson, L., Aurela, M., Holst, J., Lohila, A., Weslien, P., Vestin, P., Łakomiec, P., Peichl, M. and Tuittila, E.S., (2020). Effect of the 2018 European drought on methane and carbon dioxide exchange of northern mire ecosystems. *Philosophical Transactions of the Royal Society B*, *375*(1810), p.20190517.

Robroek, B.J., Jassey, V.E., Kox, M.A., Berendsen, R.L., Mills, R.T., Cécillon, L., Puissant, J., Meima-Franke, M., Bakker, P.A. and Bodelier, P.L., (2015). Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. *Journal of Ecology*, *103*(4), 925-934.

Robroek, B.J., Jassey, V.E., Payne, R.J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S.J., Dise, N.B., Kattge, J. and Zając, K., (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications*, *8*(1), 1-9.

Robroek, B.J., Limpens, J., Breeuwer, A. and Schouten, M.G., (2007b). Effects of water level and temperature on performance of four Sphagnum mosses. *Plant Ecology*, *190*(1), 97-107.

Robroek, B.J.M., Limpens, J., Breeuwer, A., Crushell, P.H. and Schouten, M.G.C., (2007a). Interspecific competition between Sphagnum mosses at different water tables. *Functional Ecology*, *21*(4), 805-812.

Rodwell, J.S., (1991). *British Plant Communities: Volume 5, Maritime Communities and Vegetation of Open Habitats* (Vol. 5). Cambridge University Press.

Roulet, N.T., (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: Prospects and significance for Canada. *Wetlands*, *20*(4), 605-615.

Roulet, N.T., Lafleur, P.M., Richard, P.J., Moore, T.R., Humphreys, E.R. and Bubier, J.I.L.L., (2007). Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, *13*(2), 397-411.

Rowson, J.G., Payne, R.J., Dise, N.B. and Caporn, S.J., (2012). CARBON BUDGETS FROM A FIELD SCALE MANIPULATION EXPERIMENT: THE EFFECTS OF CLIMATE CHANGE ON RAISED BOGS. 14th *International Peat Congress 1 Extended abstract No. 289*

Rowson, J.G., Worrall, F., and Evans, M.G., (2013). Predicting soil respiration from peatlands. *Science of the Total Environment*, *442*, 397-404.

Rull, V. (2010). Ecology and palaeoecology: Two approaches, one objective. *The Open Ecology Journal*, 3(1).

Ryder, E., de Eyto, E., Dillane, M., Poole, R., and Jennings, E. (2014). Identifying the role of environmental drivers in organic carbon export from a forested peat catchment. *Science of the total environment*, *490*, 28-36.

Rydin, H., and Jeglum, J.K., (2006). Peatlands around the world. In: In *The biology of peatlands*. Oxford University Press.

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., Zielińska, M., Robroek, B.J., Jassey, V.E., Buttler, A. and Chojnicki, B.H., (2018). The impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in Northern Poland. *Wetlands*, *38*(3), 551-563.

Schillereff, D.N., Chiverrell, R.C., Sjöström, J.K., Kylander, M.E., Boyle, J.F., Davies, J.A., Toberman, H. and Tipping, E., (2021). Phosphorus supply affects long-term carbon accumulation in mid-latitude ombrotrophic peatlands. *Communications Earth and Environment, 2*(*1*)*, 1-10.*

Schlünz, B. and Schneider, R.R., (2000). Transport of terrestrial organic carbon to the oceans by rivers: re-estimating flux-and burial rates. *International Journal of Earth Sciences*, *88*(4), 599-606.

Seddon, A.W., Mackay, A.W., Baker, A.G., Birks, H.J.B., Breman, E., Buck, C.E., Ellis, E.C., Froyd, C.A., Gill, J.L., Gillson, L. and Johnson, E.A., (2014). Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology*, *102*(1), 256-267.

Segers, R., (1998). Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry*, *41*(1), 23-51.

Shiller, J.A., Finkelstein, S.A. and Cowling, S.A., (2014). Relative importance of climatic and autogenic controls on Holocene carbon accumulation in a temperate bog in southern Ontario, Canada. *The Holocene*, *24*(9), 1105-1116.

Shiller, J.A., Finkelstein, S.A. and Cowling, S.A., (2014). Relative importance of climatic and autogenic controls on Holocene carbon accumulation in a temperate bog in southern Ontario, Canada. *The Holocene*, *24*(9), 1105-1116.

Simpson, G.L., (2007). Analogue Methods in Palaeoecology: Using the analogue Package. *Journal of Statistical Software*, 22(2), 1—29

Smemo, K.A. and Yavitt, J.B., (2011). Anaerobic oxidation of methane: an underappreciated aspect of methane cycling in peatland ecosystems? *Biogeosciences*, *8*(3), 779-793.

Sparling, J.H., (1967). The occurrence of Schoenus nigricans L. in blanket bogs: I. Environmental conditions affecting the growth of S. nigricans in blanket bog. *The Journal of Ecology*, 1-13.

Stocker, B.D., Roth, R., Joos, F., Spahni, R., Steinacher, M., Zaehle, S., Bouwman, L. and Prentice, I.C., (2013). Multiple greenhouse-gas feedbacks from the land biosphere under future climate change scenarios. *Nature Climate Change*, *3*(7), 666-672.

Strack, M. and Waddington, J.M., (2007). Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Global Biogeochemical Cycles*, *21*(1).

Strack, M. and Zuback, Y.C.A., (2013). Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences*, *10*(5), 2885-2896.

Strack, M., Waddington, J.M. and Tuittila, E.S., (2004). Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. *Global Biogeochemical Cycles*, *18*(4).

Strack, M., Waddington, J.M., Bourbonniere, R.A., Buckton, E.L., Shaw, K., Whittington, P., and Price, J.S., (2008). Effect of water table drawdown on peatland dissolved organic carbon export and dynamics. *Hydrological Processes: An International Journal*, *22*(17), 3373-3385.

Strack, M., Waller, M. F., and Waddington, J. M. (2006a). Sedge succession and peatland methane dynamics: A potential feedback to climate change. *Ecosystems*, *9*(2), 278-287.

Strack, M., Waddington, J.M., Rochefort, L. and Tuittila, E.S., (2006b). Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research: Biogeosciences*, *111*(G2).

Strozecki, M., Rastogi, A., Chojnicki, B., Leśny, J., Urbaniak, M., Olejnik, J., Basińska, A., Lamentowicz, M., Łuców, D., Gąbka, M. and Józefczyk, D., (2020), May. Impact of reduced precipitation and increased temperature on CH4 emission from peatland in Western Poland. In *EGU General Assembly Conference Abstracts* (p. 17989).

Swindles, G.T., (2010). Dating recent peat profiles using spheroidal carbonaceous particles (SCPs). *Mires and Peat*, *7*(03), 1-5.

Swindles, G.T., De Vleeschouwer, F. and Plunkett, G., (2010). Dating peat profiles using tephra: stratigraphy, geochemistry, and chronology. *Mires and Peat*, *7*.

Swindles, G.T., Morris, P.J., Mullan, D., Watson, E.J., Turner, T.E., Roland, T.P., Amesbury, M.J., Kokfelt, U., Schoning, K., Pratte, S. and Gallego-Sala, A., (2015). The long-term fate of permafrost peatlands under rapid climate warming. *Scientific Reports*, *5*(1), 1-6.

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J., Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T. and Barr, I.D., (2019). Widespread drying of European peatlands in recent centuries. *Nature Geoscience*, *12*(11), 922-928.

Swindles, G.T., Morris, P.J., Wheeler, J., Smith, M.W., Bacon, K.L., Edward Turner, T., Headley, A., and Galloway, J.M., (2016). Resilience of peatland ecosystem services over millennial timescales: evidence from a degraded British bog. *Journal of Ecology*, *104*(3), 621-636.

Swindles, G.T., Roland, T.P., Amesbury, M.J., Lamentowicz, M., McKeown, M.M., Sim, T.G., Fewster, R.E. and Mitchell, E.A., (2020). Quantifying the effect of testate amoeba decomposition on peat-based water table reconstructions. *European Journal of Protistology*, *74*, p.125693.

Talbot, J., Roulet, N.T., Sonnentag, O., and Moore, T.R., (2014). Increases in aboveground biomass and leaf area 85 years after drainage in a bog. *Botany*, *92*(10), 713-721.

Tang, R., Clark, J.M., Bond, T., Graham, N., Hughes, D. and Freeman, C., (2013). Assessment of potential climate change impacts on peatland dissolved organic carbon release and drinking water treatment from laboratory experiments. *Environmental Pollution*, *173*, 270-277.

Tanneberger, F., Moen, A., Joosten, H. and Nilsen, N., (2017). The Peatland Map of Europe. *Mires and Peat*, 19, p.22.

Thompson, D.K. and Waddington, J.M., (2008). Sphagnum under pressure: towards an ecohydrological approach to examining Sphagnum productivity. *Ecohydrology: Ecosystems, Land and Water Process Interactions, Ecohydrogeomorphology*, *1*(4), 299-308.

Thurman, E.M., (1985). Aquatic humic substances. In *Organic geochemistry of natural waters* (273-361). Springer, Dordrecht.

Tolonen, K. and Turunen, J., (1996). Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene*, *6*(2), 171-178.

Tsyganov, A.N., Zarov, E.A., Mazei, Y.A., Kulkov, M.G., Babeshko, K.V., Yushkovets, S.Y., Payne, R.J., Ratcliffe, J.L., Fatyunina, Y.A., Zazovskaya, E.P. and Lapshina, E.D., (2021). Key periods of peatland development and environmental changes in the middle taiga zone of Western Siberia during the Holocene. *Ambio*, 1-14.

Turetsky, M., Wieder, K., Halsey, L. and Vitt, D., (2002). Current disturbance and the diminishing peatland carbon sink. *Geophysical research letters*, *29*(11), 21-1.

Turetsky, M.R. and Louis, V.L.S., (2006). Disturbance in boreal peatlands. In *Boreal peatland ecosystems* (359-379). Springer, Berlin, Heidelberg.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D. and Tuittila, E.S., (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, *196*(1), 49-67.

Turetsky, M.R., Donahue, W. and Benscoter, B.W., (2011). Experimental drying intensifies burning and carbon losses in a northern peatland. *Nature Communications*, *2*(1), 1-5.se to climate change. *Global Change Biology*, *10*(7), 1043-1052.

Turetsky, M.R., Donahue, W. and Benscoter, B.W., (2011b). Experimental drying intensifies burning and carbon losses in a northern peatland. *Nature Communications*, *2*(1), 1-5.

Turetsky, M.R., Kane, E.S., Harden, J.W., Ottmar, R.D., Manies, K.L., Hoy, E., and Kasischke, E.S., (2011a). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, *4*(1), 27-31.

Turetsky, M.R., Manning, S.W., and Wieder, R.K., (2004). Dating recent peat deposits. *Wetlands*, *24*(2), 324-356.

Turetsky, M.R., Treat, C.C., Waldrop, M.P., Waddington, J.M., Harden, J.W. and McGuire, A.D., (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*, *113*(G3).

Turner, T.E., Swindles, G.T. and Roucoux, K.H., (2014). Late Holocene ecohydrological and carbon dynamics of a UK raised bog: impact of human activity and climate change. *Quaternary Science Reviews*, *84*, 65-85.

Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P. and Harth, C., (2001). Response of CO2 and CH4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, *11*(2), 311-326.

van Bellen, S., Shotyk, W., Magnan, G., Davies, L., Nason, T., Mullan-Boudreau, G., Garneau, M., Noernberg, T., Bragazza, L. and Zaccone, C., (2020). Carbon and nitrogen accumulation rates in ombrotrophic peatlands of central and northern Alberta, Canada, during the last millennium. *Biogeochemistry*, *151*(2), 251-272.

van Breemen, N., (1995). How Sphagnum bogs down other plants. *Trends in Ecology and Evolution*, *10*(7), 270-275.

van Loon, A.F., (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews: Water*, *2*(4), 359-392.

Vitt, D.H., (2006). Functional characteristics and indicators of boreal peatlands. In *Boreal peatland ecosystems* (9-24). Springer, Berlin, Heidelberg.

Voosen, P., (2021). Global temperatures in 2020 tied record highs. *Science*, *371*(6527), 334-335.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K. and Moore, P.A., (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, *8*(1), 113-127.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B. and Epstein, H.E., (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342-1346.

Walker, T.N., Garnett, M.H., Ward, S.E., Oakley, S., Bardgett, R.D. and Ostle, N.J., (2016). Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology*, *22*(5), 1880-1889.

Ward, S.E., Bardgett, R.D., McNamara, N.P. and Ostle, N.J., (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. *Functional Ecology*, *23*(2), 454-462.

Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H. and Bardgett, R.D., (2015). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, *96*(1), 113-123.

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A. and Bardgett, R.D., (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology letters*, *16*(10), 1285-1293.

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J. and Harth, C., (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, *9*(2), 141-151.

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K. and Chapin, C.T., (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, *81*(12), 3464-3478.

Wheeler, B.D. and Proctor, M.C.F., (2000). Ecological gradients, subdivisions, and terminology of north-west European mires. *Journal of Ecology*, *88*(2), 187-203.

Wheeler, B.D., (1984). British fens: a review. *European mires*, 237-281.

White, J.R., Shannon, R.D., Weltzin, J.F., Pastor, J. and Bridgham, S.D., (2008). Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. *Journal of Geophysical Research: Biogeosciences*, *113*(G3).

Whiting, G.J. and Chanton, J.P., (2001). Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus B*, *53*(5), 521-528.

Wiłkomirski, B. and Malawska, M., (2004). Characteristics of humic substances in peat of selected peatlands from north-eastern Poland. *Soil Science and Plant Nutrition*, *50*(6), 931-934.

Willis, K. J., Bailey, R. M., Bhagwat, S. A., and Birks, H. J. B. (2010). Biodiversity baselines, thresholds, and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology and Evolution*, 25(10), 583– 591.

Wilson, R.M., Hopple, A.M., Tfaily, M.M., Sebestyen, S.D., Schadt, C.W., Pfeifer-Meister, L., Medvedeff, C., McFarlane, K.J., Kostka, J.E., Kolton, M., and Kolka, R.K., (2016). Stability of peatland carbon to rising temperatures. *Nature Communications*, *7*(1), 1-10.

Wisser, D., Marchenko, S., Talbot, J., Treat, C. and Frolking, S., (2011). Soil temperature response to 21st century global warming: the role of and some implications for peat carbon in thawing permafrost soils in North America. *Earth System Dynamics*, *2*(1), 121-138.

Worrall, F., and Burt, T. (2004). Time series analysis of long-term river dissolved organic carbon records. *Hydrological processes*, *18*(5), 893-911.

Worrall, F., and Burt, T.P., (2008). The effect of severe drought on the dissolved organic carbon (DOC) concentration and flux from British rivers. *Journal of hydrology*, *361*(3-4), 262-274.

Worrall, F., Burt, T., Adamson, J., Reed, M., Warburton, J., Armstrong, A., and Evans, M. (2007). Predicting the future carbon budget of an upland peat catchment. *Climatic Change*, *85*(1), 139-158.

Worrall, F., Burt, T. P., and Adamson, J. K. (2006). Trends in drought frequency–the fate of DOC export from British peatlands. *Climatic Change*, *76*(3), 339-359.

Worrall, F., Burt, T. and Shedden, R., (2003). Long term records of riverine dissolved organic matter. *Biogeochemistry*, *64*(2), 165-178.

Wu, J., and Roulet, N.T., (2014). Climate change reduces the capacity of northern peatlands to absorb the atmospheric carbon dioxide: The different responses of bogs and fens. *Global Biogeochemical Cycles*, *28*(10), 1005-1024.

Xu, J., Morris, P.J., Liu, J. and Holden, J., (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena*, *160*, 134-140.

Yavitt, J.B., Williams, C.J. and Wieder, R.K., (1997). Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiology Journal*, *14*(4), 299-316.

Young, D.M., Baird, A.J., Charman, D.J., Evans, C.D., Gallego-Sala, A.V., Gill, P.J., Hughes, P.D., Morris, P.J. and Swindles, G.T., (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific Reports*, *9*(1),1-8.

Young, D.M., Baird, A.J., Gallego-Sala, A.V. and Loisel, J., (2021). A cautionary tale about using the apparent carbon accumulation rate (aCAR) obtained from peat cores. *Scientific Reports*, *11*(1), 1-12.

Yu, Z., (2006). Holocene carbon accumulation of fen peatlands in boreal western Canada: A complex ecosystem response to climate variation and disturbance. *Ecosystems*, *9*(8), 1278-1288.

Yu, Z., (2011). Holocene carbon flux histories of the world's peatlands: Global carbon-cycle implications. *The Holocene*, *21*(5), 761-774.

Zhang, D., Chen, L., Feng, Z., Ran, M., Yang, Y., Zhang, Y. and Liu, Q., (2021). Four peat humification-recorded Holocene hydroclimate changes in the southern Altai Mountains of China. *The Holocene*, p.09596836211011674.

Chapter 2: Methodology

2.1. General introduction

The purpose of this work is to integrate short-term peatland manipulation experiments with long-term high-resolution palaeoecological investigations, to better understand how these ecosystems may respond to future warming and increased drought frequency as a result of anthropogenic climate change. Integrating both approaches in this manner will improve interpretations for both approaches, helping to reduce the current uncertainty surrounding the future role of peatlands in the global climate system. To achieve this aim, it is necessary to implement a cross-disciplinary approach, integrating a suite of field, laboratory, and statistical methods from both the biological (experimental ecology) and geographical (palaeoecology) sciences.

2.2. Study site

To fulfil the objectives outlined in the previous chapter, this thesis makes use of an experimental climate manipulation experiment situated on Cors Fochno, located in mid-Wales (Figure 2.1). Cors Fochno (Lat: 52.50, Long: -4.01) is located east of the town of Borth, on the south side of the Dyfi estuary (Figure 2.1). The canalised River Leri runs through the western margin of the bog. Peat initiation began at the site around c. 6 kyr BP (Wilks, 1979). In the central raised portion of the bog, the peat attains depths greater than 7 m and the peatland surface is approximately 1 m above sea level (Wilks, 1979; Hughes and Schulz, 2001; CCW 2011). The site is underlain by estuarine silts and clays, while the underlying geology of the area is of Silurian Aberystwyth grits group (Howells, 2007).

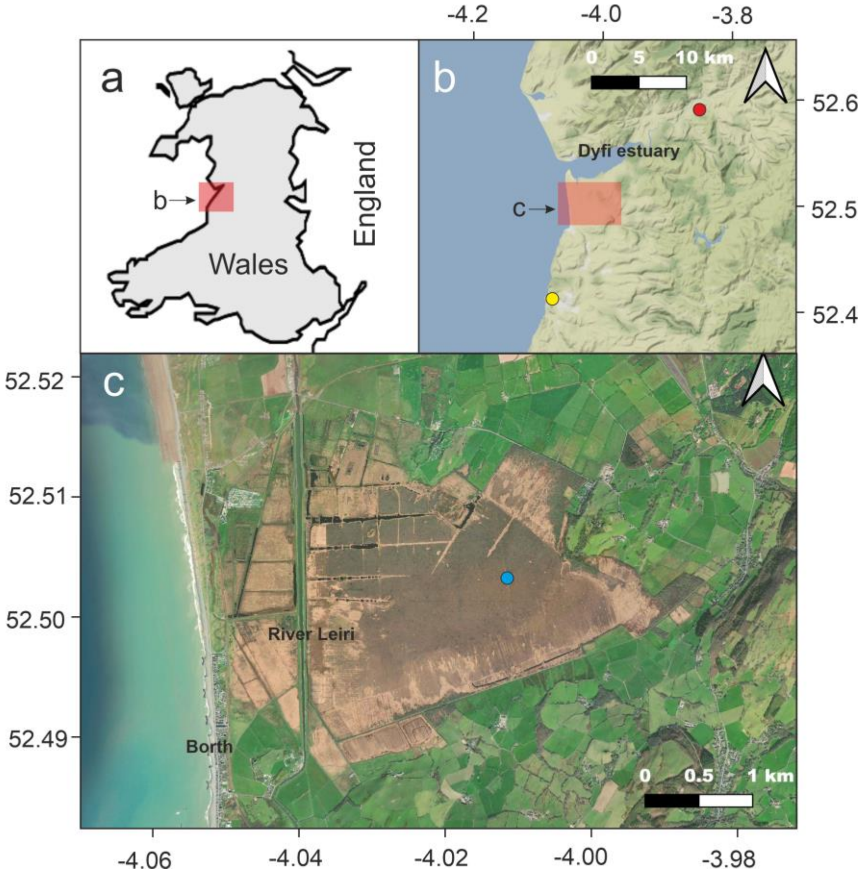


Figure 2.1. Location of the experimental site: a. Map of Wales. Red shaded areas show the area indicated by the following panel. b. topographic map showing the area from Machynlleth (red dot) to Aberystwyth (yellow dot). (Stamen terrain background). c. ESRI Satellite image of Cors Fochno showing the location of the experimental site and location of core BO17 (blue dot).

Cors Fochno is a nature reserve of international importance. It forms part of the Dyfi UNESCO Biosphere Reserve, the only example of such a reserve in Wales. It is also a Special Area of Conservation and a Site of Special Scientific Interest. It represents the type locality for estuarine raised mires and is one of the largest remaining expanses of primary surface lowland bog in Britain. The central active zone comprises c. 2 km^2 of primary surface peat, surrounded by c. 4 km^2 of degraded peatland, which was drained for peat harvesting or improved for agriculture (Poucher, 2009).

Throughout much of its history, the site experienced only low-level human activity characterised by local mining, habitation, grazing and burning (Poucher, 2009; Mighall *et al.,* 2017). Around the 10th century CE, a wooden trackway was built traversing the southern side of the bog (Page *et al.,* 2012). Human activity intensified towards the end of the 18th century, reaching its zenith during the 1940s as the war effort increased the need for agricultural land (Poucher, 2009; Page *et al.,* 2012; Mighall *et al.,* 2017). Around 1970, the first restoration efforts began to restore degraded areas of the bog. As a result of this, many formerly damaged areas are now actively regenerating and support peat-forming vegetation; however, large areas of improved acidic grassland persist, with some areas overlying peat which are still actively grazed by sheep (Poucher, 2009). In the present day, restoration work continues, with the EU-LIFE funded project New LIFE for Welsh Raised Bogs improving marginal areas and blocking former drainage channels on the site (Natural Resources Wales, 2021).

The vegetation on the central active zone compares with the National Vegetation Classification M18: *Erica tetralix – Sphagnum papillosum* raised and blanket mire (Rodwell, 1991). Figure 2.2 shows the typical vegetation community composition of the central portion of the site. Other areas feature vegetation communities resembling M1, M2, M3, M19 and M20 plant communities, all of which are classes associated with raised mires (Rodwell, 1991; Elkington et al 2001). Vegetation communities are dominated by *Sphagnum*, mostly by *S. pulchrum* (Figure 2.3), and the site is one of the last refugia for the formerly abundant species *S. austinii*. Other species abundant in the relatively undisturbed central portion of the site include *Rhynchospora alba*, *Andromeda polifolia*, *Drosera anglica*, *Eriophorum angustifolium*, *Calluna vulgaris*, *Erica tetralix* and *Myrica* *gale*. The maritime margins of the site are characterised by *Schoenus nigricans*. Degraded areas are characterised by *Molinia caerulea, Phragmites* and *Juncus* spp.,, and some areas are covered by wet woodland and areas of dense *Pteridium aquilinum* scrub.

Figure 2.2. View from the central portion of Cors Fochno (facing North) showing the vegetation community composition and microtopography of the site (*Sphagnum* carpet overlain by hummocks *Myrica gale, Calluna vulgaris* and *Rhynchospora alba*). (Photo: Luke Andrews)

Figure 2.3. Photograph of *Sphagnum pulchrum* growing on Cors Fochno, a dominant peat-forming species in the central raised portion of the bog. Each capitulum is c. 1 cm across. (Photo: Luke Andrews)

This site has been the subject of many scientific studies over many decades. These vary from studies examining the ecological effects of peatland management (Fox; 1984; Slater and Agnew, 1977; Slater, 2012), biogenic gas production and movement in peat soils (Baird *et al.,* 2004; Kettridge and Binley, 2008; Redeker *et al.,* 2015) and testing remote sensing techniques for measuring peatland hydrology (Harris *et al.,* 2006), amongst many others. Much of the research of the site has concerned the long-term history of ecological changes that have occurred since the sites' development, ranging from examination of the long-term peatland development and plant succession (Schulz, 2005; Hughes and Schulz, 2001) to changes in land use and pollution (Godwin and Newton, 1938; Hughes *et al.,* 2007; 2008; Mighall *et al.,* 2009; 2017).

2.3. Experimental setup

2.3.1. Experimental site history and purpose

The Cors Fochno experiment was established between March – June of 2010. It is a fully factorial *in-situ* climate manipulation experiment, consisting of twelve 2 x 2 m plots of *Sphagnum* lawn, replicated in three blocks along a transect (Figure 2.4). The vegetation in this area comprises mostly of *Sphagnum pulchrum* lawns. In some areas, shallow pools are populated by *Sphagnum cuspidatum*, while the sedges *Rhynchospora alba* and *Eriophorum angustifolium* are abundant in wetter areas. In drier areas, *Sphagnum capillifolium* and *Sphagnum papillosum* form hummocks which are often densely populated by the dwarf-shrubs *Calluna vulgaris, Erica tetralix* and *Myrica gale* (CCW, 2011).

Each plot is subjected to one of four experimental treatments, controls (no treatment), warming, increased drought frequency and combined warming and increased drought frequency (an additional drought every c. 2.5 years). The purpose of this experiment is to determine the effects of climate warming and drought at the range predicted for the region from the present until c. 2070 (Lowe *et al.,* 2018) upon ecosystem functions in northern ombrotrophic peatlands.

UK temperatures are projected to increase by 0.3 – 2.6 °C by 2080 – 2099 based upon the RCP2.6 climate scenario, relative to baseline temperatures for 1981 – 2000 (Lowe *et* al., 2018). Precipitation is projected to increase in winter and decrease in summer (Lowe *et al*., 2018), resulting in increasingly frequent and severe seasonal drought and rainstorms (Hanlon *et al*., 2021). Although there is a great deal of regional variation, with between 1.5 – 4.0 °C of warming, average summer drought severity is projected to increase by as much as 19 %, while days in which high-impact heavy rainfall events occur are projected to increase by 1 – 8 per year (Hanlon *et al*., 2021).

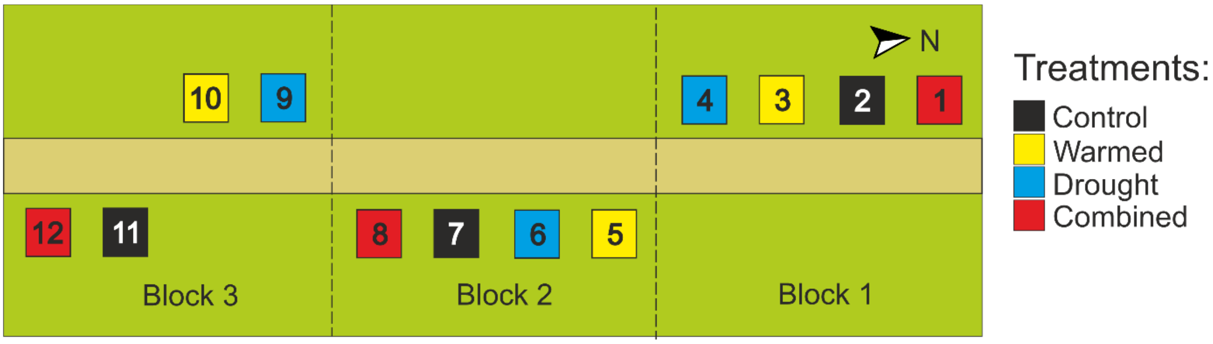


Figure 2.4. Experimental design schematic, showing the position of each experimental plot along the boardwalk (not to scale). The blocks are delineated by dashed vertical lines.

This experimental site was originally devised as part of a NERC-funded study examining the effects of nitrogen pollution upon peatland biodiversity in a warming and drying world (PEATBOG project), which ran from 2009 until 2013. The position of each plot was originally chosen along the transect so that each plot enclosed an area characterised by vegetation that was representative of the site. The Cors Fochno experiment was established to represent a relatively undisturbed mire, in comparison with a 'sister site' located in Whixall bog between Whitchurch and Ellesmere in England, which had a similar experimental design but a much higher nitrogen load, owing to historical disturbance and local sources. The study at Whixall ended in 2013, whereas the Cors Fochno experiment continued, where it was used as part of a NERC-funded PhD project examining the impacts of climate change and sea-level rise on lowland raised bog ecosystem functioning, which ran from 2013 until 2017 (Kay, 2019). Since 2017, the experimental site has continued with funding by the Leverhulme Trust for the project 'Peatland carbon balance and climate change: from the past to the future'. The results of this project culminated in this thesis.

2.3.2. Experimental climate manipulations

The Cors Fochno experiment uses open top chambers (OTCs) to passively warm the air within the chamber like a greenhouse, simulating climate warming. OTCs are a commonly used method for inducing moderate increases (typically between 0.35 – 1.0°C) in air temperature in field experiments (Aronson and McNulty, 2009; Ward *et al.,* 2013; Walker *et al.,* 2016). An example of one of the OTCs used in this project is illustrated in Figure 2.5a. The OTCs follow designs originally proposed by the International Tundra Experiment (Marion *et al.,* 1997a; 1997b; Arft *et al.,* 1999; Shaver *et al.,* 2000). OTCs were constructed from Perspex sheets 2.5mm thick, joined at the corners by cable ties inserted through four holes, drilled into the edge of each sheet.

Drought in this study refers to a period of reduced precipitation resulting in lowered groundwater levels (van Loon, 2015). In the case of this experimental study, this lowering of the groundwater (henceforth also referred to as 'drought,' as well as 'drought manipulations' or 'simulated drought') is simulated by pumping groundwater from within the plots using an automated system. Water was drawn from four excavated, plastic tube-lined wells located in the corner of each droughted plot using macerator-style pumps attached to four inlets, one for each well (Figure 2.5b, c). The drought plots were hydrologically separated from the surrounding peat using 1.5 m deep plastic piling to prevent lateral recharge of groundwater. In the non-droughted plots, the disturbance associated with their insertion was replicated by inserting 0.5 m piling, which were drilled with holes to allow water to travel between the plots and the surrounding peat. A more comprehensive description of the experimental drought setup and design is given in chapter three. Each period of experimental drought lasted four weeks, and each plot was monitored daily, with two weeks either side of the experiment used to test pre-and post-drought conditions. By the point of the completion of this current project, drought simulations had been repeated four times at the site, during 2010, 2011, 2014 and 2019. Each simulation occurred during the summer, between the months of August and September.

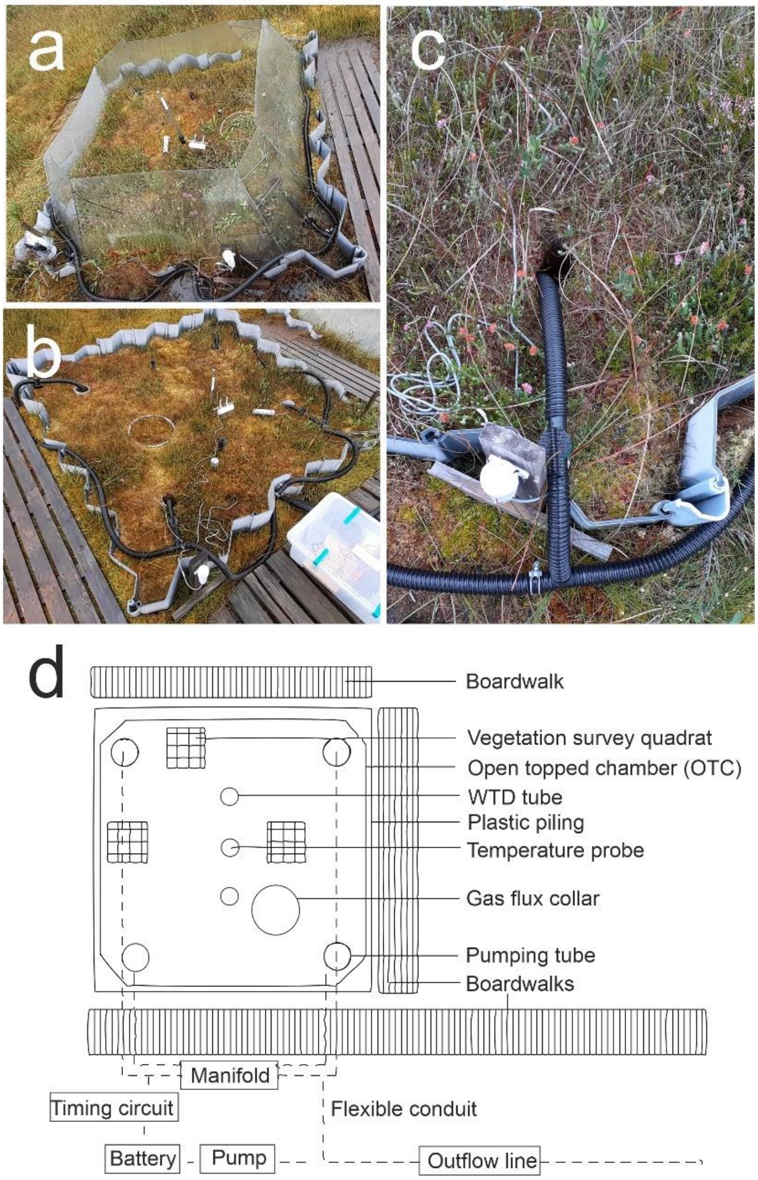


Figure 2.5. a. Warmed and drought plot with open top chamber (plastic covers) and drought simulation pumps (black cables). b. Drought plot showing internal plot-furniture and pumping mechanism. c. Close-up image of one of the corner wells from which water is pumped from within the plot. d. Plot schematic, showing the internal design of a typical plot (figure adapted from Kay, 2019).

2.3.3. Measurement of environmental conditions

Air and soil (10 cm depth) temperatures at the site were measured every six hours within each of the plots between 2010 until 2021 using HOBO Onset U10 Temperature loggers (Onset Computer Corporation; Massachusetts USA). In November 2018, these were replaced by HOBO U23 Pro v2 temperature sensors, although the Onset loggers remained in place until August 2021, ensuring adequate overlap and compatibility between measurements.

Water table depths were measured using TruTrack WT-HR 2000 water height data loggers (Trutrack, Christchurch, New Zealand), which were inserted into an excavated, plastic lined well in the centre of each plot. Logger values were converted to water table depth (WTD) by calibration against regular manual water table depth measurements, measured using a battery powered probe similar in design to those proposed by Bodley *et al.* (1989). Water table depth (relative to the height of the surface peat) was measured from two wells within each plot, both located either side of a central well which contained the TruTrack probes. Mean water table depths were calculated for each plot by averaging the two measurements between each well.

For the whole site, photosynthetically active radiation (PAR) was measured using a QSO-S PAR sensor (Apogee instruments inc., Logan, Utah, United States) at 15-minute intervals and the data were stored on a Decagon EM50 data-logger (Pullman, Washington, United States). Data were compiled throughout the experiment to achieve a near-continuous data set spanning the ten years of the project. Gaps in the data were filled using linear interpolation with temperature and water table depth records from neighbouring plots, as well as from an adjacent dip-well and weather station operated by Natural Resources Wales.

The effects of each climate manipulation treatment upon environmental conditions were tested using Generalised Linear Mixed Effect Models. The environmental variable of interest was tested as the response variable. Plots, nested in blocks and measurement date were included as random factors.

2.4. Hand coring

A 1.5 m core (BO17) was excavated from Cors Fochno in November 2017. This core was used to fulfil almost all of the palaeoecological objectives of this thesis, from which all reconstructions pertaining to the period of interest of this study (the last c. 1500 years) were made. Core BO17 was extracted using a 5 cm diameter Eijkelkamp Russian-style chamber corer (Jowsey, 1966). This type of corer secures the cored sediment within a chamber, cutting the peat with a blade that then encloses the sample, shielding it from contamination as it is extracted. Core sections 50 cm long were extracted alternatively from two holes less than 20 cm apart. Each core section overlapped by 5 cm (Jowsey, 1966).

The coring location was located c. 3 m from the experimental site, in an area between experimental plots two and three. The coring location was characterised mainly by *S. pulchrum* lawn with abundant *Rhynchospora alba.* Cores taken from lawn microtopographic features are considered to be the most sensitive to environmental change, owing to their proximity to the water table (De Vleeschouwer *et al.,* 2010). The uppermost 50 cm of core was extracted using a monolith tin, ensuring sufficient quantities of material were recovered for the multiple analyses necessary to fulfil the objectives of this thesis.

Three full-length cores (BO18 1 – 3) were also taken in November 2018 using a 5 cm-diameter Russian peat sampler from approximately equal distances along the experimental transect. These cores were used to assess the long-term average apparent rate of carbon accumulation (LORCA or LARCA) from the point of peat initiation (Korhola *et al.,* 1995; Clymo *et al.,* 1998). As with core BO17, the uppermost 50 cm of each core was extracted using a monolith tin. Extracted core sections were stored in guttering and wrapped in cling film to prevent drying. Cores were kept in a cold store at temperatures of ~4°C prior to sub-sampling.

2.5. Field measurements of carbon fluxes

2.5.1. Greenhouse gas flux measurements

To determine the effects of the experimental climate manipulations upon short-term greenhouse gas emissions and carbon cycling, fluxes of CO_2 and CH_4 and pore-water dissolved organic carbon (DOC) were measured during frequent field excursions from within each experimental plot. Measurements were made during all months of the year to capture a full range of environmental conditions

Surface exchange of the greenhouse gases CO_2 and CH_4 were measured using the closed chamber method (Alm *et al.,* 2007). Gas flux measurements were made by placing a closed chamber system upon a PVC collar inserted into the peat within each plot. A rubber seal was glued to the rim of the chamber to prevent gas from entering or escaping the chamber. To ensure a good seal between the chamber and the collar, the chamber was weighted down around the rim (Figure 2.6). Air within the chamber was circulated by a fan to prevent the stratification of gases. The type of chamber used for all measurements is shown in Figure 2.6 and 2.7. While the use of a fan may influence the advection of greenhouse gases from the soil, this effect is reduced in sites where the water table is close to the surface, since the area in which mixing and stratification of gases can occur is reduced (Redeker *et al.,* 2015). The placement of dam piling around the perimeter of the plots disconnects them from the main body of peat, therefore wind speeds are assumed to have had a negligible effect upon gas flux measurement error in this study.

For each field campaign, measurements were taken between the times of 09:00 and 16:30. As a consequence, diurnal changes in greenhouse gas emissions are not represented in this dataset (Pavelka *et al*., 2018). This may have resulted in the underestimation of CH_4 emissions, which can be higher during the night (Dooling *et al.,* 2018). The majority of measurements were taken during the summer when rates of carbon uptake are highest. This may have resulted in annual productivity rates being overestimated (Byrne *et al*., 2004; Goulsbra *et al.,* 2016).

During measurements, air within the chamber was circulated through inlets connected to a gas analyser. Between 2010 – 2016, carbon dioxide measurements were made using a factory-calibrated EGM-4 Infra-Red Gas Analyser (PP Systems, MA, USA). From 2017, a factory-calibrated Los Gatos Ultra-Portable Greenhouse Gas Analyser (Los Gatos, California) was used. The Los Gatos device simultaneously measured ambient air temperatures and the concentration of CO_2 and CH_4. Air temperatures and photosynthetically active radiation (PAR) within the chamber were measured at 1 second frequency and recorded by a Delta-T GP1 Irrigation Monitor data logger. Fluxes were monitored in real-time using a wireless user interface, allowing for a degree of quality control during sampling.

Net CO_2 balances were measured as Net Ecosystem Exchange (NEE). This is the net balance between autotrophic productivity and soil respiration. CO_2 emissions were measured as Net Ecosystem Respiration (NER), which represents respiration from autotrophs and heterotrophs. NER was measured by placing a dark cover over the chamber, while NEE was measured under ambient light conditions. Dark measurements were always taken before light measurements, to avoid warming the inside of the collar. Gross Primary Productivity (GPP) was inferred from the difference between these measurements (NEE minus NER), assuming that respiration rates are equal between light and dark measurements. GPP represents the sum of CO_2 taken up by plant photosynthetic productivity and released by autotrophic respiration. CH_4 fluxes were calculated from the measurements taken under ambient light conditions, as disturbance following placement of the chamber over the collar may have resulted in the initial displacement of pore-water CH_4 by ebullition (Hutchinson and Livingston, 1993). Each flux measurement lasted more than 120 seconds. Gas fluxes were calculated using the following equation 1, following Dossa *et al.* (2015):

$$Flux = \frac{PV}{RTA} \times \frac{\delta C}{\delta t} \qquad \text{(equation 1)}$$

Where P= pressure (atm), V=volume (m^3), R= 0.082058 L atm/mol K, T = air temperature (in K), A= Surface area of the collar, δC = Change in measured gas concentration in ppm and δt = Measurement time (in hours). For this study, collar values were V= 0.0088 m^3 and A= 0.0707. Elapsed time was δt = 0.0333. P was treated as a standard (1 atm). Both the collars and the chamber had diameters of 15 cm. Due to the relatively small size of the experimental plots and the limited footprint of the measurement collars, the spatial heterogeneity of greenhouse gas fluxes was likely underestimated in this study (Pavelka *et al.,* 2018; Lees *et al*., 2018).

Flux concentration changes were calculated using the period for each measurement where the most linear change in concentration occurred, using an Excel program. This equation gives the mass of gaseous change in terms of moles. The molecular mass of CO_2 is calculated by multiplying this value by 44, and for CH_4 this number is divided by 16. Fluxes with an r^2 less than 0.9 were visually assessed to ensure that the measurements were linear. If this was not the case, they were discarded. CO_2 and CH_4 fluxes measured by these methods are reported as g CO_2 m^{-2} h^{-1} and g CH_4 m^{-2} h^{-1}, respectively.

Figure 2.6. Photograph showing a typical gas flux measurement being taken under ambient light conditions.

Figure 2.7. Photograph of inside of flux chamber used when measuring greenhouse gas fluxes.

2.5.2. Measurements of pore water dissolved organic carbon

Rhizon samplers (pore size 1.5µm) for sampling pore-water DOC from 10 cm beneath the peat surface were inserted into each of the experimental plots in September 2017. An incision was made into the peat within each plot, and a rhizon inserted horizontally into the slit to a depth of 10 cm, before being gently pushed into the adjacent, uncut peat. Samples were not taken for four months following installation as the peat surrounding the newly implanted rhizons stabilised. Each rhizon was attached to a tube protruding from the peat surface. At the end of each tube, an attachment allowed for a syringe to draw pore-water from the sampling depth. For each sample, c. 40ml of pore water was drawn from the peat. Sampling time typically took longer during drier periods. Samples were stored in 50 ml centrifuge tubes, which were kept under cool and dark conditions after sampling, to limit sample degradation prior to laboratory analysis, usually within 1-2 days of sampling. Each sample was filtered through a 0.45 µm filter to remove particulate organic matter and microbes, and each filter was flushed using a small amount of sample to remove potential contaminants from the surface of the filter (Norrman, 1992). In some cases, it was necessary to freeze samples prior to analysis, which always occurred after filtering. DOC concentrations were analysed using an Elementar Vario TOC Select analyser and are reported as g l^{-1} in this study.

2.6. Vegetation surveys

Vegetation surveys were conducted annually during late summer (August – September) to characterise vegetation change at the species, plant functional type and community level over time. Each year, three fixed 25 x 25 cm quadrats enclosing a 5 x 5 grid were surveyed within each plot. Plant taxa were quantified using the pin-quadrat method (Levy and Madden, 1933; Rochefort *et al.,* 2013). A skewer was inserted through the top-right corner of each of the 25 squares on each grid. Total touches of each species of (living) vascular plant on the skewer were tallied for each square. Species abundance data were then summed between each square for each plot, accounting for pseudo-replication. During the surveys, all taxa were recorded to species level where possible. Surface cover (e.g., *Sphagnum* species, liverworts, bare peat) was recorded on a presence/absence basis for each segment, potentially resulting in the underestimation of surface cover species in the experimental plots. By the end of this project, a continuous, ten-year record of vegetation change from within each experimental plot had been generated. Many of the recorders were the same individuals during this 10-year period, with the author of this thesis present every summer from 2017 until 2020.

2.7. Litterbag decomposition experiment

The effects of the experimental manipulations upon organic matter decomposition at different depths were tested using the Tea Bag Index (TBI) method developed by Keuskamp *et al.* (2013). Traditional litter bag methods quantify decomposition rates in soils by measuring how much mass is lost from plant litter, requiring multiple measurements over long periods of time (Keuskamp *et al.,* 2013). These types of study typically employ locally produced plant litter to measure site-specific decomposition, making it difficult to compare the results of such studies between sites (Wider, 1982). The TBI method measures decomposition two types of substrates of differing susceptibility to decay (green tea to represent labile organic matter and rooibos tea to represent recalcitrant organic matter). This allows for decay rates (*k*) and stabilisation factors (*S*) of labile organic matter to be calculated in just a few months, while the use of consistent substrate allows for differences in these parameters to be compared between sites (Keuskamp *et al.,* 2013). *S* represents the transformation of labile organic matter into more recalcitrant compounds as a result of microbial activity and environmental conditions (Prescott, 2010; Górecki *et al.,* 2021). *S* influences long-term carbon storage, with higher values of *S* indicating greater organic matter retention (Keuskamp *et al.,* 2013). *k* reflects the rate of decomposition as a result of microbial decay and short-term carbon dynamics (Prescott, 2010; Keuskamp *et al.,* 2013). In this experiment, non-woven tetrahedron bags (Brand: Lipton) were used as opposed to the woven bags with a consistent mesh size as recommended by Keuskamp *et al.* (2013), since production of the woven mesh bags discontinued in 2017. Mesh size can affect the size of particles that entering or escaping from litterbags, therefore the use of non-woven mesh bags without consistent mesh size may reduce comparability between the tea bags used (Keuskamp *et al*., 2013). However, a study by Zhai *et al*. (2019) found that mesh size had no significant effect upon litter decay rates, therefore it is assumed that mesh size had a trivial effect upon the results of this study.

The TBI method has been tested and compared with the decomposition of other plant litter types. MacDonald *et al*., (2018) and Didion *et al*. (2016) compared how the results of the TBI method compared with those of traditional litter bag studies using different plant litters. They found that the TBI method faithfully replicated the results of traditional litter bag studies, although decomposition rates were often overestimated. Blume-Werry *et al*. (2021) compared how decomposition rates and leaching of water-soluble compounds differed between the green and rooibos tea employed by the TBI method and litter from plant species found in temperate peatlands. They found that green tea lost more mass by leaching than the leaves of the peatland species studied, however rooibos tea leached less, potentially offsetting this difference in the calculation of decomposition rates. Duddigan *et al*. (2000) subjected samples of the two types of tea used in the TBI method to experimental incubation, analysing their remains to test how changes in the stoichiometry of carbon and nitrogen compared with other litters. Both Duddigan *et al*. (2000) and Blume-Werry *et al*. (2021) concluded that the tea types used in the TBI method were suitable proxies for peatland vegetation, although Blume-Werry *et al*. (2021) noted that that green tea lost more mass than other litter types due to leaching. However, the TBI method observed similar responses to environmental variables and trends between wet and dry sites, indicating that the results of the TBI method reflect the same spatial patterns in decomposition as traditional methods.

This litter bag experiment was applied to test for differences in above and below ground decomposition between the climate manipulations. Prior to incubation, each type of tea bag was oven-dried at temperatures less than 45°C for 48 hours prior to weighing. The mass of tea was calculated per bag by subtracting the weight of each bag from the average empty bag weight, calculated from the mean weight of five empty bags for each tea type. Samples were not flushed prior to incubation, as this can inhibit compatibility between samples (Blume-Werry *et al.,* 2021).

Five replicate pairs of green and rooibos tea bags were placed onto the surface of each plot, and another five pairs were buried beneath the peat surface to a depth of c. 8cm. Samples were buried by selecting an area containing vegetation representative of the plot as a while. An incision was made into the peat and each tea bag was individually inserted to a depth of c. 8 cm. Tea bags on the surface of the plot were tied to skewers inserted into the peat. The experimental incubation began on the 12th of September 2019 and were retrieved following 92 days of field incubation on the 13th of December 2019. This time-period was chosen because leaf-fall from woody deciduous shrubs on this site occurs mostly during the autumn months. Although low temperatures may have affected decomposition rates during this time, the contribution of above-ground litter and heterotrophic respiration to net ecosystem respiration in terrestrial ecosystems is often greatest during the autumn and spring, in accordance with the increased rates of litterfall (Luo and Zhou, 2006; Jovani-Sancho *et al.*, 2021). While few studies have studied the partitioning of heterotrophic and autotrophic respiration in temperate ombrotrophic peatlands, a study of a riparian peatland in north Wales showed that enzyme activity associated with the decay of freshly accumulated above-ground litter increased following litterfall in October (Bonnett *et al.,* 2006).

Recovered bags were dried at <45°C for 48 hours after retrieval. Following drying, each bag was opened, and the contents were examined under a low-powered microscope. Foreign particles (*Sphagnum leaves,* ericaceous rootlets) were removed, although these were few. After this, the bag contents were re-weighed. Changes in mass following incubation allowed for the calculation of mass loss (%) for each bag, as well as the calculation of TBI parameters *S* and *k* using the following equations (from Keuskamp *et al.,* 2013):

$$W(t) = ae^{-kt} + (1 - a) \qquad \text{(equation 2)}$$

From this equation, *k* can be calculated. W(*t*) is the weight of the substrate following incubation time (*t),* a is the labile fraction and 1-a is the recalcitrant fraction of the tea. *S* is calculated using the equation:

$$S = 1 - \frac{a_g}{H_g} \qquad \text{(equation 3)}$$

Where a_g is the decomposable fraction and H_g is the hydrolysable fraction of green tea (given as a constant: 0.842). Calculation sheets used to determine *k* and *S* were downloaded from http://www.teatime4science.org/.

Following analysis, remaining material from the green tea bags were homogenised using a ball mill and processed using standard methods for colorimetric peat humification (Aaby and Tauber 1975; Blackford and Chambers 1993), C/N ratios (Malmer and Holm, 1984; Kuhry and Vitt, 1996), and loss on ignition (LOI) (Bouyoucos, 1934; Leifield *et al.,* 2020). This allowed the sensitivity of these palaeoecological decomposition proxies to be compared with the TBI parameters and allowed the sensitivity of each proxy to the climate manipulations to be tested.

2.8. Laboratory methods

2.8.1. Core description and sub-sampling

Core stratigraphy was described in the laboratory using the Troels-Smith method for characterising sediments (Troels-Smith, 1955). Before analysis, core sections were cleaned by scraping away c. 1 mm of surface material using a scalpel. Peat was sub-sampled throughout the core using a scalpel and a spatula. Thin nail scissors were occasionally employed to facilitate sampling of fibric peat.

2.8.2. Core dating methods

2.8.2.1. Radiocarbon dating

Radiocarbon dates were taken and measured from core BO17 to generate a core chronology, allowing for calculation of long-term carbon accumulation rates and the correlation of changes in palaeoenvironmental conditions reconstructed from this core with known periods of climate change. Samples of *Sphagnum* or other above-ground plant remains were picked from 1 cm-thick sub-samples using tweezers, extracted from points of interest within the core (e.g., changes in peat stratigraphy, core basal date). After extracting, each sample was carefully examined using a low-powered microscope at 10 – 100x magnification and rootlets and other potential sources of contamination by younger carbon were removed (Kilian *et al.,* 1995). When insufficient identifiable plant remains were present for a particular section of peat, bulk peat was analysed instead. In this case, a 1 cm thick section of peat was rinsed through a 250 µm sieve and the fine particulate fraction (<250 µm) retained, following guidelines by Piotrowska *et al.* (2011). Samples were alkali-acid washed before oven drying at <45°C. Dried, prepared samples were dated by Accelerator Mass Spectrometry (AMS) ^{14}C dating at DirectAMS, Washington, USA.

For core BO17, an initial series of three ^{14}C dates were used to determine a rough chronology for the core. Based on these measurements it was decided that palaeoecological analyses would focus on the top 1 m of peat, since this section of core represented the past c. 1500 years of interest to this study. After this, further ^{14}C dates were sampled from within this section, to refine the age-depth model within the top metre.

For cores BO18 1-3, basal dates were generated by radiocarbon dating 1 cm^3 bulk peat samples at the point of peat initiation for each core, which were processed using the same methods for bulk peat as were detailed above. All radiocarbon dates in this study were calibrated using the IntCal20 radiocarbon calibration curve in OxCal version 4.4 (Bronk-Ramsey, 2017). By calibrating radiocarbon dates, the effect that changes in atmospheric concentrations of ^{14}C through time have upon radiocarbon dates are accounted for (Reimer *et al.,* 2020).

2.8.2.2. ^{210}Pb dating of recently accumulated peat

^{210}Pb dating was used to date recently accumulated peat in core BO17 (Appleby, 1998; Turetsky *et al.,* 2004). ^{210}Pb is a naturally occurring isotope that is part of the radioactive decay chain of ^{238}U. Solid ^{210}Pb is produced as a product of the radiative decay of the gaseous ^{222}Rn, which then falls with precipitation where it can accumulate in soils. ^{210}Pb has a half-life of c. 22.3 years; therefore, changes in its concentration with depth can be a useful indicator of peat age (Appleby, 1998; Turetsky *et al.,* 2004). Contiguous, 1 cm-thick sub-samples were sampled throughout the top 30 cm of core BO17. Bulk density was measured for each sample by dividing the volume of wet peat by its weight after drying for 24 hours at <45°C (Chambers *et al.,* 2011). Sample preparation followed methods described by Appleby (1998). Samples were homogenised using scissors, weighed, and sealed in air-tight vials for three weeks, allowing for equilibrium of the daughter nucleotide ^{226}Ra within each vial. ^{210}Pb activity for each sample was measured by gamma spectroscopy using well detectors at the Consolidated Radio-Isotope Facility (CoRIF), University of Plymouth.

2.8.2.3. Spheroidal Carbonaceous Particles

An additional method for the dating of surface peat is through the use of Spheroidal Carbonaceous Particles (SCPs). SCP dating is a relatively rapid and low-cost alternative to radiometric methods for dating recently accumulated peat (Swindles, 2010). SCPs are a component of fly ash pollution and are formed by high temperature fossil fuel combustion (Rose, 2008). Samples were prepared for SCP analysis following procedures outlined by Swindles (2010). Samples of peat 1cm^3 were dried overnight at 45°C and then weighed. Dried samples were submerged in 6 ml of concentrated nitric acid (HNO_3) and were left for 24 hours. The following day, the remaining acid was evaporated away by heating the sample on a hot plate. The remaining material was mixed with 10 ml of water. This was transferred into a centrifuge tube and centrifuged for five minutes at 1500 rpm. After decanting the supernatant, this process was repeated twice more to wash the remaining acid from the sample. The residue was then transferred into an Eppendorf tube of known weight, and the weight of the tube and the sample was measured again. Samples were stirred and a quantity of the residue was transferred onto a coverslip and dried. The Eppendorf tube was re-weighed. Prepared coverslips were mounted on microscope slides using Histamount, owing to its low refractive index. Total SCPs were counted using light microscopy at x400 magnification. SCPs were identified according to criteria described by Rose (2008). SCP counts were expressed as the number of dry particles per gram of dry peat (gDM^{-1}). This was calculated using the following equation:

$$E = 100 \times (V_S - V_{SUB})/(V_S - V_E) \qquad \text{(equation 4)}$$

Where V_E is the mass of the empty Eppendorf tube, V_S is the mass of the tube containing the sample and V_{SUB} is the mass of the tube after the coverslip has been prepared.

2.8.2.4. Tephrochronology

Far-travelled volcanic ash can form discrete but sometimes invisible layers in peat soils, providing geochemically distinct isochrons that allow for correlation with eruptive events of known age (Davies, 2015). Previous studies from Cors Fochno have revealed the presence of at least three geochemically identifiable cryptotephra horizons in the top meter of peat (Watson *et al.,* 2017); therefore, it was anticipated that those results could be replicated in this study and that the identification of these cryptotephra isochrons could be used to complement and support the age-depth model of core BO17. The standard 'ashing' method (combustion of peat at 550°C) was adopted to identify cryptotephra (Swindles *et al.,* 2010; Gehrels *et al.,* 2008). Contiguous 3cm^3 samples were taken throughout the core at 3 cm resolution. Remnant material was mounted on microscope slides using Histamount and examined beneath a microscope at 400x magnification under cross-polarised light. Note was taken of the colouration and character of the glass shards.

Where tephra was identified (e.g., Figure 2.8), additional samples were extracted from the core at 1 cm resolution to identify the position of the tephra horizon more precisely. Once a precise horizon was identified, additional peat samples were extracted for geochemical analysis of cryptotephra shards. Organic matter was removed from the samples by acid digestion using sulphuric and nitric acids, as detailed by Newton *et al.* (2007). This allows for the removal of organic material without affecting the geochemical composition of the shards.

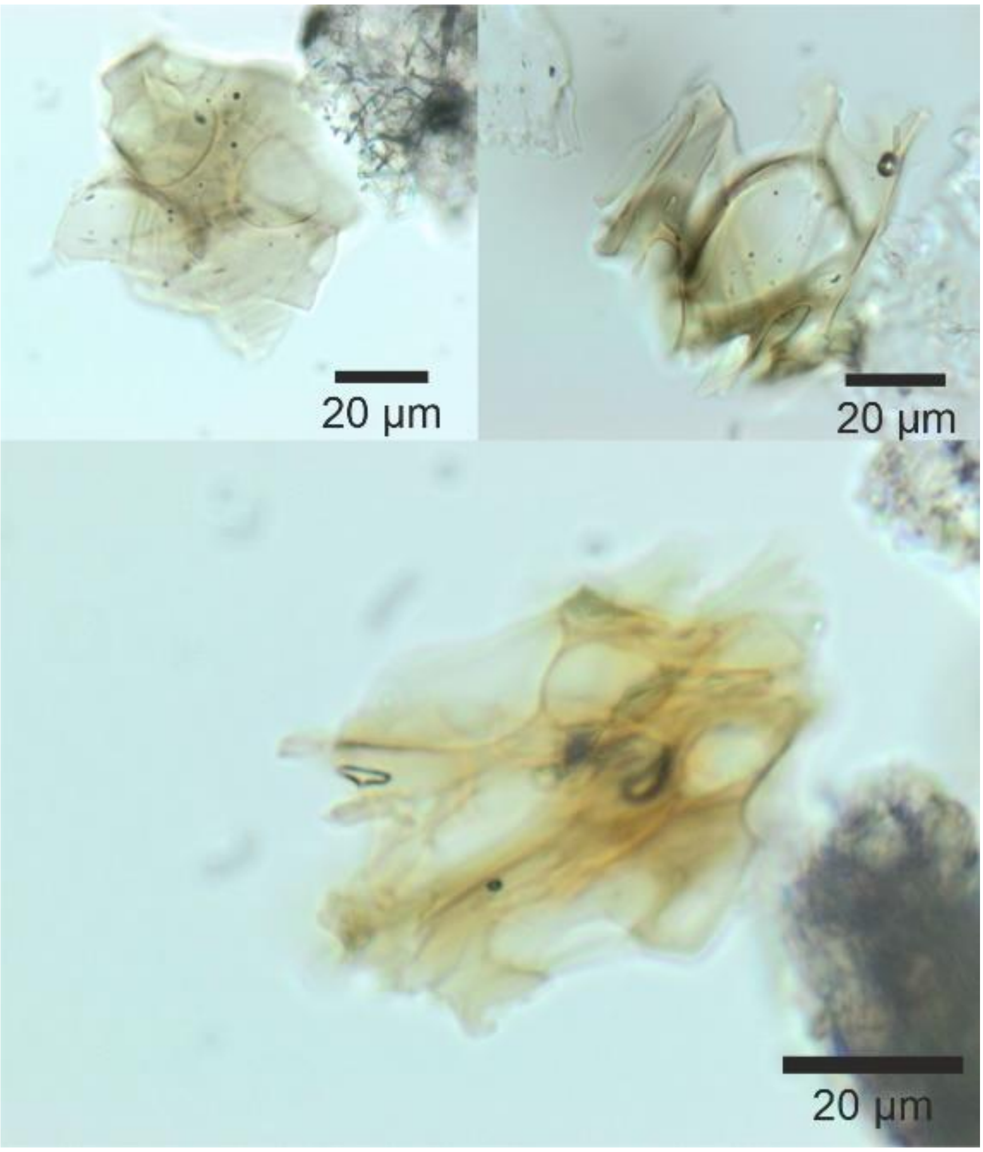


Figure 2.8. Tephra shards identified from Cors Fochno during this study. Note the vesicular morphology and brown colouration of the shards. Samples were identified at a depth between 35 – 38 cm from core BO17. Micro-photographs taken by Maria Gehrels.

Geochemical ‘fingerprinting’ of identified tephra shards along with laboratory standards (BCR2g and Lipari) was carried out at the Edinburgh Tephra Analytical Unit (TAU) using a Cameca SX100 Electron Microprobe (Hayward, 2012; Hall and Hayward, 2014). The geochemistry of each identified layer was compared with those from tephras of known origin, archived within the Tephrabase database (Newton *et al.,* 2007).

2.8.2.5. Macrocharcoal

A wildfire event that occurred in 1986 affected the central portion of the site, including the coring location (Fowles *et al.,* 2004). It was anticipated that such a significant event would leave a trace in the peat stratigraphy, as a chronostratigraphic marker of macrocharcoal likely consisting of large fragments of vegetation, indicative of burning *in-situ* (Clark, 1988). In addition, macrocharcoal was used as an indicator of wildfires resulting from human activity, since the temperate, oceanic climate of Cors Fochno precludes the probability of significant natural burning events occurring following lightning strikes. Macrocharcoal was sampled and analysed following procedures by Rhodes (1998) and Schlachter and Horn (2010). Contiguous 1 cm^3 sub-samples were taken at 1 cm resolution throughout core BO17. Each sample was submerged in 6% H_2O_2 overnight before wet-sieving through a 125 µm sieve. The larger fraction of material was retained for analysis. Charred fragments were counted under a stereomicroscope at low magnification (x10 – x100) using a Bogorov tray. Samples were reported as charcoal fragments per cubic centimetre (n cm^3).

2.8.3. Palaeoecological proxies

2.8.3.1. Plant macrofossil analysis

The long-term development of local vegetation at Cors Fochno was reconstructed throughout core BO17 using plant macrofossil analysis. 4 cm^3 sub-samples of peat were sampled at contiguous 1 cm intervals. These were submerged in 10% potassium hydroxide solution for 24 hours prior to wet sieving through a 125 µm sieve. Main peat components were assessed using a low-power stereomicroscope at 11.2x magnification, following an adapted version of the quadrat and leaf count method (Barber *et al.,* 1994) by Mauquoy *et al.* (2010). A magnified, live image of the sample beneath the microscope was projected onto a computer screen. The sample was floated in a large dish and the relative volume percentages of each primary peat component (e.g., total *Sphagnum*, *Rhynchospora alba*) were assessed by counting the number of instances in which they occurred beneath each square of a 10 x 10 grid, projected over the live image. This process was repeated 15 times, by systematically moving the dish beneath the microscope, and the results were averaged to represent the whole sample. From these values, relative percentage abundance was calculated for each component.

Seeds and other vegetative components of interest were also counted. Samples were washed through a 1 mm test sieve and both fractions were retained for analysis. Samples <1 mm were analysed at low magnification (10 – 200x) using a Bogorov tray. Material >1 mm was analysed by pouring the sample into a petri-dish, forming a single layer of material within the dish. This petri dish was underlain with numbered squares, which facilitated rapid counting of seeds and other remains, which were recorded as total counts (n).

Sphagnum percentage counts were estimated by selecting >100 leaves from each sample. A Pasteur pipette was used to draw a selection of leaves from each sample, to ensure selection was random. These were mounted on microscope slides in water and identified to species level using a high-powered stereomicroscope at 100-200x magnification. Leaf counts are expressed as percentages of the total identifiable *Sphagnum* %.

Plant macrofossils were identified with reference to Grosse-Brauckmann (1972), Smith (2004), Souto *et al*. (2016, 2017), Daniels and Eddy (1990) and Mauquoy and van Geel (2007). Plant remains were identified to species level where possible. In situations where material was insufficiently preserved to facilitate species-level identification, plant types were recorded as “undifferentiated.” Identification of seeds was achieved by referring to Cappers *et al.* (2006) and Souto *et al*. (2016). To identify *Sphagnum,* reference was made to Mauquoy and van Geel (2007) and Laine *et al.* (2011) alongside reference material collected from the site.

2.8.3.2. Peat humification

Humic acids concentrate in peat as a by-product of organic matter decay, which increases in the aerobic acrotelm under drier/warmer conditions (Clymo, 1984). Humic acids are dark brown, so darkly coloured peat is assumed to reflect a high degree of humification (de Jong *et al.,* 2010). By chemically extracting humic acids from peat and measuring the optical absorption of the resulting solution using colorimetric procedures (light spectroscopy), the degree of decomposition can be discerned. Colorimetric peat humification is commonly used as a qualitative proxy for changes in hydrological conditions in peatland palaeoecological studies (Aaby, 1976; Blackford and Chambers, 1993).

Humification was determined in this study following methods outlined by Roos-Barraclough *et al.* (2004). Contiguous 1 cm^3 sub-samples of peat 1 cm thick were sampled throughout the core BO17 and dried at <45°C for 24 hours. Samples were milled using a ball mill, and sub-samples of 0.02 g were weighed and placed into a 50 ml centrifuge tube containing 8 % sodium hydrochloride solution. Samples were agitated using a vortex mixer for ten seconds to ensure the sample was fully mixed into the solution. Stirred samples were then heated for 60 minutes in a water bath at 95°C, before filtering through Whatman type ‘0’ qualitative filter paper. Filtered samples were then diluted to 20 ml with deionised water and centrifuged at 3000 rpm for five minutes, to remove any mineral fractions of the peat that might influence results (Blackford and Chambers, 1993). Each sample was poured from the centrifuge tube into a beaker, from which sub-samples were poured into 5ml cuvettes for analysis. Humification was inferred from measurements of % light transmission using a spectrophotometer, set at 550 µm (Aaby and Tauber, 1975; de Jong *et al.,* 2010). Each measurement was replicated to ensure similar results were measured. Sample batches were limited to 20 samples for a single run, and measurements made at the beginning of a batch were re-measured at the end to ensure no colour loss had occurred. A strict time-schedule was kept, with all samples analysed sequentially, within two hours of being mixed with the alkali solution. Humification increases throughout a peat core with depth, therefore residual % transmission data were calculated based upon the linear relationship between humification and depth, to account for this effect (Chambers *et al.,* 2011).

Samples of decomposed green tea recovered from the tea bag decomposition experiment were analysed following exactly the same procedures as above, to test the effectiveness of peat humification as a proxy for decomposition.

2.8.3.3. Loss on ignition (LOI)

Loss on ignition (LOI) is commonly used in peatland palaeoecological studies as a measure of total organic matter content and is often used as a proxy for the carbon content in soils (Hoogsteen *et al.,* 2015). Inorganic matter concentrations can increase in peat as organic matter is lost by decay (Dean, 1974; Heiri *et al.,* 2001; Leifield *et al.,* 2011). To measure LOI throughout core BO17, Contiguous 1 cm thick peat sub-samples were weighed in ceramic crucibles of known weight. Samples were ashed at 550°C for 6 hours to ensure all organic matter had burned away (Heiri *et al.,* 2001). Ashed samples were re-weighed, and the percentage of mass lost calculated as % LOI following Chambers *et al.* (2011). Samples of decomposed green tea recovered from the tea bag decomposition experiment were analysed following exactly the same procedures as above, to test the effectiveness of LOI as a proxy for decomposition.

2.8.3.4. C/N ratios

Carbon (C) is preferentially lost over nitrogen (N) as a result of decomposition processes in peat; therefore, increases in the ratio of C and N percentages in peat are considered to reflect the extent of decomposition that has occurred while the peat was in the aerobic acrotelm (Malmer and Holm, 1984; Leifeld *et al.,* 2020). To measure C/N ratios throughout core BO17, contiguous 1 cm-thick peat samples were sub-sampled and dried at 45°C for 24 hours. Samples were milled using a ball mill and transferred into aluminium foil cups of known weight. The percentage mass of C and N in each sample was measured by analysing 55 ± 5 mg of milled peat using a Vario Macro Carbon/Nitrogen Analyser.

Samples of decomposed green tea recovered from the tea bag decomposition experiment were analysed following exactly the same procedures as above, to test the effectiveness of C/N ratios as a proxy for decomposition.

2.8.3.5. Testate amoebae

Testate amoebae are unicellular soil organisms that form distinctive shells that are well preserved in Holocene peat deposits (Mitchell *et al.,* 2008). They are sensitive indicators of local hydrological conditions (Booth, 2002; Mitchell *et al.,* 2008; Langdon *et al.,* 2012). Relationships between modern testate species and local hydrology can be applied to fossil testate amoebae assemblages using transfer functions, allowing for quantitative reconstruction of changes in peatland palaeohydrology, which are widely applied in peatland palaeoecological studies (Charman *et al.,* 2007; Payne and Mitchell, 2007).

Slices 1 cm thick, consisting of 2 cm^3 of peat were sub-sampled at 2 cm intervals from core BO17. Tests were extracted from the peat following adapted methods by Hendon and Charman (1997). Samples were submerged in 200ml of water along with a single lycopodium tablet (Batch number: 3862) and stirred using a glass rod. Samples were then gently heated on a hot plate for 20 minutes to disaggregate the material. Samples were sieved through a 355 µm test-sieve, and the smaller fraction was retained. These were then centrifuged at 3000 rpm for 10 minutes.

A small amount of sample residue was transferred onto a microscope slide and mounted in glycerol. Tests were counted at 200 – 400x magnification using a high-powered stereomicroscope, with minimum counts of 100 individuals achieved following recommendations by Payne and Mitchell (2009). Testate amoebae were identified with reference to Charman *et al*. (2000), Clarke (2003), Mazei and Tsyganov (2006), and Siemensma (2019).

To reconstruct approximate long-term mean average changes in water table depths through time (Booth, 2008), the weighted averaging transfer function model of Amesbury *et al*. (2016) was chosen, based on a training set of 1302 samples spanning 35° of latitude and 55° of longitude. No new local training set samples were included.

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2.9. Statistical methods

2.9.1. Net ecosystem carbon budget modelling

Multi-year carbon budgets were estimated for each experimental plot using interpolation and extrapolation methods. NER was modelled based on measured fluxes using the (2z + S) model (Rowson *et al.,* 2013). This model links the Arrhenius relationship between soil temperature and measured NER (Lloyd and Taylor, 1994) to plant functioning, accounting for feedbacks between water levels, plant root exudates and plant senescence. Seven constants required for the Rowson *et al.* (2013) model were identified using the generalised reduced gradient (GRG2) nonlinear optimisation code in Excel (Lasdon *et al.,* 1978). Model parameters were fit to the continuous temperature and water table depth time series data measured within each plot, allowing NER to be modelled. Different data combinations were explored to find the best fit for the model including modelling by plot, treatment and for measurements taken from 2010 – 2021 and 2017 – 2021. Model selection was based upon which set of models had the best predictive power (R^2) and the lowest sum of squared error (SSE).

To model GPP and CH_4, significant relationships were tested for between photosynthetically active radiation, soil and air temperatures and water table depth using simple linear regression. Where significant relationships were found, different relationships (linear, exponential, logarithmic) were tested between the response and predictor variables, and the strength of each model was tested by comparing R^2 and SEE values. Fluxes were modelled based upon interpolation using the model that provides the best fit.

The dynamics of DOC fluxes from peatland catchments are often quantified using a DOC end-member mixing model, which calculate the mixing of waters and the expected dilution of DOC from its various sources (Worrall *et al.,* 2006). This study lacked the relevant infrastructure to measure stream flow rates, and measurements were not taken of DOC from stream-waters draining from Cors Fochno, meaning that a mixing model could not be used. In order to incorporate DOC fluxes into the annual carbon budgets for Cors Fochno, a simple hydrological model previously proposed by Ridley (2014) was used. This model assumes a plug-low of DOC throughout the system, providing a rough estimate of annual DOC flux by multiplying annual total discharge with the mean average pore-water DOC concentrations measured from within each plot. Evapotranspiration rates were measured from Plas Gogerddan, Aberystwyth (600 mm m^{-2} y^{-1}) and adjusted by a conversion factor of 0.7 to account for the water-holding capacity of *Sphagnum,* resulting in an annual evaporation rate of 420 mm m^{-2} yr^{-1}. This value was subtracted from the total annual precipitation measurements from Frondirion taken between 2010 to 2019 (Justin Lyons, pers. comm). Ridley (2014) found that this model produced DOC fluxes comparable to those reported from other raised bogs, although they note that the estimated fluxes were too crude to be compared confidently with estimates from other sites. This method assumes all water not lost by evapotranspiration escapes the site via overland flow and does not account for mixing or the dilution of DOC with rainfall. Therefore, DOC fluxes are likely to be overestimated in this study. Between 8 – 9.5% of rainfall that lands upon Cors Fochno is lost via water movement through the catotelm (Baird *et al*., 2006), which is not accounted for here. Neither does this model account for increased DOC export following heavy rainfall events which may have increased annual DOC release rates from the site (Hope *et al*., 1994).

Pore-water concentrations of particulate organic carbon (POC), dissolved inorganic carbon (DIC) and dissolved gaseous carbon (CO_2 and CH_4) were not measured in this study, as these fluxes are usually assumed to be low from relatively undisturbed ombrotrophic peatlands (Lindsay, 2010). Estimates of POC and DIC fluxes were generated for Cors Fochno using values reported by Heinemeyer *et al*. (2019) and Dawson *et al.* (2002).

Annual net carbon accumulation rates were estimated by calculating the molar mass of carbon for each modelled annual flux, and adding these estimates together. Estimates for each flux were multiplied by 6 to account for the 6-hourly timeseries data used to model each gaseous flux. Net annual carbon fluxes are reported as g C m^{-2} y^{-1}.

To assess whether proportional changes between CO_2 and CH_4 emissions affected the greenhouse gas sink function of the site, CH_4 was converted to its CO_2 equivalent for 100 years by multiplying the total annual modelled CH_4 flux estimates by 28 (Ishikura *et al.,* 2018), accounting for the higher infra-red absorptivity of CH_4 relative to CO_2. CH_4 – CO_2 equivalent values were combined with NEE as a measure of the total gaseous CO_2-equivalent emissions from the site.

Differences were tested for between measured carbon fluxes, total gaseous CO_2-equivalent greenhouse gas emissions and annual carbon budgets using generalised mixed effects linear models (GLMMs). These tests were performed using the 'Lme4' package in the statistical program 'R' (Bates *et al.,* 2015; R core team, 2021). When testing gas flux measurements, environmental variables were included as model covariates, which were determined using single-term deletions. For each statistical test, plots nested in blocks and year were included as random factors to account for the repeated measures used in this study. Experimental treatments were set as fixed factors.

2.9.2. Dupont Hydrological Index

Changes in palaeohydrological conditions through time were reconstructed for core BO17 using a hydrological index based upon changes in the botanical composition of peat throughout core BO17, using plant macrofossil analysis. Changes in bog surface wetness (BSW) inferred from peatland palaeoecological proxies such as plant macrofossils provide a qualitative measure of soil moisture, which is related mostly to changes in precipitation, but also weakly linked to climate (Charman *et al.,* 2009). Weighted values are assigned to plant taxa using Dupont's hydrological index (DHI) based upon their hydrological preferences (1= wettest and 8= driest) (Dupont, 1986; Mauquoy *et al.,* 2008). Each species/taxa type were allocated a score relative to their hydrological preferences. Species that were not assigned DHI scores (following indices by Mauquoy *et al.,* 2008, with the addition of *Sphagnum denticulatum*) were removed from the dataset and relative percentage abundances recalculated. Taxa scores used to calculate the DHI are provided in the supplementary materials (Supplementary Text 2.1)

2.9.3. Analysis of changes in vegetation community composition through time

Vegetation change through time as a result of the experimental climate manipulations was tested using multivariate analysis of abundance (Wang *et al.,* 2012). Changes in vegetation (both by species and functional type) over time across all combinations of treatments were tested using the 'mvabund' package in R (Wang *et al.,* 2012; Wang *et al.,* 2020). This method fits a separate generalised linear model (GLM) to each species/group with a common set of explanatory variables (treatment, time, and the interaction between them) (Warton, 2011). This method was used because it provides greater statistical power than traditional distance-based methods often used to measure treatment effects upon multivariate data, such as principal response curves (van den Brink *et al.,* 2009, Warton, 2011, Warton *et al.,* 2012), and allows for the testing of individual species responses, as opposed to simply measuring change at the community level. Data were fitted to negative binomial models, which were chosen to account for overdispersion. The significance of the fixed effects and their interactions upon vegetation were calculated using Wald tests (Bates *et al.,* 2009), with PIT-trap resampling of 999 permutations, assuming an uncorrelated response between variables (Warton *et al*., 2017), using the package 'permute' in R (Simpson et al, 2019). Samples were restricted to plots within blocks, accounting for the hierarchical design of the experiment, and repeated measurements were accounted for by retaining the sample order when permuting the entire time series. When testing between sub-divisions of factors (e.g., control vs. combined warming and drought treatment plots) the maximum number of permutations possible (719) were used to calculate the p-value, and in these cases, there was no need to restrict sampling to blocks. Treatment effect at the community level is calculated as the summed deviance of all species in the treatment plots (Wang *et al.,* 2012).

2.9.4. Age-depth modelling

Robust age depth models are a fundamental aspect for palaeoecological studies, allowing for dates to be ascribed to climate change events and correlation between different proxy archives (Lacourse and Gajewski, 2020). In particular, a robust age-depth model is essential for generating accurate carbon accumulation rates from peat cores (Fiałkiewicz-Kozieł *et al.,* 2014). Two age-depth models were generated for core BO17. The first incorporated a mix of radiocarbon, SCP dates and a macrocharcoal chronohorizon using the package ‘rBacon’ in R (Blaauw *et al.,* 2021b), This modelling approach uses Bayesian statistics to generate accumulation histories by combining radiocarbon and other dates with prior assumptions about accumulation rates and variability (Blaauw and Christen, 2013). This model generates maximum age probabilities at set intervals (1 cm in this thesis), together with maximum and minimum ages based upon the 95% confidence interval. Radiocarbon dates were calibrated using the IntCal20 Northern Hemisphere radiocarbon age calibration curve (Reimer *et al.,* 2020). This model was used to date changes in plant community composition through time, relating changes to periods of known climate change.

A second model was used to generate carbon accumulation rates for the Late Holocene from core BO17. Data used in the former model was complemented by the incorporation of additional ^{210}Pb and tephrochronological dates. These were modelled using the package ‘rplum’ in R (Aquino-López *et al.,* 2018; Blaauw *et al.,* 2021a). This method works in a similar way to rbacon but also models ^{210}Pb dates using supported and unsupported ^{210}Pb data. This method improves on traditional techniques for modelling ^{210}Pb, allowing for the integration of ^{210}Pb dates with other dating methods without the need for re-modelling the ^{210}Pb dates, and generates model uncertainties in more statistically robust manner than traditional methods (Appleby and Oldfield, 1978; Aquino-López *et al.,* 2018, 2020).

2.9.5. Long term apparent rate of carbon accumulation (LORCA)

Holocene long term apparent average rates of carbon accumulation (LORCA) were calculated for cores BO18-1 – 3. Bulk density was measured at contiguous 10 cm resolution. Wet peat samples were weighed, and their volume was measured using water displacement, reported in cm^3. Samples were then oven dried at 45°C for 48 hours and re-weighed. Bulk density was calculated by dividing the dry weight with wet volume (Chambers *et al.,* 2011). On occasion, samples were less than 10 cm thick, and the difference in sample interval was accounted for in the calculations. %C was measured by analysing 55 ± 5 mg of milled material using a Vario Macro Carbon/Nitrogen Analyser, using birch leaf powder as an analytical standard. LORCA was calculated by dividing the sum mass of accumulated carbon by the basal date for each core (Clymo *et al.,* 1998) using the following equation by Korhola *et al.* (1995):

$$A=r\rho \qquad \text{(equation 5)}$$

Where A= dry mass accumulation , r= net rate of peat accumulation

and ρ = dry bulk density of peat. In this study, the rate of carbon accumulation is reported in units of g m^{-2} y^{-1}, net peat accumulation rate as mm y^{-1} and bulk density as g cm^3.

Net rate of peat accumulation is calculated by calculating the sum total mass of carbon accumulated throughout the peat profile and dividing this with the basal peat age, calculated from a single radiocarbon date extracted from the base of each core. The LORCA for the site was calculated as the mean value between the three cores. LORCA was reported as g C m^{-2} y-^{1}.

2.9.6. Apparent rate of carbon accumulation (aCAR)

Late Holocene apparent rates of carbon accumulation (aCAR) were calculated for core BO17. Bulk density was measured for each sample, and %C measured by analysing 55 ± 5 mg of milled material with a Vario Macro Carbon/Nitrogen Analyser**.** Samples were taken at contiguous 1 cm intervals. Carbon density was calculated by multiplying dry bulk density (g cm^3) with %C. aCAR was measured following methods by Belshe *et al.* (2019). Sedimentation rates generated from the age-depth model for core BO17 in rplum were used to calculate aCAR for each 1 cm interval. Peat accumulation rates were converted from y cm^{-1} to cm y^{-1} by converting the posterior probability density functions of the accumulation times from Gamma to inverse Gamma distributions. Carbon accumulation rates were calculated by multiplying the accumulation rate (in cm y^{-1}) by organic carbon density in units of g OC cm^{-3}. Organic carbon density were derived by multiplying bulk density with carbon % content. Mean and median aCAR rates and 95% confidence intervals were calculated from the cumulative density function (Belshe *et al.,* 2019).

2.9.7. Comparing long-term carbon accumulation with hydroclimatic change

Associations between aCAR and testate amoebae-derived water table depth reconstructions and the DHI scores were explored to test for relationships between these variables, to see how hydroclimatic changes influence aCAR. To account for the lower sampling resolution of the testate amoebae samples (1 cm thick samples every 2 cm), data were gap-filled by calculating the mid-value between adjacent samples. aCAR was also compared with broad changes in the long-term record of plant community composition derived from the plant macrofossil analysis. The effect of climate upon aCAR was tested by estimating the correlation between aCAR rates and reconstructed Northern Hemisphere temperature anomalies covering the past c. 1000 years, as well as the Central England temperature dataset (Manley, 1953; 1974; Mann *et al.,* 1999; 2008; Parker and Horton, 2005). This was done using the package 'BINCOR' in R (Polanco-Martinez *et al.,* 2018). This package allows for the correlation of two unevenly spaced time series, including instrumental and palaeoclimatic time series (Polanco-Martinez *et al.,* 2019), using binned correlation. This method resamples the irregular time series into a series of bins on a regular grid, and then assigns the mean values of each variable being tested within those bins (Mudelsee, 2010). Correlations can be calculated by estimating the cross-correlation of the binned time series.

These correlations may be affected by the resolution and accuracy of the testate amoebae-derived water table reconstructions. While testate amoebae are known to be sensitive to changes in water-table depth, comparisons between modern and fossil assemblages used to calculate these changes may be influenced by taphonomic effects relating to the preservation and distribution of tests throughout the peat profile. It is difficult to assess how the movement of testate amoebae throughout the peat profile may affect palaeoecological reconstructions (Mitchell *et al.,* 2008), however living testate amoebae exhibit only a limited degree of infaunality (Roe *et al.,* 2002), therefore the vertical movement of living testate amoebae is assumed to be small. While species with tests composed of secreted biosilica plates do not preserve well in the palaeoecological record (Swindles *et al*., 2020), this has a negligible impact upon water table reconstructions (Mitchell *et al.,* 2008). Therefore, test taphonomy is assumed to have had a minimal effect upon the resultant water table depth values reported in this study.

2.9.8. Statistical methods for the analysis of plant macrofossil data

To identify groups of stratigraphically adjacent plant community assemblages in the plant macrofossil record for core BO17, constrained incremental sum of squares cluster analysis (CONISS; Grimm, 1987) was used. Since CONISS is unable to deal with the different data types generated by the plant macrofossil analysis (Relative % abundance and count data) (Birks, 2014), only the main percentage peat components were used to partition palaeo-vegetation into zones.

2.9.9. Comparing vegetation responses to climate change

Modern vegetation assemblages from the climate manipulation experiment for all years were compared with the long-term palaeoecological record of vegetation change using a novel application of the modern analogue technique (Simpson, 2007). The modern analogue technique is normally used to identify close modern analogues (CMAs) for fossil datasets as part of transfer function assessment for palaeoecological reconstructions (Overpeck *et al.,* 1985; Simpson *et al.,* 2007). This method assigns dissimilarity scores to comparisons of every experimental survey and macrofossil sample, using methods described by Bray and Curtis (1957). A number between 0 and 1 was assigned for each pair of samples based on the statistical (dis)similarity between communities, with 0 indicating samples that are completely identical, while a coefficient of 1 indicates samples that are completely unalike. A Monte-Carlo simulation with 10,000 permutations was employed as described by Simpson (2007) to define a critical value for dissimilarity to categorise CMAs at the 95% confidence interval. This method draws two sets of data at random and compares them, recording the (dis)similarity between the two samples. This process generates a randomisation distribution of (dis)similarity values expected by random sample comparison, allowing for a threshold of similarity that is unlikely to have occurred by chance to be calculated. This method is utilised to quantify how well the vegetation within the experimental plots resembles the fossil communities, as well as the frequency with which the palaeo-vegetation communities throughout the core were close modern analogues for the vegetation within the experimental plots.

This method assumes that the relative abundance of plant functional types estimated by plant macrofossil analysis are comparable to the relative abundances of species measured using the pin-touch method in the experimental plots. This may not be the case due to methodological differences between the modern and palaeoecological methods employed in this study. For the pin-touch method, certain taxa that possess wider, taller, spreading leaves or dense growth patterns may appear to be more abundant, due to increased detection by this method (Heslehurst, 1971). *Sphagnum* and other surface cover vegetation may be underrepresented since they are only measured once per quadrat. For plant macrofossil analysis, the representation of certain taxa in the palaeoecological record will be biased, owing to differences in preservation. Robust plant remains (e.g., *Sphagnum* leaves and ericaceous roots) are preserved more commonly over more fragile remains (e.g., ericaceous woody remains and flowers) (Mauquoy and Yeloff, 2008). These differences make it difficult for quantitative comparisons to be made between palaeoecological and modern vegetation communities.

The total number of CMAs between the experimental and the palaeo-vegetation communities were used as a measure of how well the vegetation in the experimental plots resembled the vegetation within the core. Vegetation from the experimental surveys that have no analogy in the palaeoecological record were removed from the data set, in order to account for the preferential decay and absence of certain plant remains in plant macrofossil assemblages. The remaining counts were summed into taxonomic groups of *Sphagnum* (sub-genera), and into physiognomic functional groups: shrubs, sedges, and liverworts similar to those used by Ward *et al*. (2013). The relative abundance of each group was calculated. The data were square root transformed prior to analysis to reduce possible differences between the palaeoecological and experimental methods for determining plant community composition.

This was done to make the differing datasets more comparable, however this is at the expense of the loss of a great deal of information regarding differences in species-specific characteristics and behaviours (Verheijen *et al.,* 2015). Furthermore, this decision may heavily bias the results, with CMAs more likely to be detected while the species present may have been substantially different to what exist within the site presently.

2.9.10. Comparing long-term carbon accumulation with net ecosystem carbon budgets

Modelled carbon emissions were partitioned into each of their components (CO_2, CH_4, DOC) and compared to the aCAR record for core BO17. Differences in aCAR were initially compared with GPP, and each carbon flux was aggregated to GPP in turn, to see how the aggregation of different fluxes improves or compromises comparison and interpretation of contemporary carbon budgets with aCAR rates throughout the past millennium. This assumes that multi-year estimates of net ecosystem carbon balances are comparable with carbon accumulation rates derived from cores. In reality, these records are unlikely to perfectly converge. Carbon accumulation rates derived from peat cores are frequently smaller than contemporary carbon budgets from the same site

(Byrne *et al.,* 2004; Ratcliffe *et al.,* 2018). Apparent rates of carbon accumulation derived from peat cores represent full-year accumulation rates averaged over a much longer period of time than net ecosystem carbon budgets, which are typically estimated for individual years and may differ greatly depending upon annual climatic variability (Byrne *et al*., 2004). However, theoretically, when net ecosystem carbon measurements are averaged over time periods equal to the chronological resolution seen in palaeoecological studies (> 10 years), these estimates may converge (Ratcliffe *et al*., 2018).

2.9.11. Comparing the sensitivity and effectiveness of palaeoecological decomposition proxies

To determine whether vegetation communities influence decomposition, vegetation survey data measured during 2019 (the year of the litter bag decomposition experiment) were expressed as species percentage relative abundance and vegetation-groups were determined using hierarchical clustering. Ward's minimum variance method was used to identify clustering structures, and the number of clusters determined using the average silhouette approach. All analyses were performed using the package 'cluster' in R (Maechler *et al.,* 2013).

The sensitivity of each proxy to the decomposition measured by the TBI was tested using redundancy analysis. This technique is an extension of multiple linear regression, that allows regression of multiple response variables on multiple explanatory variables, aiming to maximise the amount of variance explained by the linear combination of explanatory variables (Isreals, 1984). Both explanatory (TBI parameters *k* and *S*) and response variables (% light transmission, C/N ratios, LOI) were standardised and square root transformed, owing to the dimensionally heterogenous and non-linear relationships exhibited by the variables. The magnitude and direction of change in the palaeoecological proxies were compared with the changes seen in each proxy throughout the Late Holocene record of Cors Fochno, to determine whether the magnitude and direction of changes reflect changes seen in the experimental plots.

2.10. Synopsis

This section describes the methodology employed to integrate short-term peatland manipulation experiments with long-term high resolution palaeoecological investigations. It shows how the experimental and palaeoenvironmental objectives of the thesis will be met, and what methods were used to facilitate comparison between the results of both approaches. By directly comparing the results of both approaches for the same site, this study aims to make substantive progress towards developing an understanding of how peatlands will respond to future climate changes, and whether positive or negative climate feedbacks will dominate in a warming world.

2.11. References

Aaby, B. and Tauber, H., (1975). Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Deninark. *Boreas*, *4*(1), 1-17.

Aaby, B., (1976). Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. *Nature*, *263*(5575), 281-284.

Alm, J., Shurpali, N.J., Tuittila, E.S., Laurila, T., Maljanen, M., Saarnio, S. and Minkkinen, K., (2007). Methods for determining emission factors for the use of peat and peatlands flux measurements and modelling. *Boreal Environment Research*, 12, 85-100.

Amesbury, M.J., Swindles, G.T., Bobrov, A., Charman, D.J., Holden, J., Lamentowicz, M., Mallon, G., Mazei, Y., Mitchell, E.A., Payne, R.J., and Roland, T.P., (2016). Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. *Quaternary Science Reviews*, *152*, 132-151.

Appleby, P.G. and Oldfield, F., (1978). The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. *Catena*, *5*(1), 1-8.

Appleby, P.G., (1998). *Dating recent sediments by 210 Pb: Problems and solutions* (No. STUK-A--145). Illus, E. (Ed.). Finland

Aquino-López, M.A., Blaauw, M., Christen, J.A., and Sanderson, N.K., (2018). Bayesian Analysis of 210 Pb Dating. *Journal of Agricultural, Biological and Environmental Statistics*, *23*(3), 317-333.

Aquino-López, M.A., Ruiz-Fernández, A.C., Blaauw, M. and Sanchez-Cabeza, J.A., (2020). Comparing classical and Bayesian 210Pb dating models in human-impacted aquatic environments. Quaternary Geochronology, 60, 101106.

Arft, A.M., Walker, M.D., Gurevitch, J.E.T.A., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H. and Hollister, R.D., (1999). Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, *69*(4), 491-511.

Aronson, E.L. and McNulty, S.G., (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, *149*(11), 1791-1799.

Baird, A.J., Beckwith, C.W., Waldron, S., and Waddington, J.M., (2004). Ebullition of methane-containing gas bubbles from near-surface Sphagnum peat. *Geophysical Research Letters*, *31*(21).

Baird, A. J., Eades, P. A., and Surridge, B. W. (2008). The hydraulic structure of a raised bog and its implications for ecohydrological modelling of bog development. Ecohydrology: Ecosystems, Land and Water Process Interactions, *Ecohydrogeomorphology*, 1(4), 289-298.

Barber, K.E., Chambers, F.M., Maddy, D., Stoneman, R., and Brew, J.S., (1994). A sensitive high-resolution record of late Holocene climatic change from a raised bog in northern England. *The Holocene*, *4*(2), 198-205.

Bates., D, Mächler, M., Bolker, B., Walker, S., (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1–48.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F. and Grothendieck, G., (2012). Package 'lme4'. *CRAN. R Foundation for Statistical Computing, Vienna, Austria*.

Belshe, E.F., Sanjuan, J., Leiva-Dueñas, C., Piñeiro-Juncal, N., Serrano, O., Lavery, P. and Mateo, M.A., (2019). Modeling organic carbon accumulation rates and residence times in coastal vegetated ecosystems. *Journal of Geophysical Research: Biogeosciences*, *124*(11), 3652-3671.

Birks, H.J.B., (2014). Challenges in the presentation and analysis of plant-macrofossil stratigraphical data. *Vegetation History and Archaeobotany*, *23*(3), 309-330.

Blaauw, M. and Christen, J.A., (2013). Bacon Manual v2. 3.3.

Blaauw, M. J., Christen, A. and Aquino-López, M. A. (2021a). rplum: Bayesian Age-Depth Modelling of Cores Dated by Pb-210. R package version 0.2.1.

Blaauw, M. J., Christen, A. and Aquino-López, M. A. (2021b). rbacon: Age-Depth Modelling using Bayesian Statistics. R package version 2.5.5. https://CRAN.R-project.org/package=rbacon

Blackford, J.J. and Chambers, F.M., (1993). Determining the degree of peat decomposition for peat-based paleoclimatic studies. *International Peat Journal;*(*Finland)*, *8*(5).

Blume-Werry, G., Di Maurizio, V., Beil, I., Lett, S., Schwieger, S. and Kreyling, J., (2021). Don't drink it, bury it: comparing decomposition rates with the tea bag index is possible without prior leaching. *Plant and Soil*, 1-9.

Bodley, C.L., Jeglum, J.K. and Berry, G.J., (1989). A probe for measuring depth to water surface in wells. *Canadian Journal of Soil Science*, *69*(3), 683-687

Bonnett, S. A., Ostle, N., and Freeman, C. (2006). Seasonal variations in decomposition processes in a valley-bottom riparian peatland. *Science of the Total Environment, 370*(2-3), 561-573.

Booth, R.K., (2002). Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. *Journal of Paleolimnology*, *28*(3), 329-348.

Booth, R. K. (2008). Testate amoebae as proxies for mean annual water-table depth in Sphagnum-dominated peatlands of North America. *Journal of Quaternary Science: Published for the Quaternary Research Association, 23*(1), 43-57.

Bouyoucos, G.J., (1934). A method for determining the degree of decomposition that unknown decayed vegetable organic materials have already undergone in nature. *Soil Science*, *38*(6), 477-482.

Bray, J.R. and Curtis, J.T., (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*(4), 326-349.

Byrne, K.A., Chojnicki, B., Christensen, T.R., Drosler, M., Frolking, S., Lindroth, A., Mailhammer, J., Malmer, N., Selin, P., Turunen, J. and Valentini, R., (2004). *EU peatlands: Current carbon stocks and trace gas fluxes.*

Cappers, R.T.J., Bekker, R.M. and Jans, J.E.A., (2006). *Digitale zadenatlas van Nederlands*. Groningen Archaeological Studies 4. Eelde: Barkhuis Publishing, p.502.

CCW. (2011). *Cors Fochno SAC management plan: Countryside Council for Wales core management plan, version 18*. Countryside Council for Wales

Chambers, F.M., Beilman, D.W. and Yu, Z., (2011). Methods for determining peat humification and for quantifying peat bulk density, organic matter, and carbon content for palaeostudies of climate and peatland carbon dynamics. *Mires and Peat*, *7*(7), 1-10.

Charman, D. J., Barber, K. E., Blaauw, M., Langdon, P. G., Mauquoy, D., Daley, T. J., Hughes, P. D. M., and Karofeld, E. (2009). Climate drivers for peatland palaeoclimate records. *Quaternary Science Reviews*, 28(19–20), 1811– 1819.

Charman, D.J., Blundell, A., and Accrotelm Members, (2007). A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *Journal of Quaternary Science*, *22*(3), 209-221.

Charman, D.J., Hendon, D., and Woodland, W.A., (2000). *The identification of testate amoebae* (*Protozoa: Rhizopoda) in peats; Technical Guide No. 9*, Quaternary Research Association

Clark, J.S., (1988). Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. *Quaternary research*, *30*(1), 67-80.

Clarke, K.J., (2003). *Guide to the identification of soil protozoa-testate amoebae*. Freshwater Biological Association (FBA).

Clymo, R.S., (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *303*(1117), 605-654.

Clymo, R.S., Turunen, J. and Tolonen, K., (1998). Carbon accumulation in peatland. *Oikos*, 368-388.

Countryside Council Wales (CCW) (2011). *Cors Fochno SAC management plan: COUNTRYSIDE COUNCIL FOR WALES CORE MANAGEMENT PLAN*, version 18, Countryside Council for Wales, pp 1-31.

Daniels, R.E. and Eddy, A., (1990). *Handbook of European sphagna*. HMSO.

Davies, S.M., (2015). Cryptotephras: the revolution in correlation and precision dating. *Journal of Quaternary Science*, *30*(2), 114-130.

Dawson, J. J. C., Billett, M. F., Neal, C., and Hill, S. (2002). A comparison of particulate, dissolved and gaseous carbon in two contrasting upland streams in the UK. *Journal of Hydrology*, *257*(1-4), 226-246.

de Jong, R., Blaauw, M., Chambers, F.M., Christensen, T.R., De Vleeschouwer, F., Finsinger, W., Fronzek, S., Johansson, M., Kokfelt, U., Lamentowicz, M. and Le Roux, G., (2010). Climate and peatlands. In *Changing Climates, Earth Systems and Society* (85-121). Springer, Dordrecht.

De Vleeschouwer, F., Chambers, F.M. and Swindles, G.T., (2010). Coring and sub-sampling of peatlands for palaeoenvironmental research. *Mires and peat*, *7*.

Dean, W.E., (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research*, *44*(1), 242-248.

Didion, M., Repo, A., Liski, J., Forsius, M., Bierbaumer, M., and Djukic, I. (2016). Towards harmonizing leaf litter decomposition studies using standard tea bags—a field study and model application. *Forests, 7*(8), 167.

Dossa, G.G., Paudel, E., Wang, H., Cao, K., Schaefer, D. and Harrison, R.D., (2015). Correct calculation of CO 2 efflux using a closed-chamber linked to a non-dispersive infrared gas analyzer. *Methods in Ecology and Evolution*, *6*(12), 1435-1442.

Dooling, G. P., Chapman, P. J., Baird, A. J., Shepherd, M. J., and Kohler, T. (2018). Daytime-only measurements underestimate CH_4 emissions from a restored bog. *Ecoscience*, *25*(3), 259-270.

Duddigan, S., Shaw, L. J., Alexander, P. D., and Collins, C. D. (2020). Chemical underpinning of the tea bag index: an examination of the decomposition of tea leaves. *Applied and Environmental Soil Science*, 2020.

Dupont, L.M., (1986). Temperature and rainfall variation in the Holocene based on comparative palaeoecology and isotope geology of a hummock and a hollow (Bourtangerveen, The Netherlands). *Review of Palaeobotany and Palynology*, *48*(1-3), 71-159.

Elkington, T., Dayton, N., Jackson, D., Strachan, I. (2001). *National Vegetation Classification: Field guide to mires and heaths*. JNCC

Fiałkiewicz-Kozieł, B., Kołaczek, P., Piotrowska, N., Michczyński, A., Łokas, E., Wachniew, P., Woszczyk, M. and Sensuła, B., (2014). High-resolution age-depth model of a peat bog in Poland as an important basis for paleoenvironmental studies. *Radiocarbon*, *56*(1), 109-125.

Fowles, A.P., Bailey, M.P. and Hale, A.D., (2004). Trends in the recovery of a rosy marsh moth Coenophila subrosea (Lepidoptera, Noctuidae) population in response to fire and conservation management on a lowland raised mire. *Journal of Insect Conservation*, *8*(2), 149-158.

Fox, A.D., (1984). *Aspects of the hydrology of Cors Fochno National Nature Reserve* (PhD Thesis), University of Wales, Aberystwyth.

Gehrels, M.J., Newnham, R.M., Lowe, D.J., Wynne, S., Hazell, Z.J. and Caseldine, C., (2008). Towards rapid assay of cryptotephra in peat cores: review and evaluation of various methods. *Quaternary International*, *178*(1), 68-84.

Godwin, H. and Newton, L., (1938). The submerged forest at Borth and Ynyslas, Cardiganshire. Data for the study of post-glacial history. No. I. *The New Phytologist*, *37*(4), 333-344.

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łuców, D., Kayzer, D. and Juszczak, R., (2021). Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate Sphagnum-peatland. *Science of The Total Environment*, *771*, p.145452.

Goulsbra, C., Rickards, N., Brown, S., Evans, M., Boult, S., and Alderson, D. (2016). Diurnal variations in CO2 flux from peatland floodplains: Implications for models of ecosystem respiration. *Aquatic Sciences, 78*(3), 477-489.

Grimm, E.C., (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, *13*(1), 13-35.

Grosse-Brauckmann, G. and Streitz, B., (1992). Pflanzliche Makrofossilien mitteleuropäischer Torfe. III. Früchte, samen und einige gewebe (fotos von fossilen pflanzenresten). *Telma,* 22, 53-102.

Hall, M. and Hayward, C., (2014). Preparation of micro-and crypto-tephras for quantitative microbeam analysis. *Geological Society, London, Special Publications*, *398*(1), 21-28.

Hanlon, H. M., Bernie, D., Carigi, G., and Lowe, J. A. (2021). Future changes to high impact weather in the UK. *Climatic Change*, *166*(3), 1-23.

Harris, A., Bryant, R.G., and Baird, A.J., (2006). Mapping the effects of water stress on Sphagnum: Preliminary observations using airborne remote sensing. *Remote Sensing of Environment*, *100*(3), 363-378.

Hayward, C., (2012). High spatial resolution electron probe microanalysis of tephras and melt inclusions without beam-induced chemical modification. *The Holocene*, *22*(1), 119-125.

Heinemeyer A., Vallack H.W., Morton P.A., Pateman R., Dytham C., Ineson P., McClean C., Bristow C., and Pearce-Higgins J.W. (2019) Restoration of heather-dominated blanket bog vegetation on grouse moors for biodiversity, carbon storage, greenhouse gas emissions and water regulation: comparing burning to alternative mowing and uncut management. *Final Report to Defra on Project BD5104*, Stockholm Environment Institute at the University of York, York, UK

Heiri, O., Lotter, A.F. and Lemcke, G., (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology*, *25*(1), 101-110.

Hendon, D., and Charman, D.J., (1997). The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, *7*(2), 199-205.

Heslehurst, M. R. (1971). *The point quadrat method of vegetation analysis: A review*. University of Reading, Dept. of Agriculture.

Hoogsteen, M.J., Lantinga, E.A., Bakker, E.J., Groot, J.C. and Tittonell, P.A., (2015). Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss. *European Journal of Soil Science*, *66*(2), 320-328.

Hope, D., Billett, M. F., and Cresser, M. S. (1994). A review of the export of carbon in river water: fluxes and processes. *Environmental pollution*, 84(3), 301-324.

Howells, M.F. (2007). *Wales British Regional Geology*, Nottingham: British Geological Survey.

Hughes, P. D. M. and Schulz, J., (2001). The development of the Borth Bog (Cors Fochno) mire system and the submerged forest beds at Ynyslas. M.J.C. Walker, D. McCarroll (Eds.), *The Quaternary of West Wales*. QRA Field Guide, QRA, London, 104-112

Hughes, P.D.M., Lomas-Clarke, S.H., Schulz, J., and Barber, K.E., (2008). Decline and localized extinction of a major raised bog species across the British Isles: evidence for associated land-use intensification. *The Holocene*, *18*(7), 1033-1043.

Hughes, P.D.M., Lomas-Clarke, S.H., Schulz, J. and Jones, P., (2007). The declining quality of late-Holocene ombrotrophic communities and the loss of Sphagnum austinii (Sull. ex Aust.) on raised bogs in Wales. *The Holocene*, *17*(5), 613-625.

Hunger, S., Gößner, A. S., and Drake, H. L. (2015). Anaerobic trophic interactions of contrasting methane-emitting mire soils: processes versus taxa. *FEMS Microbiology Ecology*, *91*(5).

Hutchinson, G.L. and Livingston, G.P., (1993). Use of chamber systems to measure trace gas fluxes. In: *Agricultural ecosystem effects on trace gases and global climate change*, American Society of Agronomy/Crop Science Society of America/Soil Science Society of America, *55*, 63-78.

Ishikura, K., Darung, U., Inoue, T. and Hatano, R., (2018). Variation in soil properties regulate greenhouse gas fluxes and global warming potential in three land use types on tropical peat. *Atmosphere*, *9*(12), p.465.

Israels, A.Z., (1984). Redundancy analysis for qualitative variables. *Psychometrika*, *49*(3), 331-346.

Jovani-Sancho, A. J., Cummins, T., and Byrne, K. A. (2021). Soil carbon balance of afforested peatlands in the maritime temperate climatic zone. *Global Change Biology, 27*(15), 3681-3698.

Jowsey, P.C., (1966). An improved peat sampler. *New Phytologist*, *65*(2), 245-248.

Kay, M., (2019). *Impacts of Warming, Drought, and Sea Level Rise on Ombrotrophic Peatlands* (PhD thesis), Manchester Metropolitan University.

Kettridge, N., and Binley, A. (2008). X-ray computed tomography of peat soils: Measuring gas content and peat structure. Hydrological Processes: An International Journal, 22(25), 4827-4837.

Keuskamp, J.A., Dingemans, B.J., Lehtinen, T., Sarneel, J.M. and Hefting, M.M., (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution*, *4*(11), 1070-1075.

Kilian, M.R., van Geel, B. and van der Plicht, J., (2000). 14C AMS wiggle matching of raised bog deposits and models of peat accumulation. *Quaternary Science Reviews*, *19*(10), 1011-1033.

Korhola, A., Tolonen, K., Turunen, J. and Jungner, H., (1995). Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. *Radiocarbon*, *37*(2), 575-584.

Kuhry, P. and Vitt, D.H., (1996). Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology*, *77*(1), 271-275.

Lacourse, T. and Gajewski, K., (2020). Current practices in building and reporting age-depth models. *Quaternary Research*, *96*, 28-38.

Laine, J., Harju, P., Timonen, T., Laine, A., Tuittila, E.S., Minkkinen, K., and Vasander, H. (2011). *The intricate beauty of Sphagnum mosses - a Finnish guide to* *identification.* University of Helsinki Department of Forest Sciences Publications, Hel

Langdon, P.G., Brown, A.G., Caseldine, C.J., Blockley, S.P.E. and Stuijts, I., (2012). Regional climate change from peat stratigraphy for the mid-to late Holocene in central Ireland. *Quaternary International*, *268*, 145-155.

Lasdon, L.S., Waren, A.D., Jain, A. and Ratner, M., (1978). Design and testing of a generalized reduced gradient code for nonlinear programming. *ACM Transactions on Mathematical Software* (*TOMS)*, *4*(1), 34-50.

Lees, K. J., Quaife, T., Artz, R. R. E., Khomik, M., and Clark, J. M. (2018). Potential for using remote sensing to estimate carbon fluxes across northern peatlands–A review. *Science of the Total Environment*, *615*, 857-874.

Leifeld, J., Klein, K. and Wüst-Galley, C., (2020). Soil organic matter stoichiometry as indicator for peatland degradation. *Scientific reports*, *10*(1), 1-9.

Levy, E. N., and Madden, E. A. (1933). The Point Method of Pasture Analysis*. New Zealand Journal of Agriculture 46*, 267-79.

Lindsay, R. (2010). *Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change*. University of East London, Environmental Research Group.

Lloyd, J. and Taylor, J.A., (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 315-323.

Lowe, J.A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G. and Fung, F. (2018). UKCP18 science overview report. *Met Office Hadley Centre: Exeter, UK*.

Luo, Y., and Zhou, X. (2010). *Soil respiration and the environment*. Elsevier.

MacDonald, E., Brummell, M.E., Bieniada, A., Elliot, J., Engering, A., Gauthier, T.L., Saraswati, S., Touchette, S., Tourmel-Courchesne, L. and Strack, M., (2018). Using the Tea Bag Index to characterize decomposition rates in restored peatlands. *Boreal Environment Research. 23,* 221-235.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. and Studer, M., (2013). Package 'cluster'.

Malmer, N. and Holm, E., (1984). Variation in the C/N-quotient of peat in relation to decomposition rate and age determination with 210 Pb. *Oikos*, 171-182.

Manley, G., (1953). The mean temperature of central England, 1698–1952. *Quarterly Journal of the Royal Meteorological Society*, *79*(340), 242-261.

Manley, G., (1974). Central England temperatures: monthly means 1659 to 1973. *Quarterly Journal of the Royal Meteorological Society*, *100*(425), 389-405.

Mann, M.E., Bradley, R.S. and Hughes, M.K., (1999). Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters*, *26*(6), 759-762.

Mann, M.E., Zhang, Z., Hughes, M.K., Bradley, R.S., Miller, S.K., Rutherford, S. and Ni, F., (2008). Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. *Proceedings of the National Academy of Sciences*, *105*(36), 13252-13257.

Marion, G.M., Bockheim, J.G. and Brown, J. (1997a). Arctic soils and the ITEX experiment. *Global Change Biology*, *3*(S1), 33-43.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., Levesque, E., Molau, U., Mølgaard, P., Parsons, A.N. and Svoboda, J., (1997b).

Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, *3*(S1), 20-32.

Mauquoy, D., and Yeloff, D. (2008). Raised peat bog development and possible responses to environmental changes during the mid-to late-Holocene. Can the palaeoecological record be used to predict the nature and response of raised peat bogs to future climate change? *Biodiversity and Conservation*, 17(9), 2139– 2151.

Mauquoy, D. and van Geel, B. (2007). Plant macrofossil methods and studies: mire and peat macros. In *Encyclopedia of Quaternary Science*, 2315-2336. Elsevier Science.

Mauquoy, D., Hughes, P.D.M. and van Geel, B., (2010). A protocol for plant macrofossil analysis of peat deposits. *Mires and Peat*, *7*(6), 1-5.

Mauquoy, D., Hughes, P.D.M. and van Geel, B., (2010). A protocol for plant macrofossil analysis of peat deposits. *Mires and Peat*, *7*(6), 1-5.

Mauquoy, D., Yeloff, D., van Geel, B., Charman, D.J. and Blundell, A., (2008). Two decadally resolved records from north-west European peat bogs show rapid climate changes associated with solar variability during the mid–late Holocene. *Journal of Quaternary Science*, *23*(8), 745-763.

Mazei, Y. and Tsyganov, A.N. (2006). *Freshwater testate amoebae*. *KMK, Moscow*, *302*.

Mighall, T., Timberlake, S., Martínez-Cortizas, A., Silva-Sánchez, N., and Foster, I.D.L., (2017). Did prehistoric and Roman mining and metallurgy have a significant impact on vegetation? *Journal of Archaeological Science: Reports*, *11*, 613-625

Mighall, T.M., Timberlake, S., Foster, I.D., Krupp, E. and Singh, S., (2009). Ancient copper and lead pollution records from a raised bog complex in Central Wales, UK. *Journal of Archaeological Science*, *36*(7), 1504-1515.

Mitchell, E.A., Charman, D.J. and Warner, B.G., (2008). Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present, and future. *Biodiversity and Conservation*, *17*(9), 2115-2137.

Mudelsee, M. (2010). *Climate Time Series Analysis: Classical Statistical and Bootstrap Methods*. Springer.

Natural Resources Wales (2021). New LIFE for Welsh Raised Bogs. [Online]. Available at: <https://naturalresources.wales/about-us/our-projects/nature-projects/new-life-for-welsh-raised-bogs/?lang=en> [Accessed 17 December 2021].

Newton, A.J., Dugmore, A.J. and Gittings, B.M., (2007). Tephrabase: tephrochronology and the development of a centralised European database. *Journal of Quaternary Science*, *22*(7), 737-743.

Norrman, B., (1993). Filtration of water samples for DOC studies. *Marine Chemistry*, *41*(1-3), 239-242.

Overpeck, J.T., Webb, T.I.I.I. and Prentice, I.C., (1985). Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research*, *23*(1), 87-108.

Page, N., Hughes, G., Jones, R. and Murphy, K., (2012). Excavations at Erglodd, Llangynfelyn, Ceredigion: prehistoric/Roman lead smelting site and medieval trackway. *Archaeologia Cambrensis*, *161*, 285-356.

Parker, D. and Horton, B., (2005). Uncertainties in central England temperature 1878–2003 and some improvements to the maximum and minimum series. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *25*(9), 1173-1188.

Pavelka, M., Acosta, M., Kiese, R., Altimir, N., Brümmer, C., Crill, P., Darenova, E., Fuß, R., Gielen, B., Graf, A. and Klemedtsson, L., (2018). Standardisation of chamber technique for CO2, N2O and CH4 fluxes measurements from terrestrial ecosystems. *International Agrophysics*, 32(4).

Pawson, R. R., Lord, D. R., Evans, M. G., and Allott, T. E. H. (2008). Fluvial organic carbon flux from an eroding peatland catchment, southern Pennines, UK. *Hydrology and Earth System Sciences, 12*(2), 625-634.

Payne, R.J., and Mitchell, E.A., (2007). Ecology of testate amoebae from mires in the Central Rhodope Mountains, Greece, and development of a transfer function for palaeohydrological reconstruction. *Protist*, *158*(2), 159-171.

Payne, R.J., and Mitchell, E.A., (2009). How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. *Journal of Paleolimnology*, *42*(4), 483-495.

Piotrowska, N., Blaauw, M., Mauquoy, D. and Chambers, F.M., (2011). Constructing deposition chronologies for peat deposits using radiocarbon dating. *Mires and Peat*, *7*(10), 1-14.

Polanco-Martínez, J.M., Korpela, M., Mudelsee, M. and Polanco-Martínez, M.J.M., (2018). *Package 'BINCOR'.* CRAN-r project.

Polanco-Martínez, J.M., Medina-Elizalde, M.A., Sánchez-Goñi, M.F. and Mudelsee, M., (2019). BINCOR: An R package for estimating the correlation between two unevenly spaced time series. *The R Journal; 11:* 170–184. *doi: 10.32614*.

Poucher P. (2009). *Wetland Margins Survey: Cors Fochno*. Dyfed Archaeological Trust

Prescott, C.E., (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils?. *Biogeochemistry*, 101(1), 133-149.R Core

Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ramsey, C.B., (2017). Methods for summarizing radiocarbon datasets. *Radiocarbon*, *59*(6), 1809-1833.

Ratcliffe, J., Andersen, R., Anderson, R., Newton, A., Campbell, D., Mauquoy, D. and Payne, R., (2018). Contemporary carbon fluxes do not reflect the long-term carbon balance for an Atlantic blanket bog. *The Holocene*, *28*(1), 140-149.

Redeker, K.R., Baird, A.J. and Teh, Y.A., (2015). Quantifying wind and pressure effects on trace gas fluxes across the soil–atmosphere interface. *Biogeosciences*, *12*(24), 7423-7434.

Reimer, P.J., Austin, W.E., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M. and Grootes, P.M., (2020). The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, *62*(4), 725-757.

Rhodes, A.N., (1998). A method for the preparation and quantification of microscopic charcoal from terrestrial and lacustrine sediment cores. *The Holocene*, *8*(1), 113-117.

Ridley, L.M., (2014). *Study of dissolved organic matter in peatlands: molecular characterisation of a dynamic carbon reservoir*. (PhD thesis), University of Edinburgh.

Ritson, J. P., Brazier, R. E., Graham, N. J., Freeman, C., Templeton, M. R., and Clark, J. M. (2017). The effect of drought on dissolved organic carbon (DOC) release from peatland soil and vegetation sources. *Biogeosciences,* 14(11), 2891-2902.

Rochefort, L., Isselin-Nondedeu, F., Boudreau, S. and Poulin, M. (2013). Comparing survey methods for monitoring vegetation change through time in a restored peatland. *Wetlands Ecology and Management, 21*(1), 71-85.

Rodwell, J.S., (1991). *British Plant Communities: Volume 5, Maritime Communities and Vegetation of Open Habitats* (Vol. 5). Cambridge University Press.

Roe, H. M., Charman, D. J., and Roland Gehrels, W. (2002). Fossil testate amoebae in coastal deposits in the UK: implications for studies of sea-level change. *Journal of Quaternary Science: Published for the Quaternary Research Association,* 17(5-6), 411-429.

Roos-Barraclough, F., van der Knaap, W.O., van Leeuwen, J.F.N. and Shotyk, W., (2004). A Late-glacial and Holocene record of climatic change from a Swiss peat humification profile. *The Holocene*, *14*(1), 7-19.

Rose, N.L., (2008). Quality control in the analysis of lake sediments for spheroidal carbonaceous particles. *Limnology and Oceanography: Methods*, *6*(4), 172-179.

Rosset, T., Binet, S., Rigal, F., and Gandois, L. (2022). Peatland Dissolved Organic Carbon Export to Surface Waters: Global Significance and Effects of Anthropogenic Disturbance. *Geophysical Research Letters, 49*(5), e2021GL096616.

Rowson, J.G., Worrall, F., and Evans, M.G., (2013). Predicting soil respiration from peatlands. *Science of the Total Environment*, *442*, 397-404.

Schlachter, K.J. and Horn, S.P., (2010). Sample preparation methods and replicability in macroscopic charcoal analysis. *Journal of Paleolimnology*, *44*(2), 701-708.

Schulz, J., (2005). *Late Holocene mire development of the lowland raised bogs Cors Caron and Cors Fochno: A palaeoecological approach using high resolution macrofossil analysis*. (PhD. thesis), University of Southampton.

Shaver, G.R., Canadell, J., Chapin III, F.S. and Gurevitch, J., (2000). Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience*, 50(10), p.871.

Siemensma, F., (2019). *Microworld – world of amoeboid organisms*. [online] Arcella.nl. Available at: <https://www.arcella.nl/> [Accessed 1 March 2019].

Simpson, G.L., (2007). Analogue Methods in Palaeoecology: Using the analogue Package Journal of Statistical Software, 22(2), 1—29

Simpson, G.L., R Core Team, Bates, D.M., Oksanen, J. and Simpson, M.G.L., (2019). *Package 'permute'.* CRAN-r project.

Slater, F.M. and Agnew, A.D.Q., (1977). Observations on a peat bog's ability to withstand increasing public pressure. *Biological Conservation*, *11*(1), 21-27.

Slater, F.M., (2012). Surface profile change at Cors Fochno (Borth Bog), Wales, UK. International Peat Congress, Stockholm, Sweden, 3-8 June 2012. *Proceedings of the 14th International Peat Congress*.

Smith, A.J.E. (2004). *The moss flora of Britain and Ireland*. Cambridge University Press.

Souto, M., Castro, D., Pontevedra-Pombal, X., Garcia-Rodeja, E. and Fraga, M.I. (2017). Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: bryophytes. *Mires and Peat*, *19*.

Souto, M., Castro, D., Pontevedra-Pombal, X., Garcia-Rodeja, E. and Fraga, M.I. (2016). Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: vascular plants. *Mires and Peat*, *18*, 1-21.

Swindles, G.T., (2010). Dating recent peat profiles using spheroidal carbonaceous particles (SCPs). *Mires and Peat*, *7*(03), 1-5.

Swindles, G.T., De Vleeschouwer, F. and Plunkett, G., (2010). Dating peat profiles using tephra: stratigraphy, geochemistry, and chronology. *Mires and Peat*, *7*.

Swindles, G.T., Roland, T.P., Amesbury, M.J., Lamentowicz, M., McKeown, M.M., Sim, T.G., Fewster, R.E. and Mitchell, E.A., (2020). Quantifying the effect of testate amoeba decomposition on peat-based water-table reconstructions. European Journal of Protistology, 74, p.125693.

Troels-Smith, J., (1955). Karakterisering af løse jordarter. *Danmarks Geologiske Undersøgelse IV. Række*, *3*(10), 1-73.

Turetsky, M.R., Manning, S.W., and Wieder, R.K., (2004). Dating recent peat deposits. *Wetlands*, *24*(2), 324-356.

van den Brink, P.J., Den Besten, P.J., bij de Vaate, A. and ter Braak, C.J., (2009). Principal response curves technique for the analysis of multivariate biomonitoring time series. *Environmental Monitoring and Assessment*, *152*(1-4), p.271.

van Loon, A.F., (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews: Water*, *2*(4), 359-392.

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H., Kattge, J., and Van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology, 21*(8), 3074-3086.

Walker, T. N., Ward, S. E., Ostle, N. J., and Bardgett, R. D. (2015). Contrasting growth responses of dominant peatland plants to warming and vegetation composition. *Oecologia*, *178*(1), 141-151.

Walker, T.N., Garnett, M.H., Ward, S.E., Oakley, S., Bardgett, R.D. and Ostle, N.J., (2016). Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology*, *22*(5), 1880-1889.

Wang, Y., Naumann, U., Wright, S., Warton, D. and Wang, M.Y (2021). Package ‘mvabund’. CRAN-r project

Wang, Y.I., Naumann, U., Wright, S.T., and Warton, D.I., (2012). mvabund–an R package for model‐based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, *3*(3), 471-474.

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A. and Bardgett, R.D., (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, *16*(10), 1285-1293.

Warton, D.I., (2011). Regularized sandwich estimators for analysis of high‐dimensional data using generalized estimating equations. *Biometrics*, *67*(1), 116-123.

Warton, D.I., Thibaut, L., and Wang, Y.A., (2017). The PIT-trap—A “model-free” bootstrap procedure for inference about regression models with discrete, multivariate responses. *PloS one*, *12*(7), 1-18.

Warton, D.I., Wright, S.T. and Wang, Y., (2012). Distance‐based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, *3*(1), 89-101.

Watson, E.J., Swindles, G.T., Lawson, I.T., Savov, I.P. and Wastegård, S., (2017). The presence of Holocene cryptotephra in Wales and southern England. *Journal of Quaternary Science*, *32*(4), 493-500.

Wider, R.K. and Lang, G.E., (1982). A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, *63*(6), 1636-1642.

Wilks, P.J., (1979). Mid-Holocene sea-level and sedimentation interactions in the Dovey Estuary area, Wales. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *26*, 17-36.

Worrall, F., Burt, T. P., and Adamson, J. K. (2006). Trends in drought frequency–the fate of DOC export from British peatlands. *Climatic Change*, *76*(3), 339-359.

Zhai, J., Cong, L., Yan, G., Wu, Y., Liu, J., Wang, Y., Zhang, Z. and Zhang, M., (2019). Influence of fungi and bag mesh size on litter decomposition and water quality. *Environmental Science and Pollution Research*, 26(18), 18304-18315.

Chapter 3: Plant community responses to experimental climate manipulation in a Welsh ombrotrophic peatland and their palaeoenvironmental context

Running title: Peatland plant responses to climate change

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Peatlands, vegetation, climate change, palaeoecology, carbon, testate amoebae, experimental climate manipulation.

3.1. Abstract

We test whether vegetation community composition from a 10-year climate manipulation experiment on a Welsh peat bog resembles vegetation communities during periods of climate change inferred from a peat core. Experimentally warmed and combined warmed and droughted treatments drove significant increases in ericaceous shrubs but *Sphagnum* was unaffected. Similarly, *Calluna vulgaris* seeds increase during inferred warmer periods in the palaeoecological record. Experimental short-term episodic drought (four 4-week drought treatments) did not affect vegetation. Plant community composition has undergone several abrupt changes throughout the past c. 1500 years, often in response to human disturbance. Only slight changes occurred during the Medieval Climate Anomaly (c. 950–1250 Common Era [CE]) in vegetation and hydrology, while abrupt changes occurred during the Little Ice Age (c. 1300–1850 CE) when water tables were highest, suggesting that these shifts were driven by changes in water table, modulated by climate. A period of water table drawdown c. 1800, synchronous with historical records of increased drainage, corresponds with the development of the present-day vegetation community. Modern analogues for fossil material, characterized by abundant *Rhynchospora alba* and *Sphagnum pulchrum*, are more common after this event. Vegetation changes due to climate inferred from the palaeo record differ from those observed in the experiments, possibly relating to differences in the importance of drivers of vegetation change over varying timescales. Whereas temperature is frequently identified as the dominant driver of plant community change in experiments, sustained changes in water table appear to be more important in the long-term record. We find evidence that recent climate change and other anthropogenic stressors (e.g., drainage, heavy metal, and nitrogen pollution) may

promote the development of novel plant communities without analogues in the fossil record. These communities may be poorer at sequestering carbon and may respond differently to future climate change.

3.2. Introduction

Peatlands accumulate vegetative material over thousands of years, which preserves as peat under anaerobic and cool conditions beneath the water table (Yavitt *et al.,* 1997). As peat grows, carbon is retained, and can be stored indefinitely (Belyea, 2009; Davidson and Janssens, 2006). Peatlands contain approximately 30% of all terrestrial soil carbon, estimated at c. 500 ± 100 billion tonnes (GT) (Gorham, 1991; Yu, 2012; Yu *et al.,* 2010) despite only occupying c. 3% of global land area (Waddington *et al.,* 2015). Peatlands emit atmospheric carbon via gaseous exchange of carbon dioxide (CO_2) and methane (CH_4) while also losing carbon via hydrological pathways in dissolved and particulate forms (Blodau, 2002; Freeman *et al.,* 2004). This constant carbon cycling produces both positive and negative climate feedbacks (Bridgham *et al.,* 1995; Gorham, 1995; Moore *et al.,* 1998). Overall, pristine peatlands are considered net carbon sinks, cooling global climate (Frolking and Roulet, 2007).

Anthropogenic climate change is projected to alter global temperatures and weather patterns, with the most pronounced changes in temperature and precipitation rates predicted for the Northern Hemisphere (IPCC, 2021). Temperature, water table depth (WTD) and atmospheric CO_2 concentrations are important climatic variables that govern peatland resilience and functioning (Turetsky *et al.,* 2012). Increased temperatures and lower water tables may promote vascular plant growth at the expense of *Sphagnum* mosses (e.g., Dieleman *et al.,* 2015; Metcalfe *et al.,* 2011; Trinder *et al.,* 2008). *Sphagnum* is important for maintaining ecosystem functioning and resilience to climatic or anthropogenic perturbations in many northern peatlands (Bragazza *et al.,* 2013; Kuiper *et al.,* 2014). By modifying the hydrology and biochemistry of the soil, *Sphagnum* creates waterlogged and acidic substrates that decay slowly (van Breemen, 1995). If *Sphagnum* cover is reduced in favour of vascular plants, decomposition may be accelerated, as the supply of readily decomposed (labile) exudates from vascular plant roots increases, coinciding with fewer inhibitory polyphenol compounds released by *Sphagnum* (Bragazza *et al.,* 2013; Fenner and Freeman, 2011). This may significantly impact peatland ecosystem functioning, decreasing its carbon sink capacity (Dieleman *et al.,* 2015). Other indirect climate change impacts, such as drought and wildfire, may also weaken or reverse peatland carbon sink functioning (Blodau, 2002; Grillakis, 2019; Norby *et al.,* 2019; Rouse *et al.,* 1997). By understanding how changes in climate and hydrology will affect peatland plant communities, we can better anticipate future peatland ecosystem responses to anthropogenic climate change. A complete understanding of these responses and their associated feedbacks may lead to future improvements in global climate models (Frolking *et al.,* 2009).

We compare changes in plant community composition following 10 years of climate manipulation (warming and episodic drought) on Cors Fochno, an ombrotrophic peatland in Wales, with the long-term palaeo-vegetation history of the bog. We generate a high-resolution testate amoebae-derived hydroclimatic reconstruction for the past c. 1500 years from a peat core, relating hydrological shifts with changes in plant community composition in the long-term record. We compare vegetation community composition within the experimental plots and test the hypothesis that vegetation community composition within the experimentally warmed and droughted plots resembles that of dry/warm periods over the past one and a half millennia.

Climate manipulation studies simulate climatic and hydrological changes in peatlands (e.g., Dieleman *et al.,* 2015; Ward *et al.,* 2013), allowing examination of ecosystem responses to a range of environmental stressors. However, such experiments are frequently short-lived, rarely exceeding five growing seasons and therefore become increasingly imprecise for predicting how peatlands will respond to climate change over longer timescales. Nevertheless, peatlands also record a sensitive archive of environmental and climatic change over long-term (decadal to millennial) timescales (Barber, 1993; Chambers and Charman, 2004). Changes in environmental conditions may be inferred from biological or physical proxies that record changes in precipitation, reinforced by temperature (Charman *et al.,* 2004, 2009) and may be compared with changes in vegetation (e.g., Chambers *et al.,* 1999; De Vleeschouwer *et al.,* 2009; Turner *et al.,* 2014). Such studies can be limited by the difficulty of discerning climatic effects from anthropogenic impacts in some instances, dating uncertainties and differential preservation of biological proxies (Kuhry and Turunen, 2006; Mauquoy and Yeloff, 2008; Swindles *et al.,* 2020).

Studies incorporating both climate manipulation studies and centennial or millennial-scale proxy records are rare (Lamentowicz *et al.,* 2016). However, the methods are complementary and can be applied together to improve the understanding of peatland vegetation responses to climate change (Lamentowicz *et al.,* 2016; Rull, 2010; Seddon *et al.,* 2014). Interpretation of the results of long-term *in situ* climate manipulation experiments may also be improved by considering the present state of an ecosystem in the context of its long-term history (Lamentowicz *et al.,* 2016; Willis *et al.,* 2010). Lamentowicz *et al.* (2016) considered the long-term palaeo-vegetation history for two experimental sites at Linje mire, northern Poland and Mukhrino in western Siberia, and found that the vegetation cover in both sites had changed during the past c. 200 years: due to human activities (drainage) on Linje mire and following changes in climate and bog microforms on the relatively pristine Mukhrino. They argue changes in vegetation following anthropogenic disturbances and climate changes have modified ecosystem functioning in peatlands.

For the palaeo-vegetation reconstruction at Cors Fochno, we focus on the past c. 1000 years, as temperature variation during this period (c. 0.2°C, Mann *et al.,* 2009) likely resembled the simulated temperature differences imparted by the experiment (Bradley and Jonest, 1993; Mann *et al.,* 2009). Climatic variability during the past millennium for the Northern Hemisphere included relatively warm conditions from the mid-9th to the mid-13th century Common Era (CE), followed by cooler conditions from the 14th to the mid-19th century CE (Mann *et al.,* 1999). These events are loosely termed the Medieval Climate Anomaly (MCA) and Little Ice Age (LIA) respectively (Lamb, 1965; Mann *et al.,* 2002). The timing and magnitude of both events vary widely across regions, and neither were periods of ubiquitous warming or cooling (Broecker, 2001; Mann *et al.,* 2002; Matthews and Briffa, 2005; Neukom *et al.,* 2019). The MCA was a period of generally warmer conditions over much of the Northern

Hemisphere, characterized by a predominantly positive North Atlantic Oscillation (Trouet *et al.,* 2009). The LIA was characterized by pronounced cooling over the Northern Hemisphere and a predominantly negative North Atlantic Oscillation (Lamb, 1965; Mann *et al.,* 2009; Matthes, 1939). Marine palaeoclimate reconstructions show that North Atlantic Sea surface temperatures were warmer during the MCA and fell during the LIA (Cunningham *et al.,* 2013), corresponding with palaeoclimate data showing that conditions were generally drier throughout much of Britain during the MCA and wetter or more variable throughout the LIA (Charman and Hendon, 2000; Lamb, 1965; Proctor *et al.,* 2000).

Previous studies have made great strides towards understanding peatland vegetation responses to climate change (e.g., Buttler *et al.,* 2015; Malhotra *et al.,* 2020; Weltzin *et al.,* 2003); however, to our knowledge, no previous study has attempted to combine *in situ* temperature and water table manipulation with palaeoecological approaches to test how well the changes in these experimental studies replicate past changes. Comparing plant community composition changes in the experimental and palaeoecological record over the past c. 1000 years provides insights on how well climate manipulation experiments reflect actual long-term ecological changes and if changes in past vegetation community composition can serve as useful analogies for future responses to anthropogenic climate change.

3.3. Study site, methods, and materials

3.3.1. Study site

Cors Fochno is a *Sphagnum*-dominated raised (ombrotrophic) bog near the Ceredigion coast, Wales, east of the town of Borth (Lat: 52.50, Long: −4.01) (Figure 3.1). It is the largest expanse of primary surface lowland raised bog in Wales, with a central active zone comprising c. 2 km^2 of primary surface peat, surrounded by c. 4 km^2 of degraded peatland (Poucher, 2009). The vegetation on the central dome is consistent with the UK National Vegetation Classification M18: *Erica tetralix–Sphagnum papillosum* raised and blanket mire-type vegetation communities, dominated by *Sphagnum pulchrum* lawns (Rodwell, 1991). Cors Fochno overlays tidal mud flats, and the underlying geology is of Silurian Aberystwyth grits group (Howells, 2007). Peat initiation began at the site around c. 6000 BCE (Wilks, 1979). The peat attains a maximum depth above 7 m in the central raised dome, which sits c. 1 m above sea level (CCW, 2011; Hughes and Schulz, 2001; Wilks, 1979). Based upon local measurements, annual precipitation rate (1981–2019), average air temperature (2010–2019) and average wind speed were 1236 mm $year^{-1}$, 11.1°C and 3.1 m s^{-1} respectively (unpublished data).

The site has experienced low-level disturbance from human activities such as agriculture, peat cutting and mining activities throughout much of its history, which intensified at the end of the 18th century (Mighall *et al.,* 2017; Page *et al.,* 2012; Poucher, 2009). Population increases at this time drove demand for increased agriculture and fuel, resulting in the excavation of extensive drainage channels after 1815 and the conversion of large areas of the bog to farmland (Poucher, 2009). Annual burning of peripheral areas of the site began in the early 19th century and continued at a near annual basis until 1986 (CCW, 2011). Drainage and peat cutting continued until the 1970s, at which time restoration work began, restoring former water levels and re-establishing peat bog conditions in degraded areas (Poucher, 2009).

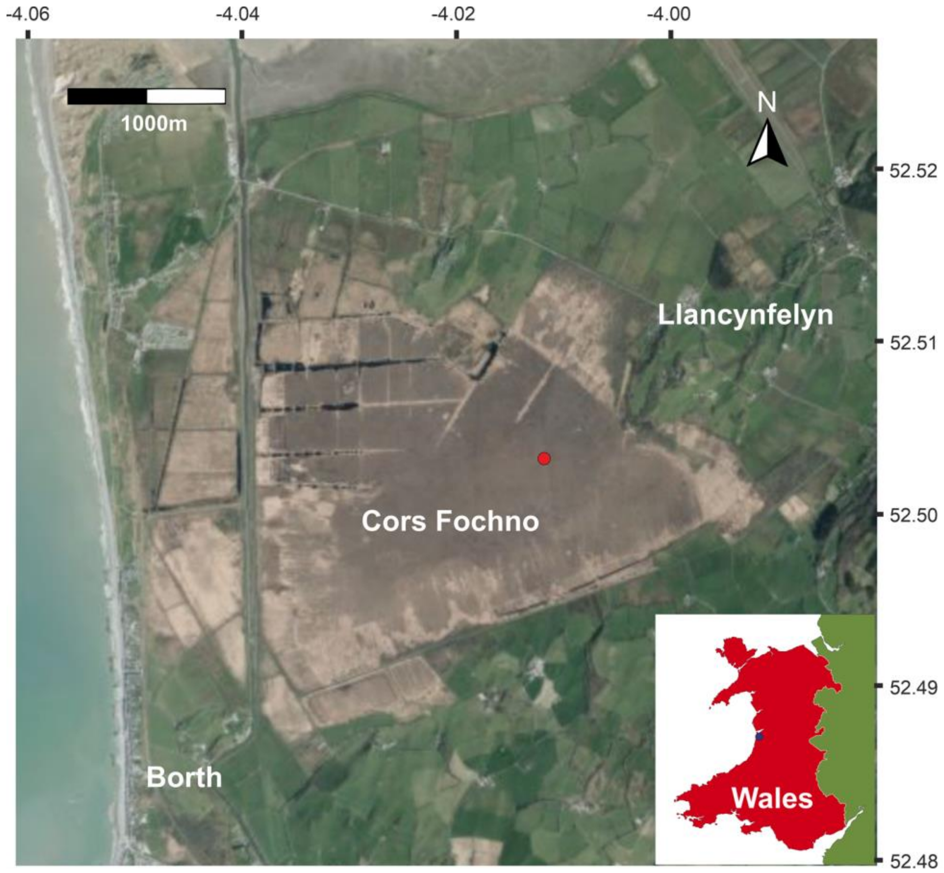

Figure 3.1. Satellite image of Cors Fochno, Ceredigion, West Wales. The red dot denotes the location of the experimental plots and core. The inset map shows the location of Cors Fochno within Wales (blue dot). Satellite image sourced from Bing maps

3.3.2. Experimental set-up

The Cors Fochno experiment is a long-term (10-year), fully factorial *in situ* climate manipulation experiment consisting of hydrologically isolated plots of *Sphagnum* lawn (Figure 3.2). The intention of the experiment is to determine the effects of climate warming and drought upon ecosystem functions in northern ombrotrophic peatlands.

This project uses open top chambers (OTCs) to simulate climate warming (Figure 3.2); these are commonly used to moderately elevate air and soil temperatures in field experiments (Aronson and McNulty, 2009). OTCs were constructed from 2.5-mm thick Perspex sheets, joined at the corners by cable ties, following designs used by the International Tundra Experiment (Arft *et al.,* 1999; Marion, Bockheim, *et al.,* 1997; Marion, Henry, *et al.,* 1997; Shaver *et al.,* 2000). OTCs passively warm the air within the chamber like a greenhouse, with studies typically reporting a 0.35–1.0°C air temperature increase (Walker *et al.,* 2016; Ward *et al.,* 2013).

Table 3.1. Experimental treatments in the Cors Fochno climate manipulation experiment. The two experimental levels are denoted by shading of the table rows. The presence of open top chambers (OTCs) and groundwater pumping treatments (Pumped) are denoted by an X. Combined warming and drought plots are referred to as 'combined'

Treatment	OTC	Pumping	Number of plots	Plot ID
OTC	**x**		6	1, 3, 5, 8, 10, 12
Pumped		**X**	6	1, 4, 6, 8, 9, 12
Control			3	2, 7, 11
Warmed	**x**		3	3, 5, 10
Drought		**X**	3	4, 6, 9
Combined	**x**	**X**	3	1, 8, 12

Drought in this study refers to reduced precipitation resulting in lowered groundwater levels (van Loon, 2015). Drought simulation was achieved by automated groundwater pumping from within the plots. In the corner of each drought plot, we inserted a 1-m-long, 11-cm-diameter perforated tube vertically into the peat and removed the peat inside. During drought simulation, plots were drained by macerator-style pumps attached to inlets (fitted with one-way valves to prevent water backflow) for each tube. Plastic piling, 1.5 m long, hydrologically separates the plots from the surrounding peat, preventing lateral flow into the drought plots. Shorter, 0.5 m piling drilled with holes were inserted into warmed and control plots to replicate this disturbance while still allowing for lateral water exchange to take place. Drought simulation was repeated during 2010, 2011, 2014 and 2019, each time lasting four weeks between August and September. This study tests the effects of increased drought incidence upon vegetation over 10 years, rather than the effects of long-term, sustained water table drawdown.

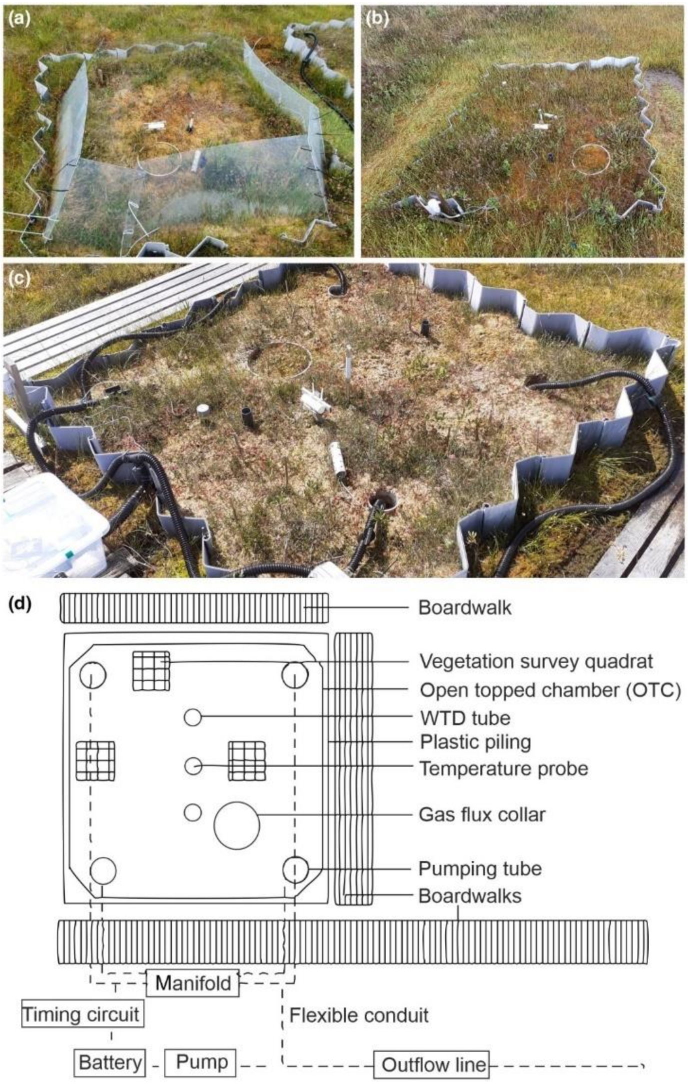

Figure 3.2. Cors Fochno Experiment climate manipulation plots: (a) plot with open top chamber; (b) control plot; (c) drought plot undergoing drought manipulation; and (d) schematic of plot design (Kay, 2019)

Each plot was equipped with HOBO Onset U10 Temperature loggers (Onset Computer Corporation) measuring air and soil (10 cm depth) temperature. These were later replaced with HOBO U23 Pro v2 temperature sensors in 2018. TruTrack WT-HR 2000 water-height data loggers (Trutrack) record water table height. Logger values were converted to WTD by calibration against regular manual WTD measurements. Data gaps were filled by linear interpolation with temperatures and WTD records from neighbouring plots, as well as from an adjacent dip-well and weather station operated by Natural Resources Wales.

3.3.3. Vegetation survey within experimental plots

Three fixed 25 × 25 cm quadrats, each enclosing a 5 × 5 grid, were used to quantify the plant community composition and abundance in each plot. The quadrats were surveyed annually using the pin-quadrat method (Levy and Madden, 1933; Rochefort *et al.,* 2013). A pin was pushed through the top-right corner of the 25 grid squares. Total touches for each species of vascular plant were tallied for each plot. *Sphagnum* (recorded to species), liverworts and bare peat were recorded on a presence/absence basis for each segment.

3.3.4. Core collection and storage

We extracted a 1.5-m-long core (BO17) from the bog in November 2017 using a 5-cm diameter Russian corer, with 5 cm of overlap between core sections (Jowsey, 1966). The coring location was proximal to the experimental site and was characterized by a *S. pulchrum* lawn. The uppermost 50 cm was extracted using a monolith tin to ensure sufficient additional material for later analysis. Extracted cores were stored in guttering, wrapped in cling film, and refrigerated at 4°C.

3.3.5. Chronology

Sphagnum or other above-ground plant remains were hand-picked from 1 cm thick subsamples in the core for Accelerator Mass Spectrometry ^{14}C dating. Rootlets were removed to avoid contamination by younger carbon (Kilian *et al.,* 1995). When insufficient identifiable plant remains were present, we analysed bulk peat. In those cases, a 1 cm thick, 1 cm^3 section of peat was washed through a 250 µm sieve and the fine particulate fraction (<250 µm) retained for analysis, following Piotrowska *et al.* (2011). Samples were alkali-acid washed before oven drying at <45°C.

Recently accumulated peat was dated using spheroidal carbonaceous particles (SCPs). SCPs are a component of black carbon that are only formed through fossil fuel combustion at high temperatures. SCP samples were prepared following procedures outlined by Swindles (2010). Changes in SCP concentrations throughout the soil profile are related to known ages of historical fuel combustion and can be compared with known fallout rates from other dated sedimentary sequences (Rose and Appleby, 2005; Swindles, 2010). SCP dating is a relatively rapid and low-cost alternative to radiometric methods for dating recently accumulated peat. SCPs are less mobile in peat than some radiometric isotopes such as ^{137}Cs; however, some chronological accuracy may be lost compared to the absolute, continuous dating possible with ^{210}Pb (Turetsky *et al.,* 2004). Contiguous 1 cm^3 samples of peat were subsampled from the top 30 cm of the core at 1 cm resolution. SCPs were identified following criteria described by Rose (2008) using a high-powered microscope at 400× magnification. SCP concentration is reported as the number of particles per gram of dry mass (g DM^{-1}).

An additional chronostratigraphic marker is provided by a well-documented wildfire affecting the coring site during 1986 (Fowles *et al.,* 2004). Such an event would provide a clear subsurface chrono-horizon of macrocharcoal consisting of the remains of identifiable peatland species. Macrocharcoal was sampled and analysed following the procedures by Rhodes (1998) and Schlachter and Horn (2010). Contiguous 1 cm^3 subsamples were taken at 1 cm resolution. Each sample was submerged in 6% H_2O_2 overnight before wet sieving through a 125 µm sieve, retaining the larger fraction. Charred fragments were counted under a stereomicroscope at low magnification (10 – 100x) using a Bogorov tray.

Age-depth models were generated using the package 'rBacon' (Blaauw *et al.,* 2021a), incorporating all SCPs, macrocharcoal and ^{14}C dates. This Bayesian model generates a maximum age probability at set (1 cm in this study) intervals together with maximum and minimum ages, based upon the 95% confidence interval. Dates within this study are reported as the median age probability prefixed circa (c.), and the max-min age range is given as cal CE. Year notations are reported as CE dates, following the Gregorian calendar.

3.3.6. Palaeo-vegetation

We used plant macrofossil analysis to determine palaeo-vegetation community change through the core. Peats of 4 cm^3 were sampled at contiguous 1 cm intervals. These were submerged in 10 % potassium hydroxide solution for 24 h prior to rinsing through a 125 µm sieve.

Primary peat components were assessed using a low-power stereomicroscope at 11.2× magnification following an adapted version of the quadrat and leaf count method (Barber *et al.,* 1994) by Mauquoy *et al.* (2010). Components (e.g., total *Sphagnum*, *Rhynchospora alba* stem) were expressed as percentages of total peat components. Plant macrofossils were identified with reference to Grosse-Brauckmann and Streitz (1972), Smith (2004), Souto *et al.* (2016, 2017), Daniels and Eddy (1990) and Mauquoy *et al*. (2010). Plant remains were identified to species level where possible. *In situ*ations where material was insufficiently preserved to facilitate species-level identification, plant types were recorded as ‘undifferentiated’’.

Each sample was washed through a 1-mm test sieve, with both fractions retained. A Bogorov tray was used to count seeds within the <1 mm fraction, whereas material >1 mm was counted by creating a single layer of material in a Petri dish underlain with numbered squares. Seeds and other objects (e.g., *Myrica gale* bud scales) were identified and counted for each square within the Petri dish. Seed identification was achieved by referring to Cappers *et al.* (2006) and Souto *et al*. (2016). Seeds were counted under a low-power stereomicroscope at 10 – 200× magnification and are presented as total counts.

Sphagnum percentage counts were estimated by selecting >100 leaves from each sample for identification to species level. *Sphagnum* leaves were identified under a high-powered stereomicroscope at 100 – 200× magnification, with reference to Mauquoy and van Geel (2007) and Laine *et al.* (2011) alongside reference material collected from the site. Leaf counts are expressed as percentages of the total identifiable *Sphagnum*. *Sphagnum* nomenclature follows Daniels and Eddy (1990), bryophytes follow Smith (2004) and vascular plants follow Stace (2010).

3.3.7. Testate amoebae

Testate amoebae are unicellular soil organisms, useful as proxies for hydrological change in peatlands (Langdon *et al.,* 2012). Testate community composition changes in response to WTD, with species distributions reflecting their ecological optima (Booth, 2008; Mitchell *et al.,* 2008). Their shells (tests) often allow identification to species level and are frequently preserved in peat (Mitchell *et al.,* 2008). Quantitative reconstruction of WTD based on fossil assemblages is possible following the development of numerical transfer function methods using present-day species–environment relationships (Charman *et al.,* 2007; Payne and Mitchell, 2007).

We used the weighted averaging transfer function model of Amesbury *et al.* (2016) based on a training set of 1302 samples spanning 35° of latitude and 55° of longitude. The efficacy of the model (tolerance down weighted with inverse de-shrinking) has been rigorously tested by both statistical validation and comparison with independent test sets with associated instrumental data by Swindles *et al.* (2015).

Samples of 2 cm^3 (1 cm thick) were subsampled at 2 cm intervals. Tests were extracted following an adaptation of protocols by Hendon and Charman (1997). Each sample was submerged in water with a lycopodium tablet (Batch: 3862) then washed through a 355-µm test sieve, retaining the smaller fraction. These were then centrifuged at 30 Hz for 10 min before mounting in glycerol. Tests were counted at 250× magnification using a high-powered stereomicroscope, with minimum counts of 100 individuals achieved following Payne and Mitchell (2009). Testate amoebae are identified with reference to Charman *et al.* (2000), Clarke (2003), Mazei and Tsyganov (2006) and Siemensma (2019).

3.3.8. Statistical analyses

All analyses were carried out using the statistical package 'R' (R core team, 2021). Further details (fixed effects, accounting for hierarchical and repeated measure design of the experiment). Statistical differences in temperature and water table between treatments were tested for using mixed effects linear models using the 'lme4' package in R (Bates *et al.,* 2015), and significant differences tested for using likelihood ratio tests (LRT). These tests assesses the goodness of fit of two statistical models, one with and another without the fixed effect of treatment against time, based on the ratio of their likelihoods. The environmental variable of interest was the dependent variable, and the experimental treatments were fixed factors. Plots, nested in block, and measurement time were included in the model as random factors.

Changes in vegetation (by species and physiognomic functional type) over time across all combinations of treatments were tested by generalized linear models (GLMs) using the 'mvabund' package (Wang *et al.,* 2012, 2020). GLMs are an extension of linear regression, relating linear models to their response variable via link functions. More information regarding the statistical methods used here is included in the supplementary information (Supplementary Text 1.1). Functional type data were compared by removing vegetation from the modern data with no analogy in the palaeoecological record, due to differential preservation of vegetation types in plant macrofossil assemblages (Mauquoy and Yeloff, 2008), although this is likely to bias the results, potentially causing CMAs to be detected where the vegetation were quite different at the species level.. Furthermore, by reducing plant species data to static plant functional types, a large amount of detail related to species-specific properties and behaviours may be lost (Verheijen *et al*., 2015).

Stratigraphically constrained incremental sum of squares cluster analysis (CONISS; Grimm, 1987) was used to identify the groups of stratigraphically adjacent plant community assemblages, indicating changes have occurred between identified clusters throughout core BO17. Since CONISS is unable to deal with the different data types (relative % abundance and counts) in the plant macrofossil data (Birks, 2014), only the percentage peat component data were used to partition palaeo-vegetation zones.

To compare palaeoecological plant community composition with modern experimental vegetation communities, we used analogue matching using the ‘analogue’ package (Simpson, 2007). This is a technique used to identify close modern analogues (CMAs) for fossil data sets (Overpeck *et al.,* 1985; Simpson, 2007). Similarity coefficients were calculated between experimental and fossil communities using methods described by Bray and Curtis (1957). A number between 0 and 1 is assigned for each pair of samples based on the statistical (dis)similarity between communities, with 0 indicating that samples are identical, while a coefficient of 1 indicates samples are completely unalike. A Monte-Carlo simulation with 10,000 permutations was employed as described by Simpson (2007) to define a critical value for dissimilarity to categorize CMAs at the 95% confidence interval. Data were square root transformed prior to analysis to reduce possible differences between the two methods.

3.4. Results

3.4.1. Air temperature

To determine if the experimental treatments affected soil and air temperature or WTD, we analysed temperature data from 2019 as a representative year and WTD measurements from the 2019 drought manipulation experiment. OTCs have a significant warming effect on air temperature (LRT: $\chi^2(1) = 11.64$, $p = <.001$), increasing it by an average of 0.47°C throughout 2019 (Figure 3.3a). Temperature differences were greatest during summer months, differing by as much as c. 7.4°C, with mean temperature differences greatest between 12 PM and 6 PM (Figure 3.3a–c). During winter months, mean temperatures are often slightly cooler within the OTCs than in controls (Figure 3.3c), with a maximum cooling of 3.4°C. This is likely due to sheltering by the OTCs, restricting heat transport by wind passing over the vegetation canopy (Samson *et al.,* 2018).

3.4.2. Soil temperature

The OTCs significantly increased soil temperature (10 cm depth) by an average of 0.45°C (95% CI: 0.09 – 0.80°C) throughout 2019 (Figure 3.3b). Soil warming in plots with OTCs was slightly higher during the winter months, indicative of a lag between air and soil temperatures (Figure 3.3b – d).

3.4.3. Water table depth

Significant differences occurred in WTD due to pumping during the 2019 water table drawdown experiment (LRT: $\chi^2(1) = 1835.3$, $p = <.001$) (Figure 3.4). Pumping reduced WTDs by an average of 16.1 cm (95% CI: 13.7 – 18.4 cm) during the pumping period, comparable to the average WTDs within the plots during a drought that affected much of Europe between June and August 2018 (16.4 cm).

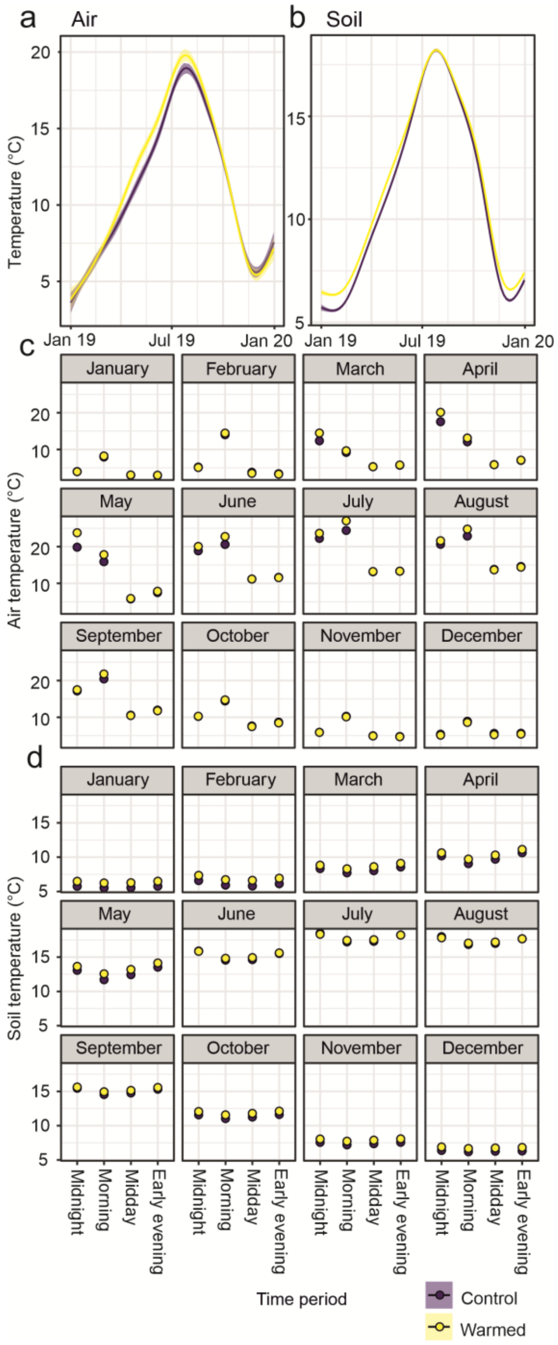

Figure 3.3. Temperature variations between treatments for the year 2019. Temperatures for plots without open top chambers (OTCs) are shown in purple; plots with OTCs are in yellow. (a, b) LOESS curves showing the differences in a. air and b. soil temperatures throughout the year. (c, d) Differences in monthly mean air (c) and soil (d) temperatures during different time periods for different times of year. Periods = midnight c. 12 AM; morning c. 6 AM; midday c. 12 PM; and early evening c. 6 PM

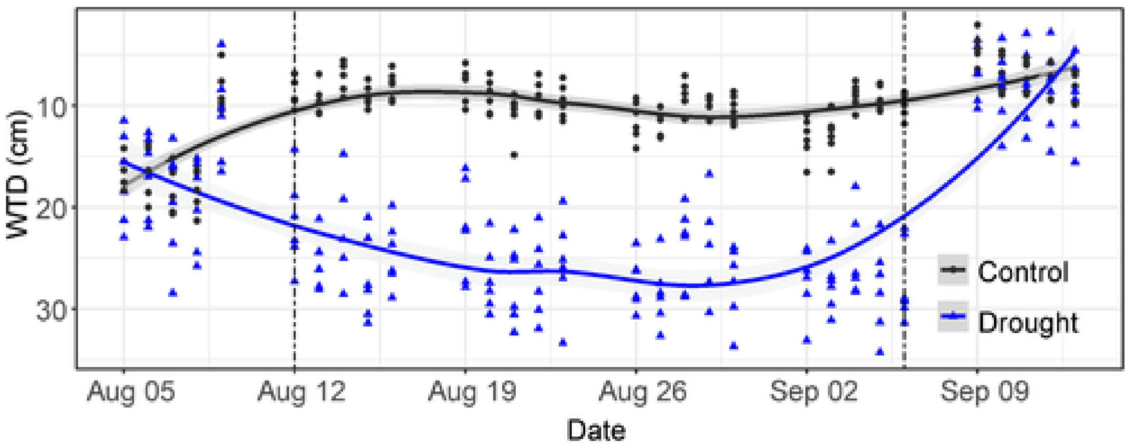

Figure 3.4. Difference in water table depths (WTD) between pumped (blue) and not pumped (black) plots during the 2019 drought manipulation experiment. Six weeks of daily WTD measurements are shown, including week-long measurements post- and pre-drought manipulation. Dashed vertical lines indicate the start (12 August) and end (6 September) of the drought manipulation for this year

3.4.4. Vegetation changes in the 10-year experimental study

A total of 21 plant taxa occur within the experimental plots. The most abundant species, *R. alba*, constitutes 30.2 ± 12.6% (1*σ*) of mean vegetation coverage in the plots. The second most abundant species recorded was *S. pulchrum*, at 28.4 ± 11.1%.

Although this number is consistent with the countryside council for Wales (CCW, 2011) estimate that *Sphagnum* represent >25% of the primary bog surface, species abundances may have been underestimated due to the sampling method used. As a ground-cover species, *Sphagnum* were only allocated one touch per quadrat, whereas the abundance of widely branching species such as *Rhynchospora alba* were frequently counted, potentially overestimating their relative cover.

Other *Sphagnum* species were less abundant within the plots. The most common species after *Sphagnum pulchrum* was *Sphagnum papillosum*, with a mean coverage of only 4.9 ± 6.6 % of the total assemblage. *Sphagnum capillifolium* and *Sphagnum* *cuspidatum* represented 1.4 ± 3.9 % and 1.3 ± 3.3 % respectively. Mean values for *Sphagnum medium* and *Sphagnum tenellum* represented <1 % of the total plant cover within the experimental plots. Supplementary figures 1.1 – 1. 1.6 illustrate changes in functional type and species differences between various treatments. The results of the Wald tests between each treatment are given in Table 3.2.

Shrub abundance significantly increased under both warmed and combined treatments relative to controls. However, this effect only significantly affected overall plant community composition in the plots with OTCs, which increased by >200 % (rising from 4 % of total cover within the plots to 29 %) between 2010 and 2020, relative to >90 % (increase in cover 14 %–26 %) in the combined treatment plots and a >7 % decrease in the control plots during this time. Shrub taxa were less abundant in the warmed and combined treatment plots at the beginning of the experiment, which is in part a consequence of the small number of experimental plots (three for each treatment), a practical limitation of this study. However, in both cases, the 95 % CIs overlapped with controls at the start, and in both cases the increase in shrubs was logarithmic, reaching a plateau in 2016, six years after the start of treatments (Figure 3.5). Drought had no significant effect upon vegetation abundance, indicating that the significant increase in shrubs in the combined treatments was due to warming alone. The presence of OTCs had a significant effect upon the plant community at the species level relative to controls. This was mostly driven by increases in *Calluna vulgaris*, which doubled in abundance between 2010 and 2020, and increased significantly in the warmed plots. *C. vulgaris* is relatively uncommon in the plots, achieving a mean relative abundance of 5.6 % of the entire community by 2020.

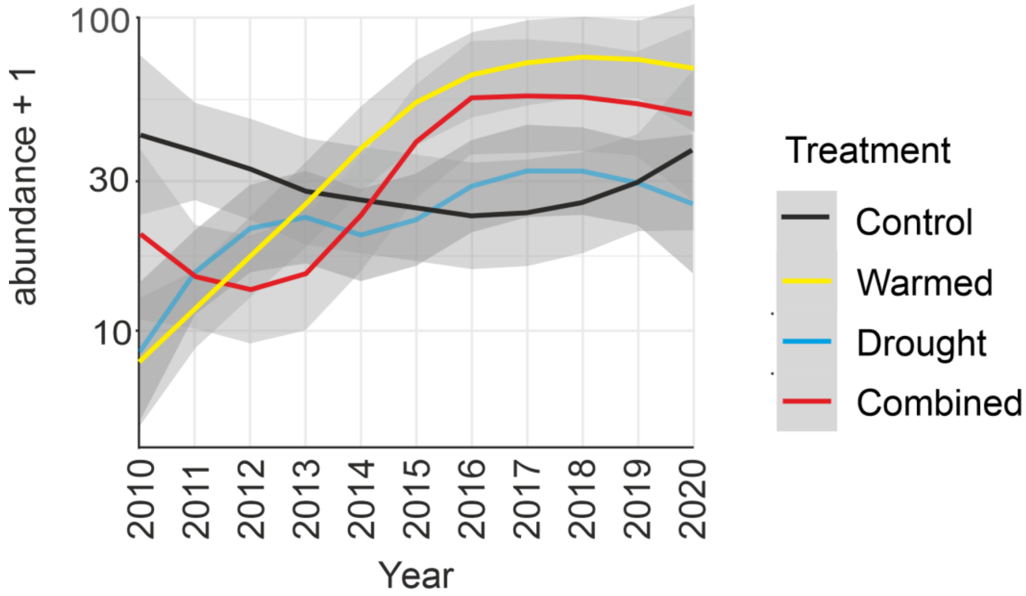

Figure 3.5. Responses of shrubs to treatments relative to controls over the 10-year experiment. The y-axis abundance is total summed counts for each plot +1, plotted on a log-linear scale. Shading indicates the 95 % confidence interval.

3.4.5. Core chronology

The results of the radiocarbon analyses are shown in Table 3.3. Dates are in stratigraphic order, except for the 44 and 50 cm depths, where the median date for the overlying sample is older than that of the underlying sample. The age ranges for these two depths overlap completely, indicating that their ages are statistically indistinguishable. This is the same for 75 and 80 cm depths. All other ages are significantly different from each other. These overlaps are likely to reflect non-linearity in the IntCal20 terrestrial calibration curve (Figure 3.6). The calibration curve exhibits periods of decline for both periods for which pairs of radiocarbon dates overlap. For both of these periods, several centuries of radiocarbon years equate to around one century of calendar years. Blaauw *et al*. (2003) found similar overlap in radiocarbon dates from a peat core, with equivalent differences in depth between samples to those in this study.

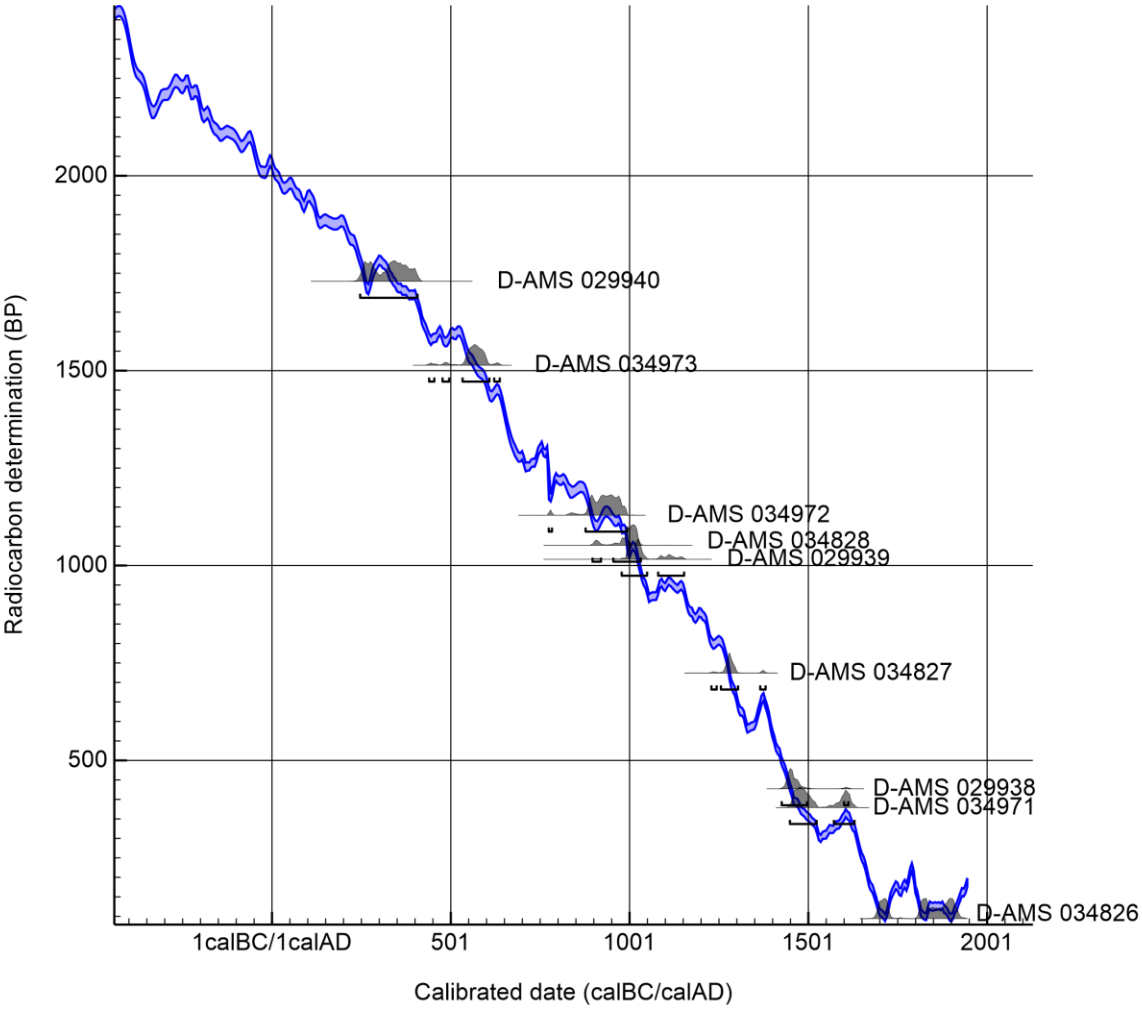

Figure 3.6. Probability distribution functions of calibrated radiocarbon dates (grey shapes) from core BO17 compared with the IntCAL20 calibration curve in blue (Reimer *et al*., 2020). Figure generated using OxCal version 4.4 (Bronk-Ramsey, 1995).

Table 3.2. Results of the statistical tests for vegetation differences between plots. Each plot with OTCs (OTC in table) and each pumped plot (Pumped in table) are compared against the plots without OTCs and plots that are not pumped as controls. The results of these tests are unshaded in the table. All other comparisons are made between individual treatments: control, warmed, drought and combined (combined warming and drought), these tests are shaded in light blue. Significant results are highlighted in bold and delineated by an asterix.

Control					
Functional Types	Res.DF	DF.diff	Wald	p. val	Functional types
OTC	110	10	7.493	0.055	Shrubs (Wald: 7.493; p=0.035)
Pumped	110	10	7.828	0.359	NA
Warmed	44	10	12.892	**0.001***	Shrubs (Wald: 10.897; p=0.001)
Drought	44	10	10.636	0.10	NA
Combined	44	10	9.579	0.20	Shrubs (Wald: 7.744; p=0.033)
Individual taxa	Res.DF	DF.diff	Wald	p. val	Species
OTC	110	10	16.70	**0.039***	No single species
Pumped	110	10	12.871	0.324	NA
Warmed	44	10	13.825	0.35	*Calluna vulgaris* (Wald: 7.108; p=0.013)
Drought	44	10	13.291	0.20	NA
Combined	44	10	13.088	0.60	NA
Warmed					
Functional Types	Res.DF	DF.diff	Wald	p. val	Functional types
Drought	44	10	8.145	**0.05***	No single species
Combined	44	10	6.168	0.75	NA
Individual taxa	Res.DF	DF.diff	Wald	p. val	Species
Drought	44	10	12.524	0.35	NA
Combined	44	10	11.455	0.60	NA
Drought					
Functional Types	Res.DF	DF.diff	Wald	p. val	Functional types
Combined	44	10	8.145	0.35	NA
Individual taxa	Res.DF	DF.diff	Wald	p. val	Species
Combined	44	10	11.900	0.20	NA

Table 3.3. Table of AMS ^{14}C dates from BO17 core, Cors Fochno. Dates were calibrated using the IntCal20 calibration curve (Reimer *et al.,* 2020) in OxCal version 4.4 (Bronk-Ramsey, 1995)

Depth (CM)	**Lab code**	**Material dated**	**^{14}C Age**	**^{14}C error**	**Calibrated age range (years CE) 95.4%**	**Median age Years**
29	D-AMS 034826	*Sphagnum* stems and leaves	94	26	1690-1922	1837
44	D-AMS 029938	*Sphagnum* stems and leaves	427	26	1426-1613	1455
50	D-AMS 034971	*Sphagnum* stems and leaves	379	24	1449-1630	1498
60	D-AMS 034827	*Sphagnum* stems and leaves	724	29	1230-1381	1281
70	D-AMS 034972	*Sphagnum* stems and leaves	1129	25	775-994	933
75	D-AMS 029939	*Sphagnum* stems and leaves	1016	31	979-1153	1022
80	D-AMS 034828	*Sphagnum* stems and leaves	1052	27	897-1032	1002
100	D-AMS 034973	Fine fraction of bulk peat	1514	27	400-638	569
135	D-AMS 029940	*Racomitrium lanuginosum* stems and leaves	1729	33	247-408	334

SCP concentrations in the core (Figure 3.7) were relatively low compared to other studies within the United Kingdom (e.g., Rose and Appleby, 2005), probably due to the predominantly westerly winds blowing relatively clean air from the Irish and Atlantic seas. The SCP profile is bimodal, with peaks at 13 and 20 cm. Such a double peak has been identified in previous SCP profiles from Cors Fochno and nearby sites (Rose *et al.,* 1995; Schulz, 2005). The upper profile is consistent with typical SCP profiles for Britain and Northern Ireland (Rose *et al.,* 1995), with the sharp decline above 10 cm reflecting the success of air pollution legislation in the last decades of the 20th century. The age distribution of a calibrated radiocarbon date of 1922–1690 CE at 29 cm makes it difficult to ascertain whether the SCPs within the deeper part of the profile were deposited *in situ* or relate to downward mobility of SCPs resulting from water table fluctuations. Because of this, only a single date could be tentatively ascribed: 1976 ± 3 for the subsurface peak at 13 cm based upon comparison of SCP profiles from Lakes in north and central Wales with corresponding ^{210}Pb age-depth profiles (Rose and Appleby, 2005).

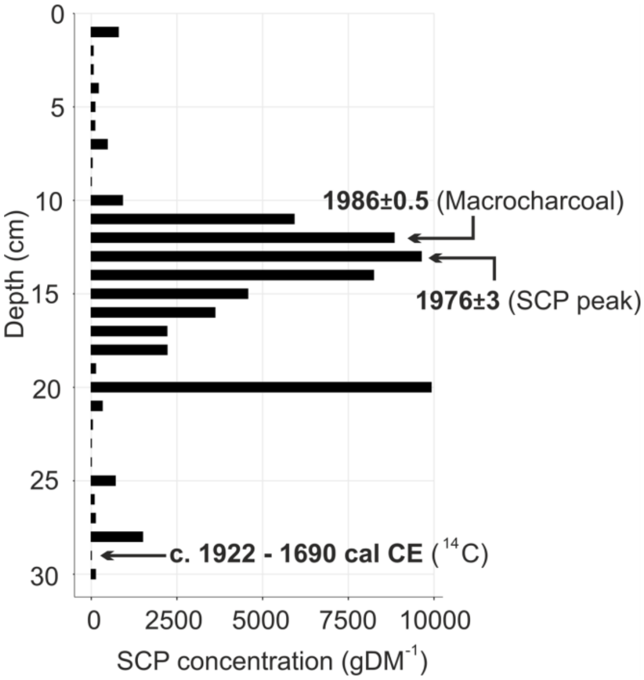

Figure 3.7. Spheroidal carbonaceous particle (SCP) concentration (gDM^{-1}) profile for Cors Fochno core (BO17). The radiocarbon date given for 29 cm is the calibrated date for the sample. At 12 cm, a macrocharcoal layer containing >10 mm fragments of charred peatland vegetation is considered to reflect the position within the core relating to the 1986 fire (see Figure 3.9).

The age-depth model for BO17 (Figure 3.8) has a mean 95% confidence range of 185 years and a maximum range of 287 years between 35 and 65 cm. All dates used overlap with the model, producing a relatively linear trend as is commonly observed in peat (Belyea and Clymo, 2001). A maximum sampling depth of 100 cm was chosen for all palaeoecological analyses based on the age-depth model, capturing the past c. 1000 years within the mean 95% CI of the model while providing sufficient prior environmental context.

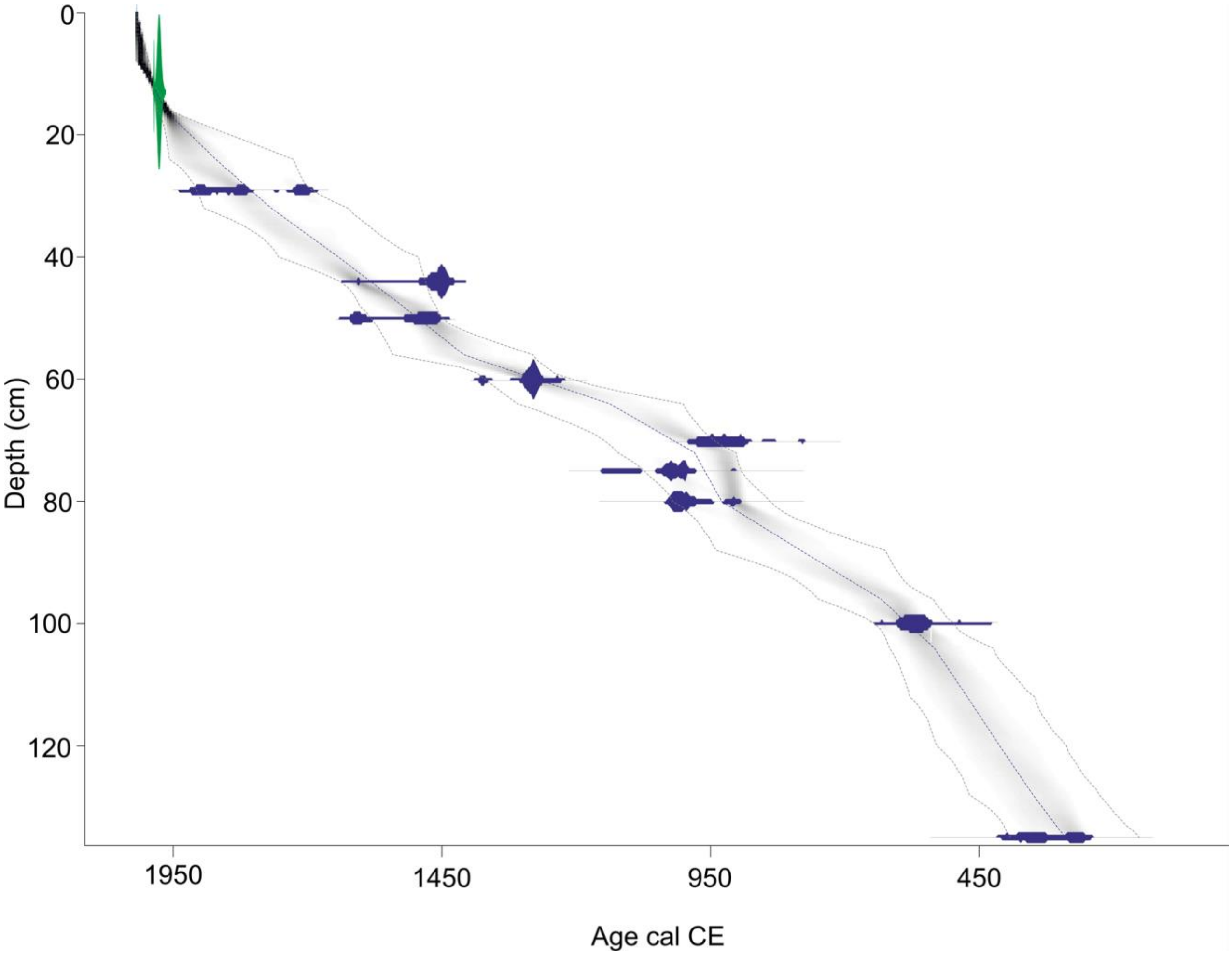

Figure 3.8. Age depth model for core BO17, based on integrated radiocarbon, macrocharcoal and spheroidal carbonaceous particles (SCPs). The model was generated using rBacon (Blaauw *et al.,* 2021b; Blaauw and Christen, 2011, 2013). Probability distribution functions (PDFs) for ^{14}C dates are shown in blue, and PDFs for calendar dates (SCPs and macrocharcoal) are shown in green. Black shading denotes interpolated age distributions for all depths. 95% confidence intervals are denoted by dashed lines. Plots for model performance are presented in Supplementary Figure 1.8.

3.4.6. Plant macrofossils

Sphagnum is the principal plant macrofossil, accounting for 31.6 ± 17.6 % of peat components (Figure 3.9). Other abundant components include monocotyledon radicells (22.0 ± 12.4 %), ericaceous rootlets (21.1 ± 12.4 %) and unidentified organic matter (20.8 ± 13.8 %). Above-ground remains (e.g., identifiable leaves, stems, and flowers) of vascular plants are poorly represented. Nine phases of significant vegetation development were identified. Large quantities of UOM below the depth of the acrotelm may indicate that beneath this depth, more readily decomposed species were present that are no longer represented in the plant macrofossil record. Therefore, plant community composition below this depth may be biased towards species possessing remains that are resilient to decay.

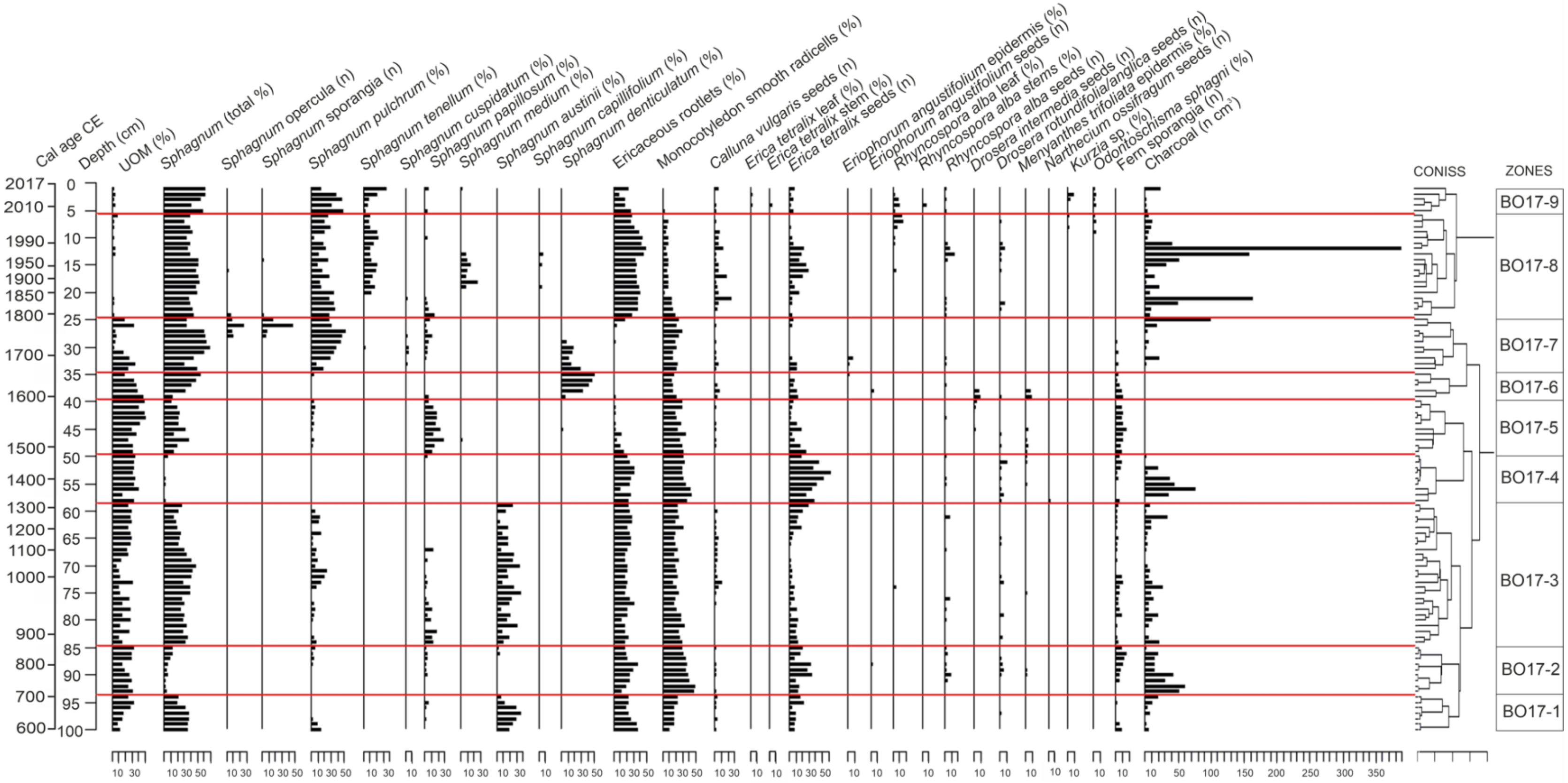

Figure 3.9. Plant macrofossil diagram for core BO17. CONISS illustrates the hierarchical clustering upon which the diagram zonation is based, red horizontal lines indicate zone boundaries. A broken stick model was used to determine the number of significant zones (Bennett, 1996). Peat components accounting for less than 5% of the overall percentage abundance and seeds with count numbers less than five in all levels are omitted although these data are included in all other analyses.

3.4.7. Testate amoebae

The stratigraphic profile of core BO17 is mainly characterized by the species *Amphitrema wrightianum*, *Archerella flavum*, *Arcella discoides* and *Phryganella arcopodia*. These are indicators of wet conditions (Charman *et al.,* 2000) and occur throughout the profile. Dry periods are indicated by abundant *Difflugia pulex* and *Cryptodifflugia oviformis* types. The former typically prefers slightly wetter to intermediate conditions (e.g., Charman *et al.,* 2007), although these are rare in modern samples and thus have poorly constrained optima (Swindles, *et al.,* 2015). The latter prefers deeper water tables (Amesbury *et al.,* 2012; Lamentowicz and Mitchell, 2005). The relative abundance of testate amoebae throughout the stratigraphy of core BO17 is provided in Supplementary Figure 1.7. The water table reconstruction for core BO17 is shown in Figure 3.10. The reconstruction indicates that water tables gradually increased from c. 600 to c. 1800 CE, with a slight period of increasing WTD between c. 1000 and 1300 CE. Mean values were above the peat surface from c. 1550 to 1750, suggesting the coring location underwent an aquatic phase at this time. This is followed by a significant increase in water table depths from c. 1800 to 1970 CE, where the highest depths are attained, until water tables abruptly increase to their prior levels until the end of the profile.

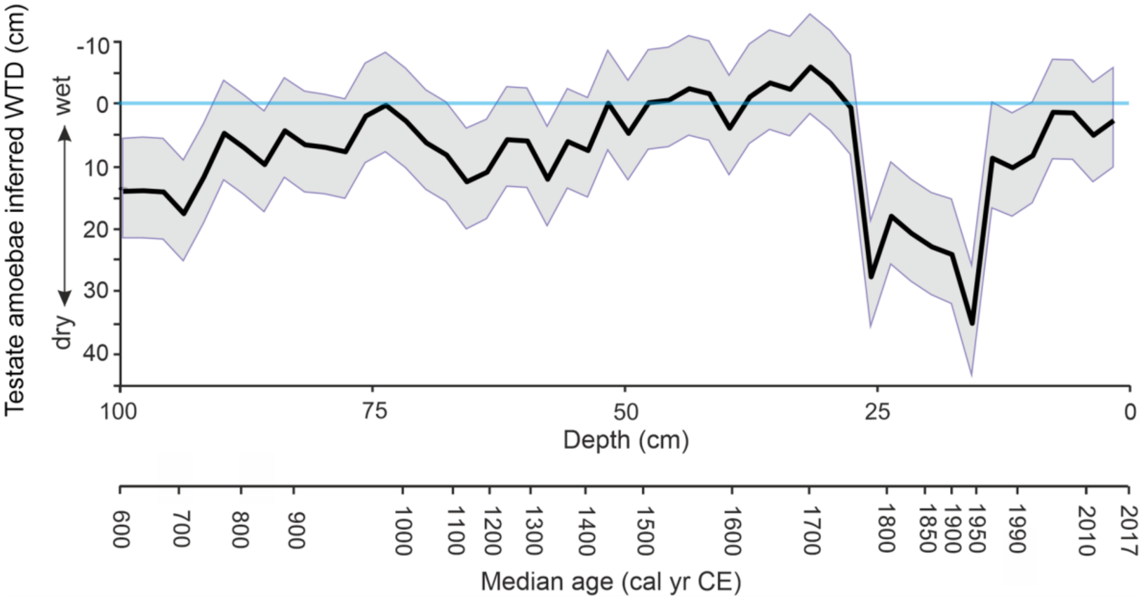

Figure 3.10. Testate amoebae inferred water table depth reconstruction generated using the pan-European training set developed by Amesbury *et al*. (2016). Age is given as the median age probability. Shaded areas denote sample-specific errors, based on 1000 bootstrapping cycles. WTD: water table depth

3.4.8. Comparing experimental vegetation composition and palaeoecological data

The methods used to quantify plant populations differ between the experimental (pin-touch and quadrat) and palaeoecological (leaf count) studies; both have limitations of their own (Birks, 2007; Goodall, 1952; Mauquoy and Yeloff, 2008) in addition to the sources of error when comparing between them. For example, certain taxa (e.g., *R. alba*) may have elevated counts from the pin-touch method due to their wide, tall, spreading shape and the density in which they can grow together (Heslehurst, 1971), whereas the representation of certain taxa in the palaeoecological record may be biased by taphonomic effects favouring more recalcitrant remains (e.g., *Sphagnum* leaves) over more labile remains (e.g., ericaceous woody remains) (Mauquoy and Yeloff, 2008). Even within *Sphagnum*, certain species are more robust than others (Bengtsson *et al.,* 2016) and are therefore likely to be preserved better and be more readily identified, falsely inflating their apparent abundance in palaeoecological records (Johnson and Damman, 1991). This may have the effect of reducing the visibility of certain plant types with high rates of biomass turnover, such as grasses, sedges, and woody shrubs (Greenwood and Donovan, 1991). Some *Sphagnum* species also lose their leaves more readily from their branches, and therefore contribute leaves to the palaeoecological record in differing quantities (Barber, 1981). These differences and limitations hinder our ability to make quantitative comparisons between palaeoecological and modern vegetation communities from peatlands. However, comparisons can still be made on a qualitative basis.

The result of the CMA analysis is presented in Figure 3.11. From the experimental communities, 237 samples counted as CMAs for 52 fossil samples using a Bray–Curtis (dis)similarity cut-off of 0.1106. These were only 1.8 % of the total number of comparisons made, indicating that the current vegetation composition in all the plots (control and treatments) is unlike nearly all the inferred plant communities in the bog over the last 1500 years. CMAs appear to relate to the abundance of the two most common functional groups within the modern data sets: sedges and *Sphagnum* sect. *sphagnum*, while showing little correspondence with periods of hydroclimatic change (Figure 3.11). Most of the CMAs were from control (77) and combined treatment communities (71), with warmed and droughted plots less likely to be CMAs (47 and 42 respectively). The dominant vegetation within the experimental plots is *S. pulchrum* and *R. alba*, members of these functional groups. Most (70.5 %) of the CMAs occurred within the top 28 cm of the core, between c. 1822 and 2012 cal CE. This period is dominated by ericaceous roots, *S. pulchrum* and *S. tenellum*. The depth with the most CMAs occurred at 26 cm, which matched with 36 experimental vegetation communities. This sampling interval represents c. 1840 cal CE and is characterized by high *Sphagnum* sect. Cuspidatum (50 %) and sedge abundance (35 %), with shrubs representing a further 11 % and *Sphagnum* sect. *Sphagnum* representing only 4 % of the total assemblage. Most of the CMAs for this depth were from control (14) and combined (13) plots.

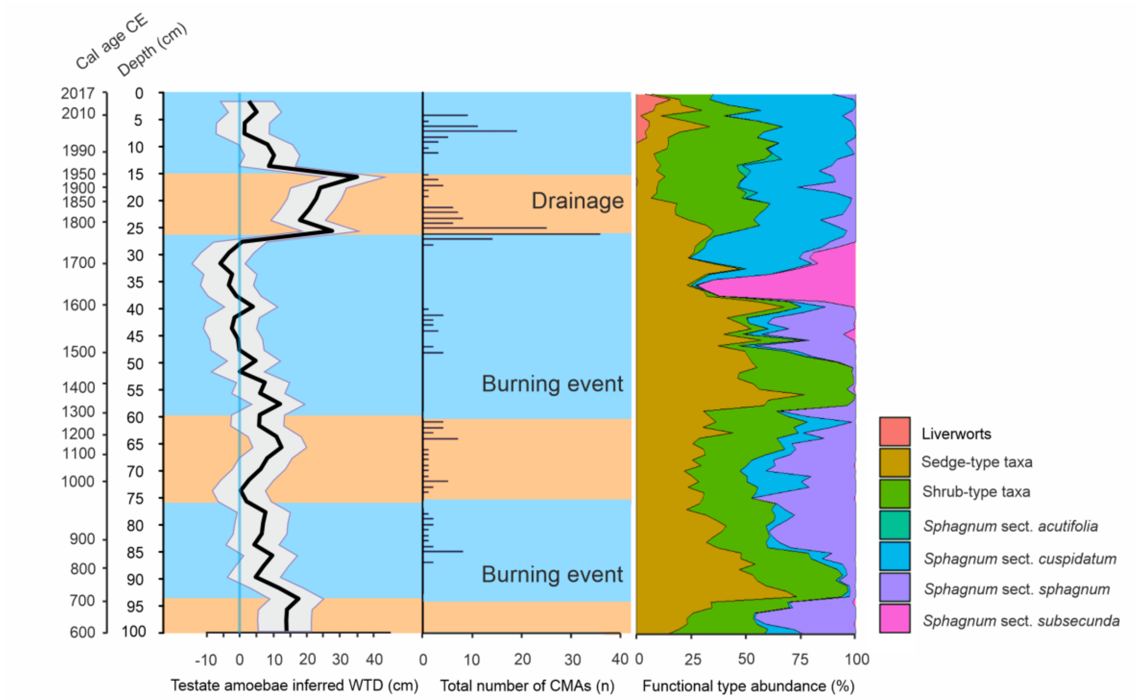

Figure 3.11. Relative changes in plant functional types and total number of close modern analogues of vegetation community composition (CMAs) for each sampling interval from core BO17. Horizontal coral-coloured bars denote periods of lower water table (drier/warmer periods), blue bars denote periods of higher water table (wetter/cooler periods), as inferred from the testate amoebae based palaeohydrological reconstruction. Age cal BP is given as the median age probability. WTD, water table depth.

Groupings of CMAs also occur between c. 815 and 940 cal CE, c. 975 and 1280 cal CE, c. 1510 and 1525 cal CE, and between c. 1570 and 1615 cal CE (Figure 3.11). Climatic conditions and species composition vary between these periods. Between c. 815 and

940 cal CE, the vegetation community composition composed predominantly of sedges (c. 40 %) and the formerly abundant *S. austinii* (c. 27 %), a species within the *Sphagnum* sect. *Sphagnum*. The period c. 970 to 1280 cal CE covers the timing of the MCA, where shrubs (31 %), sedges (30 %) and *Sphagnum* sect. *Sphagnum* (25%) type taxa dominated, mainly *S. austinii*. Groupings between c. 1510 and 1525 cal CE and between c. 1570 and 1615 cal CE occur during the LIA and are characterized by high abundances of sedge (50%) and *Sphagnum* sect. *Sphagnum* (30 %), the latter represented by *S. papillosum*.

3.5. Discussion

3.5.1. Effect of experimental warming and drought upon peatland vegetation

Ericaceous shrubs became more abundant in response to warming over 10 years. Increased ericaceous shrub cover is commonly reported with warming in climate manipulation experiments in peatlands. For example, Weltzin *et al*. (2003) reported a 50% increase in shrub cover in a bog mesocosm experiment following summer temperature increases between 1.6 and 4.1°C over five years, comparable to the temperature changes in this study. Buttler *et al.* (2015) conducted an *in-situ* climate warming experiment using OTCs on an ombrotrophic bog in the Jura mountains, finding that *Andromeda polifolia* increased over five years due to increased rooting depth. Malhotra *et al.* (2020) found similar results in an entire ecosystem manipulation experiment on a forested ombrotrophic bog in northern Minnesota. Increased soil temperatures expanded the below-ground growing season, increasing root density.

This finding has several implications for peatland ecosystem functions including the peatland carbon sink. Increased ericaceous shrub dominance due to warming may initially increase the rate of CO_2 sequestration due to their high productivity, although this may be offset by increased carbon respiration resulting from increased root exudates and a reduction in the quality of plant litter (Bell *et al.,* 2018; Fenner *et al.,* 2007; Ward *et al.,* 2013; Weltzin *et al.,* 2000). In addition, vascular plant expansion may affect local evapotranspiration rates, particularly where grasses increase in cover (Hirano *et al*., 2016). This can result in reduced soil moisture and peat aeration, (Admiral and Lafleur, 2007), allowing aerobic decomposition to occur. Other vegetation types, particularly *Sphagnum*, may be suppressed by shrubs due to shading and enhanced water use, increasing the depth to the water table (Norby *et al.,* 2019). Loss or decline in *Sphagnum* is an important indicator of the future direction of peatland functioning under climate change due to its importance as a peat-former and ecosystem engineer in many northern peatlands (van Breemen, 1995).

The relatively slow rate of change seen in *Calluna vulgaris* abundance in this experiment suggests that peatland vegetation changes to future warming will occur at a similar pace. However, it is possible that the presence of OTCs may have delayed the rates of vegetation change within the plots. OTCs can prevent new species from establishing and may shield the plants inside from pollination by wind and insects (Totland and Eide, 1999; Richardson *et al*., 2000).

No significant changes occurred for *Sphagnum* due to increases in air temperature of 0.3 – 0.7°C over ten years (Figure 3.3), which is in-line with low range UK temperature projections until c. 2070 (Lowe *et al.,* 2018). Weltzin *et al.* (2000, 2003) found no significant change in Sphagnum cover in bog mesocosms with increased summer soil temperatures of 1.6 – 4.1°C. Similarly, Walker *et al*. (2006) found that *Sphagnum* cover did not significantly change with 1 – 3°C of warming across multiple sites in Arctic regions. Some studies even suggest that modest warming may increase the production of certain *Sphagnum* species (Dorrepaal *et al.,* 2004; Robroek *et al.,* 2007). However, a critical temperature for *Sphagnum* decline appears to exist. Dieleman *et al.* (2015) found that *Sphagnum* from a poor (nutrient deficient) fen in Ontario, Canada declined significantly following temperature increases of 8°C in a mesocosm experiment. A transplantation study by Bragazza *et al*. (2016) of peat mesocosms from a Swiss ombrotrophic bog to a warmer location (+ 5°C) reduced the productivity of *S. fallax* by 60 %. Norby *et al.* (2019) found that *Sphagnum* productivity in an ombrotrophic bog in northern Minnesota initially increased with warming but declined at temperature increases above 5°C, declining by nearly 100 % with warming of 9°C.

The experiment therefore showed that the expected change in climate by the mid-century for this region does not reach the critical temperature threshold for *Sphagnum* decline over a 10-year period. However, it does not rule out a change in Sphagnum over the longer term, either in direct response to a sustained temperature/water table change, or indirectly through a community shift driven by the influx of shrubs. Projections for temperature increases in Northern Hemispheric regions by 2100 range from 2°C to above 8°C relative to 1850 – 1900 baselines, based on predictions by the IPCC (IPCC, 2021), with increased temperatures and faster rates of change projected for higher-latitude areas (Masson-Delmotte *et al.,* 2018; IPCC, 2021).

The negative effect of experimental warming to such a rapid and dramatic increase in temperature upon *Sphagnum* is commonly achieved using infrared heat lamps, which may scorch the *Sphagnum* and unrealistically increase soil drying (Harte and Shaw, 1995; Johnson *et al.,* 2013). Whether the effects of high temperatures on *Sphagnum* cover using infrared heat lamps should be considered realistic responses to warming or experimental artefacts depends on how rapidly we expect temperatures to increase in these regions. Sim *et al.* (2021) found that *Sphagnum* populations in permafrost peatlands demonstrated remarkable resilience to warming despite temperatures increasing two to three times faster than global averages (Masson-Delmotte *et al.,* 2018), supporting the notion that *Sphagnum* may be resilient to warming above this threshold in areas where rapid increases in temperature are projected to occur.

Our results suggest that increased drought frequency did not significantly influence peatland vegetation in our experimental site, at least over a 10-year period. This disagrees with the results of other water table drawdown experiments (e.g., Bragazza *et al.,* 2013; Murphy *et al.,* 2009; Strack *et al.,* 2006). However, our study differs from previous studies since we simulate repeated episodes of temporary seasonal drought, rather than inducing a permanent step-change in the water table.

Despite being an abundant species across most of the central portion of the site, no significant changes occurred in *Rhynchospora alba* abundance following ten years of experimental warming and increased drought frequency. In Cors Fochno, where water-tables are generally close to the surface, the high abundance of *R. alba* indicates that the site may emit substantial quantities of CH_4 into the atmosphere (Strack, 2006). However, while *R. alba* is a common species in the central dome area of Cors Fochno, its relative abundance may have been overestimated in the experimental study due to increased detection by the pin-touch method.

3.5.2. Vegetation changes in the palaeoecological record

Vegetation and inferred water tables were stable for much of the palaeo-vegetation record of Cors Fochno. For example, between c. 850 and 1300 cal CE, during the warmer MCA, there were few changes in vegetation community composition, and only slight changes in hydrology towards drier conditions (Figure 3.11). The stability of peatland flora and hydrology during the MCA is typical of many peatland palaeoecological studies (e.g., Magnan *et al.,* 2019). Plant communities and their functional diversity often exhibit remarkable stability due to several autogenic feedback mechanisms that result in a degree of homeostasis in peatland hydrology (Belyea, 2009). These have moderated peatland responses to past changes in climate (Churchill *et al.,* 2015; Dise, 2009; Swindles *et al.,* 2012). Peatland feedback mechanisms are known to operate over a range of timescales (Belyea, 2009), and it may be that peatland vegetation is resilient to short-term changes in water table but may rapidly shift to a new composition in response to long-term shifts.

This stability in the Cors Fochno palaeo-vegetation record is punctuated by relatively abrupt changes in vegetation which occur without obvious changes in water table depth. These seem to occur either because of anthropogenic disturbances (burning) or may be mediated by hydroclimatic changes, reflecting interspecific competition between *Sphagnum* and other plant species in response to long-term, gradual changes in water table depth (Robroek *et al.,* 2007). For example, between c. 1300 and 1500 CE, *Sphagnum austinii* disappears and *E. tetralix* reach a peak following a burning event at c. 1400 CE. Peatlands are known to undergo changes in plant community composition following wildfire (Guêné-Nanchen *et al*., 2022). Controlled burns on peatlands may have a lasting negative effect upon *Sphagnum* cover (Noble *et al*., 2018), while large, uncontrolled fires can remove *Sphagnum* entirely (Maltby *et al.,* 1990). It can take between 10 to 40 years for *Sphagnum* to re-establish following wildfire (Kuhry, 1994; Clarke *et al*., 2015). In the immediate aftermath of a fire, pioneer species (typically sedges) rapidly colonise the burnt areas (Bret-Harte *et al*., 2013). In a palaeoecological study of a UK upland blanket peatland, the disappearance of *Sphagnum* and its replacement by *Calluna vulgaris* occurred following a fire event (Blundell and Holden, 2015). It appears that similar processes occurred following wildfire events at Cors Fochno, with *Sphagnum austinii* being replaced by *Erica tetralix* twice throughout the 1500-year record.

Sphagnum austinii was a formerly common and important peat-forming species in Europe until its pronounced decline in the past 2000 years (Swindles, *et al.,* 2015). Many environmental and anthropogenic causes for this decline have been suggested (Swindles, Turner, *et al.,* 2015). In core BO17, it is virtually absent by c. 1300 CE, later than the formerly established date of its extinction from this site of 1100 cal CE by Hughes and Schulz (2001). While it is beyond the scope of this paper to identify the cause of the *S. austinii* extinction, its timing in the core following a fire event suggests possible anthropogenic influence.

During the c. 1200-year period between the start of the record until c. 1800 CE, water table depth is relatively stable, exhibiting a general monotonic trend towards wetter conditions. A sudden shift towards more aquatic vegetation occurred around c. 1500 CE and lasted until c. 1800 CE. This shift is an indicative of the development of a bog pool, reflected in the palaeo-hydrology of the site, where average reconstructed water tables rise above the peatland surface (Figure 3.10). Other studies also document dramatic shifts in vegetation following the onset of the LIA (Magnan *et al.,* 2019; Mauquoy *et al.,* 2002). The correspondence of this shift with increasingly wet, cool conditions suggests it was climatically mediated, with thresholds for compositional change defined by the position of the water table. These changes in water table depth agree with several studies which often show generally wetter conditions in Britain during the MCA and drier conditions during the LIA (Charman and Hendon, 2000; Lamb, 1965; Turner *et al.,* 2014), although other records disagree, likely due to a lack of spatial coherence between proxy precipitation records across Britain (Proctor *et al.,* 2000).

3.5.3. Comparing past and future vegetation responses to climate change

This study demonstrates that ericaceous shrubs increased in abundance with warming in both experimental and palaeoecological studies from the same site. This correspondence suggests that where ericaceous cover has increased in response to warming in peatlands in the past, it may continue to do so with future climate change. The lack of a significant effect of increased drought in our experimental study can neither be supported nor be refuted by the palaeo record because the experimental droughts simulate short, episodic water table drawdown, rather than prolonged periods of water table drawdown as are recorded by the long-term palaeo record (e.g., between c. 1800 and 1970 CE). We see that during that time there is a shift in vegetation, with bog pool vegetation (particularly *S. denticulatum*) making way for more terrestrial species, including hummock-forming *Sphagnum* species such as *S. medium* and *S. capillifolium*. During this time, ericaceous rootlets increase after having previously declined during the very wet preceding conditions. This event corresponds to a period of intensive drainage at Cors Fochno (Poucher, 2009). The palaeo record suggests that water tables returned to pre-drainage levels by c. 1970 CE, likely in response to drainage blocking and peatland restoration taking place around this time (Poucher, 2009). No large changes in peatland vegetation occurred following this restoration (Figures 3.8 and 3.10). These findings suggest that while sustained water table drawdown may have a dramatic effect upon vegetation communities, increased hydrological droughts at the frequency, magnitude and timescale imparted by our study (four × 4-week simulated droughts over 10 years) are unlikely to result in significant changes in vegetation, although we cannot be sure that this will remain the case over longer timescales. Manipulation experiments are unlikely to capture changes resulting from slow, long-term changes in climate which can be seen in the palaeo record. Conversely, the palaeo record may not be sufficiently fine-scaled to identify annual to decadal-scale changes in vegetation that may respond more to temperature change than to water table fluctuations.

Sedge-type taxa were present throughout the past c. 1500 years at Cors Fochno. Although their above-ground remains are poorly preserved, the seeds of *R. alba* occur regularly throughout the peat profile, along with abundant monocot radicells. The abundance of these remains fell during apparent warmer or drier periods, possibly in response to long-term increases in water table depth (figure 3.11). This suggests that sedge abundance may decrease on Cors Fochno, should future projected warming result in a lowering of the water table at the site. This agrees with the results of some studies where higher water tables facilitated sedge expansion into peatlands (Churchill *et al.*, 2015; Olefeldt *et al*., 2017) Despite this, how sedges will respond to climate warming remains unclear. Some studies suggest that sedge abundance is unaffected by climate change (e.g., Dieleman *et al*., 2015), while other show that fluctuations in water table depth can reduce their abundance in ombrotrophic peatlands (Strack *et al.,* 2006; Breeuwer *et al*., 2009). In other cases, sedge abundance increased with drying, at the expense of *Sphagnum* (Weltzin *et al*., 2003; Dieleman *et al*., 2015; Łucow *et al*., 2017). Sedge abundance may also increase in peatlands as a result of future increases in nitrogen deposition (Berendse *et al*., 2001).

Increased sedge abundance may alter carbon cycling in peatlands, with sedges exhibiting rapid biomass turnover and priming decomposition by supplying root exudates and oxygen to deeper peat (Breeuwer *et al*., 2009; Armstrong *et al*., 2012; Zeh *et al.,* 2019). Additionally, sedges provide a conduit for CH_4 to travel from the sub-peat, bypassing methanotrophs in the oxic layer and increasing net CH_4 emissions (Strack *et al*., 2006). The effects of sedge abundance upon CH_4 emissions relates to the height of the water table, with wetter conditions facilitating greater release with sedges present, while under drier conditions sedges appear to ameliorate CH_4 emissions (Strack *et al*., 2006). The effects of sedges upon greenhouse gas fluxes are more pronounced in fens than bogs (Weltzin *et al.,* 2000).

We find that the current vegetation composition of Cors Fochno, including the species within the experimental plots, has few analogues in the palaeo record as far back as 600 CE. We find most CMAs are from control or combined treatments, rather than warmed or droughted plots. This suggests that these treatments produce fewer analogues since periods of warming typically coincide with periods of drying. Most close analogues occur near the top of the profile, following the development of the modern-day vegetation community in the central dome of the site, around c. 1800 CE (Poucher, 2009). This is contemporaneous with a period of enhanced human activity and peatland drainage, as indicated by the macrocharcoal and palaeohydrological reconstructions (Figures 3.8 and 3.9). This suggests that changes in the modern-day plant communities are a consequence of human activity during recent centuries.

The later development of the modern-day vegetation community is likely to have resulted in a change in carbon sequestration, with the dominant *S. pulchrum* being a member of the subgenera *Sphagnum* sect. *Cuspidatum* that produces more readily decomposed litter, meaning more carbon is lost to the atmosphere by decay (as CO_2) then is retained in the soil (Bengtsson *et al.,* 2016); however, the waterlogged lawn environments that this species occupies delays their decomposition. *Sphagnum* sect. *Sphagnum* type species (e.g., *S. austinii*) have similar productivity rates but are less prone to decomposition and, like *S. pulchrum*, used to occupy lawns (Bengtsson *et al.,* 2016; Mauquoy and van Geel, 2007). Therefore, this change in dominant species is likely to have resulted in a net decline in carbon sequestration rates.

The intensification of anthropogenic impacts on peatlands over the past c. 300 years may have driven threshold shifts in plant communities (Swindles *et al.,* 2019). Even where apparently pristine conditions have been maintained or restored, peatlands may still be affected by climate change, past disturbance, or atmospheric pollution (e.g., Berendse *et al.,* 2001; Swindles *et al.,* 2016; Talbot *et al.,* 2014). In palaeoecological studies, anthropogenic effects are the dominant drivers of many palaeoecological proxies (Gauthier *et al.,* 2019; Turner *et al.,* 2014). Differences in the relative importance of the drivers of vegetation change over time represents an important distinction between the results of palaeoecological and experimental studies. Whereas temperature is frequently identified as the dominant driver of change in experiments (Breeuwer *et al.,* 2008; Dieleman *et al.,* 2015; Heijmans *et al.,* 2013; Weltzin *et al.,* 2000), in palaeoecological studies, hydrological conditions are often of greater importance (Charman *et al.,* 2009). This suggests that the importance of the main drivers of vegetation change differ between short (sub decadal) and long (multidecadal to millennial) timescales, although this may also be a consequence of the low-temperature sensitivity of peatland palaeo records (Payne, 2014). This study supports the notion that peatlands are less resistant to direct anthropogenic disturbances such as burning or drainage than they are to climate change. This agrees with Swindles *et al.* (2016) who found that multiple anthropogenic disturbances at Swarth Moor over 50 years overcame the site's capacity to resist vegetation succession.

Approximately 15 % of the world's peatlands are in a state of degradation (Joosten *et al.,* 2012) and many of Europe's peatlands have undergone substantial drying throughout the past c. 300 years on account of human activity (Swindles *et al.,* 2019). Species turnover and functional diversity affect peatland ecosystem service provision (Dieleman *et al.,* 2015; Ward *et al.,* 2009), and these are, in turn, impacted by anthropogenic disturbance (Gatis *et al.,* 2016). Atmospheric deposition of sulphuric and nitric acid has been shown to have negatively affected *Sphagnum* as well as other bryophytes in UK peatlands, in some cases causing localised extinctions (Ferguson *et al.,* 1978; Gorham *et al*., 1984; Hogg *et al*., 1995). The combined effects of anthropogenic climate change, drainage, burning and environmental pollution may result in the development of novel vegetation communities (Alexander *et al.,* 2015; Ordonez *et al.,* 2016). Woody plant encroachment and the establishment of generalists and exotic species has been related to the effects of climate change (Gunnarsson *et al.,* 2004; Pellerin and Lavoie, 2003). In some cases, peatlands that have experienced significant levels of disturbance have remained resilient to changes in climate. Despite initial changes in ecosystem functioning and vegetation following drainage, degraded peatlands are often able to recover to their previous condition (Swindles *et al*., 2016; Łuców *et al.,* 2020), although this recovery can be slow (Page and Baird, 2016).

The degree of disturbance and atmospheric deposition of anthropogenic pollutants varies regionally and latitudinally. For example, the deposition of anthropogenic pollutants is more pronounced in temperate regions than in the northernmost latitudes, reflected by the decreasing bioaccumulation gradients of pollutants from south to north across the Northern Hemisphere (Pakarinen and Tolonen, 1976; Ross, 1987; Galloway *et* *al*., 2004). However, permafrost thaw and increasing rates of atmospheric deposition may still lead to increased nitrogen availability in these regions (Galloway *et al*., 2004; Keuper *et al*., 2012) encouraging the encroachment of vascular plants at the expense of *Sphagnum* (Berendse *et al*., 2001; Sim *et al*., 2021). Historically, peatland degradation in the Northern Hemisphere has mostly occurred in Europe and North America (Xu *et al*., 2019), however peatlands are susceptible to a range of anthropogenic disturbances (e.g., burning and wildfire, peat extraction, oil sands mining, conversion to agriculture or forestry) (Turetsky *et al*., 2002).

It is important to note that the results of this study are based upon the analysis of a single core. The climatic sensitivity of different coring locations within a site can vary depending upon differences in the climatic sensitivity of different macroforms (Loisel and Garneau 2010). The spatial distribution of microforms vary in space and time, depending upon differences in the availability of moisture, nutrients, and light, as well as interactions with nearby vegetation within sites (Andersen *et al.,* 2011). As a result of the microscale variability of peatland surface cover, different cores from within the same site, even those taken a short distance from one another, may exhibit differing patterns of vegetation change over time (Charman *et al*., 1999). While studies have shown that adjacent cores can exhibit broadly similar patterns of past vegetation (e.g., Chiverrell *et al*., 2001) substantial differences may occur (e.g., Mauquoy *et al*., 2002). Therefore, while not invalidating the results of this study, these findings should not be considered as representative of past changes in vegetation across the site as a whole.

Similarly, while the vegetation community composition within the experimental plots was characteristic of the plant community composition that characterises the central raised dome, which represents approximately one-third of the site, a further two-thirds are dominated by *Molinia caerulea*, *Phragmites* and *Juncus* s (Poucher, 2009; CCW, 2011). The presence of these species suggests that these areas receive more groundwater influence and nutrients than the experimental site and have also been subjected to a greater degree of disturbances such as drainage and peat cutting (Hughes *et al*., 2007; Poucher, 2009; Swindles *et al*., 2016). Such areas are likely to be less resilient to the effects of climate change (Page and Baird, 2016; Swindles *et al*., 2016) and are also likely to show greater rates of carbon loss than the central dome, owing to increased erosion, decomposition, and differences in vegetation cover as a result of disturbance (Frolking *et al*., 2011; Aslan-Sungur *et al.,* 2019; Burdun *et al*., 2021). While this study was focused on the response of relatively intact ombrotrophic peatlands to future changes in climate, it does not consider how degraded areas will respond (Leifeld and Menichetti, 2018).

Changes in vegetation are likely to impact ecosystem functions (Hájek, 2009; Johnson and Damman, 1991; Swindles *et al.,* 2019). Consequently, past peatland responses to climate changes may differ from future responses and may not be accurately represented within the palaeo record. It is for this reason that we recommend long-term experimental climate manipulation studies continue, since these can provide clues as to the direction of future changes under post-disturbance baselines. Palaeoecological records may still provide an important source of information on how peatlands have responded to climate change under pre-disturbance conditions, improving our understanding by documenting responses to environmental and climatic changes beyond those that can be obtained from experimental studies alone (Graumlich, 2002).

They are also useful, as in the case of this study, for contextualizing experimental studies against the long-term history of a site, elucidating past vegetational changes and disturbances. It is also important to acknowledge that some sites, such as those in the highest latitudes, exhibit near pristine conditions, therefore palaeoecological studies from these sites may remain useful sources of information for future peatland climate responses.

3.6. Conclusions

Our study compares the peatland vegetation response to a 10-year climate manipulation experiment with those inferred over the last 1500 years from the palaeo record in response to climate and habitat change. The results of our experimental study showed that warming increased the abundance of shrub-type vegetation over 10 years, a result supported by most warming experiments in peatland ecosystems. This result is corroborated by increases in *C. vulgaris* seeds during apparently warmer periods in the long-term vegetation record, supporting the likelihood of increased shrub dominance in peatlands with warming. We see no evidence for a significant change in *Sphagnum*, likely since the c. 0.5°C warming imparted by this study, in line with changes expected over the next 70 years for the United Kingdom, does not appear to exceed a critical threshold for *Sphagnum* decline. An increase in ericaceous shrub dominance may result in changes in the carbon balance of peatlands, potentially resulting in increased carbon losses due to enhanced root exudates and a reduction in litter quality. The persistence of *Sphagnum*, at least over the short term, may ameliorate this change. However, we cannot rule out that *Sphagnum* may eventually decline in response to either sustained warming as is projected to occur in the northernmost latitudes, or due to ecological changes, particularly increases in shrub cover.

Vegetation community composition in ombrotrophic bogs is resilient to increases in short-term episodic droughts at the severity imparted by our manipulations (four additional 4-week droughts over a 10-year period). The long-term palaeoecological record does not record individual drought events but rather periods of long-term water table drawdown, therefore this result could not be corroborated by the palaeoecological record. The results of the experimental study suggest that the predicted increase in short-term episodic droughts may not compound the effects of warming upon peatland vegetation in the near future. Our palaeoecological study, on the other hand, suggests vegetation composition may change in response to long-term sustained water table drawdown, which agrees with experimental studies that replicate such a scenario.

Based on this study, we suggest that studying the response of modern peatlands to climate change, either through experiments, resurveys, or through targeted gradient studies, provides the best way to predict peatland responses to climate change over the next few decades or more. Since all such studies benefit from understanding the long-term environmental and disturbance context of a site, peatland palaeoecological studies are still highly valuable in our understanding of peatland ecosystem dynamics. To better predict future climate change responses, long-term studies have the capacity to identify the long-term drivers of changes in vegetation, possibly allowing for the identification of tipping points that drive the large magnitude changes in vegetation communities frequently observed in palaeoecological studies. Responses in vegetation community composition to climate change inferred from the peatland palaeoecological record may be unreliable as an analogue for future change because many peatlands, even seemingly ‘pristine’ ones, have been influenced by anthropogenic drivers such as drainage or air pollution. Such anthropogenic impacts have become stronger drivers of change in peatland plant community composition than climate, and peatland autogenic feedbacks do not confer the same level of resistance to these impacts. It is important to stress, however, that the findings of this study are based upon the results of a single experimental site and a single core within a relatively undisturbed area of original surface peatland, and therefore may not be representative of changes over the site as a whole, or of global peatlands more generally.

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Conflict of interest

The authors declare no conflict of interest.

3.8. References

Admiral, S. W., & Lafleur, P. M. (2007). Partitioning of latent heat flux at a northern peatland. *Aquatic Botany, 86*(2), 107-116.

Alexander, J. M., Diez, J. M., and Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525(7570), 515– 518.

Andersen, R., Poulin, M., Borcard, D., Laiho, R., Laine, J., Vasander, H., & Tuittila, E. T. (2011). Environmental control and spatial structures in peatland vegetation. *Journal of Vegetation Science*, 22(5), 878-890.

Amesbury, M. J., Barber, K. E., and Hughes, P. D. M. (2012). The relationship of fine-resolution, multi-proxy palaeoclimate records to meteorological data at Fågelmossen, Värmland, Sweden and the implications for the debate on climate drivers of the peat-based record. *Quaternary International*, 268, 77– 86.

Amesbury, M. J., Swindles, G. T., Bobrov, A., Charman, D. J., Holden, J., Lamentowicz, M., Mallon, G., Mazei, Y., Mitchell, E. A. D., Payne, R. J., Roland, T. P., Turner, T. E., and Warner, B. G. (2016). Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. *Quaternary Science Reviews*, 152, 132– 151.

Arft, A. M., Walker, M. D., Gurevitch, J. E. T. A., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., and Hollister, R. D. (1999). Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, 69(4), 491– 511.

Armstrong, A., Holden, J., Luxton, K., & Quinton, J. N. (2012). Multi-scale relationship between peatland vegetation type and dissolved organic carbon concentration. *Ecological Engineering*, 47, 182-188.

Aronson, E. L., and McNulty, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149(11), 1791– 1799.

Aslan-Sungur, G., VanLoocke, A., Moore, C., Bernacchi, C., & Ferin, K. (2019). Process-based Models as a Gap Filling Method for Eddy Covariance Measurements of Net Ecosystem CO 2 Exchange: A Case Study for the Perennial Grass Miscanthus. In *AGU Fall Meeting Abstracts* (Vol. 2019, B41K-2499).Barber, K. E. (1981). *Peat stratigraphy and climatic change: A palaeoecological test of the theory of cyclic peat bog regeneration*. Balkema, 219

Barber, K. E. (1993). Peatlands as scientific archives of past biodiversity. *Biodiversity and Conservation*, 2(5), 474– 489.

Barber, K. E., Chambers, F. M., Maddy, D., Stoneman, R., and Brew, J. S. (1994). A sensitive high-resolution record of late Holocene climatic change from a raised bog in northern England. *The Holocene*, 4(2), 198– 205.

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1– 48.

Bell, M. C., Ritson, J. P., Verhoef, A., Brazier, R. E., Templeton, M. R., Graham, N. J., Freeman, C., and Clark, J. M. (2018). Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma*, 331, 29– 37.

Belyea, L. R. (2009). Nonlinear dynamics of peatlands and potential feedbacks on the climate system. In: A. J. Baird, L. R. Belyea, X. Comas, A. S. Reeve, and L. D.

Slater (Eds.), *Carbon cycling in Northern Peatlands* (Vol. 184, 5– 18). American Geophysical Union.

Belyea, L. R., and Clymo, R. S. (2001). Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1473), 1315– 1321

Bengtsson, F., Granath, G., and Rydin, H. (2016). Photosynthesis, growth, and decay traits in *Sphagnum*—A multispecies comparison. *Ecology and Evolution*, 6(10), 3325– 3341

Bennett, K. D. (1996). Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132(1), 155– 170.

Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., Lee, J. A., Mitchell, E., Saarinen, T., Vasander, H., and Wallén, B. (2001). Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Global Change Biology*, 7(5), 591– 598.

Birks, H. H. (2007). Plant macrofossil introduction. *Encyclopedia of Quaternary Science*, 3, 2266– 2288.

Birks, H. J. B. (2014). Challenges in the presentation and analysis of plant-macrofossil stratigraphical data. *Vegetation History and Archaeobotany*, 23(3), 309– 330.

Blaauw, M., Heuvelink, G. B., Mauquoy, D., van der Plicht, J., & van Geel, B. (2003). A numerical approach to 14C wiggle-match dating of organic deposits: best fits and confidence intervals. *Quaternary Science Reviews, 22*(14), 1485-1500.

Blaauw, M. J., Christen, A., and Aquino-López, M. A. (2021a). *rplum: Bayesian age-depth modelling of cores dated by Pb-210. R package version 0.2.1*.

Blaauw, M. J., Christen, A., and Aquino-López, M. A. (2021b). *rbacon: Age-depth modelling using Bayesian statistics. R package version 2.5.5*.

Blaauw, M., and Christen, J. A. (2011). Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis*, 6(3), 457– 474.

Blaauw, M., and Christen, J. A. (2013). *Bacon manual v2. 3.3*. Queens University Belfast.

Blodau, C. (2002). Carbon cycling in peatlands a review of processes and controls. *Environmental Reviews*, 10(2), 111– 134.

Blundell, A., & Holden, J. (2015). Using palaeoecology to support blanket peatland management. *Ecological Indicators*, 49, 110-120.

Booth, R. K. (2008). Testate amoebae as proxies for mean annual water table depth in Sphagnum-dominated peatlands of North America. *Journal of Quaternary Science,* 23(1), 43– 57.

Bradley, R. S., and Jonest, P. D. (1993). 'Little Ice Age' summer temperature variations: their nature and relevance to recent global warming trends. *The Holocene*, 3(4), 367– 376.

Bragazza, L., Buttler, A., Robroek, B. J., Albrecht, R., Zaccone, C., Jassey, V. E., and Signarbieux, C. (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, 22(12), 4114– 4123.

Bragazza, L., Parisod, J., Buttler, A., and Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, 3(3), 273– 277.

Bray, J. R., and Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4), 325– 349.

Breeuwer, A., Heijmans, M. M., Robroek, B. J., and Berendse, F. (2008). The effect of temperature on growth and competition between *Sphagnum* species. *Oecologia*, 156(1), 155– 167.

Breeuwer, A., Robroek, B. J., Limpens, J., Heijmans, M. M., Schouten, M. G., & Berendse, F. (2009). Decreased summer water table depth affects peatland vegetation. *Basic and Applied Ecology, 10*(4), 330-339.

Bret-Harte, M.S., Mack, M.C., Shaver, G.R., Huebner, D.C., Johnston, M., Mojica, C.A., Pizano, C. and Reiskind, J.A., (2013). The response of Arctic vegetation and soils following an unusually severe tundra fire. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 368(1624), p.20120490.

Bridgham, S. D., Pastor, J., McClaugherty, C. A., and Richardson, C. J. (1995). Nutrient-use efficiency: A litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. *The American Naturalist*, 145(1), 1– 21.

Broecker, W. S. (2001). Was the medieval warm period global? *Science*, 291(5508), 1497– 1499.

Burdun, I., Kull, A., Maddison, M., Veber, G., Karasov, O., Sagris, V., & Mander, Ü. (2021). Remotely sensed land surface temperature can be used to estimate ecosystem respiration in intact and disturbed northern peatlands. *Journal of Geophysical Research: Biogeosciences*, 126(11), e2021JG006411.

Buttler, A., Robroek, B. J., Laggoun-Défarge, F., Jassey, V. E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E. A., and Bragazza, L. (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science*, 26(5), 964– 974.

Cappers, R. T. J., Bekker, R. M., and Jans, J. E. A. (2006). *Digitale zadenatlas van Nederlands. Groningen archaeological studies 4*. Barkhuis Publishing.

CCW. (2011). *Cors Fochno SAC management plan: Countryside Council for Wales core management plan, version 18*. Countryside Council for Wales.

Chambers, F. M., and Charman, D. J. (2004). Holocene environmental change: Contributions from the peatland archive. *The Holocene*, 14(1), 1– 6.

Chambers, F. M., Mauquoy, D., and Todd, P. A. (1999). Recent rise to dominance of *Molinia caerulea* in environmentally sensitive areas: New perspectives from palaeoecological data. *Journal of Applied Ecology*, 36(5), 719– 733.

Charman, D. J., Hendon, D., & Packman, S. (1999). Multiproxy surface wetness records from replicate cores on an ombrotrophic mire: implications for Holocene palaeoclimate records. *Journal of Quaternary Science: Published for the Quaternary Research Association, 14*(5), 451-463.

Charman, D. J., Barber, K. E., Blaauw, M., Langdon, P. G., Mauquoy, D., Daley, T. J., Hughes, P. D. M., and Karofeld, E. (2009). Climate drivers for peatland palaeoclimate records. *Quaternary Science Reviews*, 28(19–20), 1811– 1819.

Charman, D. J., Blundell, A., and Members, A. (2007). A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *Journal of Quaternary Science*, 22(3), 209– 221.

Charman, D. J., Brown, A. D., Hendon, D., and Karofeld, E. (2004). Testing the relationship between Holocene peatland palaeoclimate reconstructions and instrumental data at two European sites. *Quaternary Science Reviews*, 23(1–2), 137– 143.

Charman, D. J., and Hendon, D. (2000). Long-term changes in soil water tables over the past 4500 years: Relationships with climate and North Atlantic atmospheric circulation and sea surface temperature. *Climatic Change*, 47(1), 45– 59.

Charman, D. J., Hendon, D., and Woodland, W. A. (2000). *The identification of testate amoebae* (*Protozoa: Rhizopoda) in peats*. Technical guide no. 9, Quaternary Research Association.

Churchill, A. C., Turetsky, M. R., McGuire, A. D., and Hollingsworth, T. N. (2015). Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen. *Canadian Journal of Forest Research*, 45(2), 185– 193.

Chiverrell, R. C. (2001). A proxy record of late Holocene climate change from May Moss, northeast England. *Journal of Quaternary Science: Published for the Quaternary Research Association*, 16(1), 9-29.

Clarke, K. J. (2003). *Guide to the identification of soil protozoa-testate amoebae*. Freshwater Biological Association (FBA).

Clarke, P. J., Keith, D. A., Vincent, B. E., & Letten, A. D. (2015). Post-grazing and post-fire vegetation dynamics: long-term changes in mountain bogs reveal community resilience. *Journal of Vegetation Science, 26(*2), 278-290.

Cunningham, L. K., Austin, W. E. N., Knudsen, K. L., Eiríksson, J., Scourse, J. D., Wanamaker, A. D., Butler, P. G., Cage, A. G., Richter, T., Husum, K., Hald, M., Andersson, C., Zorita, E., Linderholm, H. W., Gunnarson, B. E., Sicre, M.-A., Sejrup, H. P., Jiang, H., and Wilson, R. J. S. (2013). Reconstructions of surface ocean conditions from the northeast Atlantic and Nordic seas during the last millennium. *The Holocene*, 23(7), 921– 935.

Daniels, R. E., and Eddy, A. (1990). *Handbook of European sphagna*. HMSO.

Davidson, E. A., and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165– 173

De Vleeschouwer, F., Piotrowska, N., Sikorski, J., Pawlyta, J., Cheburkin, A., Le Roux, G., Lamentowicz, M., Fagel, N., and Mauquoy, D. (2009). Multiproxy evidence of 'Little Ice Age' palaeoenvironmental changes in a peat bog from northern Poland. *The Holocene*, 19(4), 625– 637.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology*, 21(1), 388– 395.

Dise, N. B. (2009). Peatland response to global change. *Science*, 326(5954), 810– 811.

Dorrepaal, E., Aerts, R., Cornelissen, J. H., Callaghan, T. V., and van Logtestijn, R. S. (2004). Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure, and production in a sub-arctic bog. *Global Change Biology*, 10(1), 93– 104

Fenner, N., and Freeman, C. (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, 4(12), 895– 900.

Fenner, N., Freeman, C., Lock, M. A., Harmens, H., Reynolds, B., and Sparks, T. (2007). Interactions between elevated CO_2 and warming could amplify DOC exports from peatland catchments. *Environmental Science and Technology*, 41(9), 3146– 3152.

Ferguson, P., Lee, J. A., & Bell, J. N. B. (1978). Effects of sulphur pollutants on the growth of Sphagnum species. *Environmental Pollution,* 16(2), 151-162.

Fowles, A. P., Bailey, M. P., and Hale, A. D. (2004). Trends in the recovery of a rosy marsh moth *Coenophila subrosea* (Lepidoptera, Noctuidae) population in response to fire and conservation management on a lowland raised mire. *Journal of Insect Conservation*, 8(2–3), 149– 158.

Freeman, C., Ostle, N. J., Fenner, N., and Kang, H. (2004). A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biology and Biochemistry*, 36(10), 1663– 1667.

Frolking, S., and Roulet, N. T. (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, 13(5), 1079– 1088.

Frolking, S., Roulet, N., and Lawrence, D. (2009). *Issues related to incorporating northern peatlands into global climate models*. Carbon Cycling in Northern Peatlands, Geophysical Monographs Series 184 (19– 35).

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S. and Roulet, N., (2011). Peatlands in the Earth's 21st century climate system. *Environmental Reviews*, *19*(NA), 371-396.

Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A. and Karl, D.M., (2004). Nitrogen cycles: past, present, and future. *Biogeochemistry, 70*(2), 153-226.

Gatis, N., Luscombe, D. J., Grand-Clement, E., Hartley, I. P., Anderson, K., Smith, D., and Brazier, R. E. (2016). The effect of drainage ditches on vegetation diversity and CO_2 fluxes in a *Molinia caerulea* dominated peatland. *Ecohydrology*, 9(3), 407– 420.

Gauthier, E., Jassey, V. E. J., Mitchell, E. A. D., Lamentowicz, M., Payne, R., Delarue, F., Laggoun-Defarge, F., Gilbert, D., and Richard, H. (2019). From climatic to anthropogenic drivers: A multi-proxy reconstruction of vegetation and peatland development in the French Jura mountains. *Quaternary*, 2(4), 38.

Goodall, D. W. (1952). Some considerations in the use of point quadrats for the analysis of vegetation. *Australian Journal of Biological Sciences*, 5(1), 1– 41.

Gorham, E. (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1(2), 182– 195.

Gorham, E. (1995). The biogeochemistry of northern peatlands and its possible responses to global warming. In: G. M. Woodwell and F. T. Mackenzie (Eds.), *Biotic feedbacks in the global climate system: Will the warming feed the warming* (169– 187). Oxford University Press, Inc.

Gorham, E., Bayley, S. E., & Schindler, D. W. (1984). Ecological effects of acid deposition upon peatlands: a neglected field in" acid-rain" research. *Canadian Journal of Fisheries and Aquatic Sciences*, 41(8), 1256-1268.

Graumlich, L. J. (2002). Long-term vegetation change in mountain environments: Palaeoecological insights into modern vegetation dynamics. In M. Beniston (Ed.), *Mountain environments in changing climates* (158– 168). Routledge.

Greenwood, D. R., & Donovan, S. K. (1991). The taphonomy of plant macrofossils. *The processes of fossilization*, 141-169.

Grillakis, M. G. (2019). Increase in severe and extreme soil moisture droughts for Europe under climate change. *Science of the Total Environment*, 660, 1245– 1255.

Grimm, E. C. (1987). CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences*, 13(1), 13– 35.

Grosse-Brauckmann, G., and Streitz, B. (1972). Pflanzliche Makrofossilien mitteleuropäischer Torf 3 d (On plant macrofossils in central European peat. I. Remnants of vascular plant tissues and their characteristics). *Telma,* 2, 19–55 (in German).

Guêné-Nanchen, M., LeBlanc, M. C., & Rochefort, L. (2022). Post-fire peatland vegetation recovery: a case study in open rich fens of the Canadian boreal forest. *Botany, 100*(5), 435-447.

Gunnarsson, U., Granberg, G., and Nilsson, M. (2004). Growth, production, and interspecific competition in Sphagnum: effects of temperature, nitrogen, and sulphur treatments on a boreal mire. *New Phytologist*, 163(2), 349– 359.

Hájek, T. (2009). Habitat and species controls on Sphagnum production and decomposition in a mountain raised bog. *Boreal Environment Research*, 14(6), 947– 958.

Harte, J., and Shaw, R. (1995). Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. *Science*, 267(5199), 876– 880.

Heijmans, M. M., van der Knaap, Y. A., Holmgren, M., and Limpens, J. (2013). Persistent versus transient tree encroachment of temperate peat bogs: Effects of climate warming and drought events. *Global Change Biology*, 19(7), 2240– 2250.

Hendon, D., and Charman, D. J. (1997). The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, 7(2), 199– 205.

Heslehurst, M. R. (1971). *The point quadrat method of vegetation analysis: A review*. University of Reading, Dept. of Agriculture.

Hirano, T., Yamada, H., Takada, M., Fujimura, Y., Fujita, H., & Takahashi, H. (2016). Effects of the expansion of vascular plants in Sphagnum-dominated bog on evapotranspiration. *Agricultural and forest meteorology*, 220, 90-100.

Hogg, P., Squires, P., & Fitter, A. H. (1995). Acidification, nitrogen deposition and rapid vegetational change in a small valley mire in Yorkshire. *Biological Conservation,* 71(2), 143-153.

Howells, M. (2007). *Wales: British regional geology*. British Geological Survey.

Hughes, P. D. M., and Schulz, J. (2001). The development of the Borth Bog (Cors Fochno) mire system and the submerged forest beds at Ynyslas. In M. J. C. Walker and D. McCarroll (Eds.), The Quaternary of West Wales. QRA field guide (104– 112). QRA.

Hughes, P. D. M., Lomas-Clarke, S. H., Schulz, J., & Jones, P. (2007). The declining quality of late-Holocene ombrotrophic communities and the loss of Sphagnum austinii (Sull. ex Aust.) on raised bogs in Wales. *The Holocene, 17*(5), 613-625.

IPCC. (2021). Summary for policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (Eds.), *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* (5– 21). Cambridge University Press.

Johnson, L. C., and Damman, A. W. (1991). Species-controlled sphagnum decay on a South Swedish raised bog. *Oikos*, 61(2), 234– 242.

Johnson, C. P., Pypker, T. G., Hribljan, J. A., and Chimner, R. A. (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO_2/CH_4 dynamics in a northern Michigan peatland. *Ecosystems*, 16(5), 736– 748.

Joosten, H., Tapio-Biström, M. L., and Tol, S. (2012). *Peatlands: Guidance for climate change mitigation through conservation, rehabilitation, and sustainable use*. Food and Agriculture Organization of the United Nations.

Jowsey, P. C. (1966). An improved peat sampler. *New Phytologist*, 65(2), 245– 248.

Kay, M. (2019). *Impacts of warming, drought, and sea level rise on ombrotrophic peatlands* (PhD thesis). Manchester Metropolitan University.

Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, 18(6), 1998-2007.

Kilian, M. R., van der Plicht, J., and van Geel, B. (1995). Dating raised bogs: new aspects of AMS ^{14}C wiggle matching, a reservoir effect and climatic change. *Quaternary Science Reviews*, 14(10), 959– 966.

Kuhry, P. (1994). The role of fire in the development of Sphagnum-dominated peatlands in western boreal Canada. *Journal of Ecology*, 899-910.

Kuhry, P., and Turunen, J. (2006). The postglacial development of boreal and subarctic peatlands. In R. Kelman Wieder and D. H. Vitt (Eds.), *Boreal peatland ecosystems* (25– 46). Springer.

Kuiper, J. J., Mooij, W. M., Bragazza, L., and Robroek, B. J. (2014). Plant functional types define magnitude of drought response in peatland CO_2 exchange. *Ecology*, 95(1), 123– 131.

Laine, J., Harju, P., Timonen, T., Laine, A., Tuittila, E. S., Minkkinen, K., and Vasander, H. (2011). *The intricate beauty of Sphagnum mosses—A Finnish guide to identification*. University of Helsinki Department of Forest Sciences Publications.

Lamb, H. H. (1965). The early medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 1, 13– 37.

Lamentowicz, M., and Mitchell, E. A. (2005). The ecology of testate amoebae (Protists) in Sphagnum in north-western Poland in relation to peatland ecology. *Microbial Ecology*, 50(1), 48– 63.

Lamentowicz, M., Słowińska, S., Słowiński, M., Jassey, V., Chojnicki, B., Reczuga, M., Zielińska, M., Marcisz, K., Barabach, J., Samson, M., and Kołaczek, P., (2016). Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of Sphagnum peatlands to drought, fire and warming. *Mires and Peat*, 18, 20.

Langdon, P. G., Brown, A. G., Caseldine, C. J., Blockley, S. P. E., and Stuijts, I., (2012). Regional climate change from peat stratigraphy for the mid-to late Holocene in central Ireland. *Quaternary International*, 268, 145– 155

Leifeld, J., & Menichetti, L. (2018). The underappreciated potential of peatlands in global climate change mitigation strategies. *Nature Communications, 9*(1), 1-7.

Levy, E. N., and Madden, E. A., (1933). The point method of pasture analysis. *New Zealand Journal of Agriculture*, 46, 267– 279.

Loisel, J. and Garneau, M., (2010). Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*(3-4), 493-533.

Lowe, J. A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G., and Fung, F., (2018). *UKCP18 science overview report*. Met Office Hadley Centre.

Łuców, D., Basińska, A., Chojnicki, B., Gąbka, M., Józefczyk, D., Juszczak, R., & Lamentowicz, M. (2017). The response of vegetation structure to active warming and precipitation reduction of the Sphagnum peatland. In *EGU General Assembly Conference Abstracts* (p. 8001).

Łuców, D., Lamentowicz, M., Obremska, M., Arkhipova, M., Kittel, P., Łokas, E., Mazurkevich, A., Mróz, T., Tjallingii, R. and Słowiński, M., (2020). Disturbance and resilience of a Sphagnum peatland in western Russia (Western Dvina Lakeland) during the last 300 years: a multiproxy, high-resolution study. The Holocene, 30(11), 1552-1566.

Magnan, G., Le Stum-Boivin, É., Garneau, M., Grondin, P., Fenton, N., and Bergeron, Y., (2019). Holocene vegetation dynamics and hydrological variability in forested peatlands of the Clay Belt, eastern Canada, reconstructed using a palaeoecological approach. *Boreas*, 48(1), 131– 146.

Magnan, G., Sanderson, N.K., Piilo, S., Pratte, S., Väliranta, M., van Bellen, S., Zhang, H. and Garneau, M., (2022). Widespread recent ecosystem state shifts in high-latitude peatlands of northeastern Canada and implications for carbon sequestration. *Global Change Biology*, 28(5), 1919-1934.

Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J., and Iversen, C. M., (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences of the United States of America*, 117(30), 17627– 17634.

Maltby, E., Legg, C. J., & Proctor, M. C. F. (1990). The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. *The Journal of Ecology*, 490-518.

Mann, M. E., Bradley, R. S., and Hughes, M. K. (1999). Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters*, 26(6), 759– 762.

Mann, M. E., Hughes, M. K., Cook, E. R., and Esper, J. (2002). Tree-ring chronologies and climate variability. *Science*, 296(5569), 848– 849.

Mann, M. E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., Ammann, C., Faluvegi, G., and Ni, F., (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, 326(5957), 1256– 1260.

Marion, G. M., Bockheim, J. G., and Brown, J., (1997). Arctic soils and the ITEX experiment. *Global Change Biology*, 3(S1), 33– 43.

Marion, G. M., Henry, G., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. N., Svoboda, J., and Virginia, R. A. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3(Suppl 1), 20– 32.

Masson-Delmotte, V., Zhai, P., Pörtner, H.O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R. and Connors, S., (2018). *An IPCC Special Report on the impacts of global warming of Global warming of 1.5 C,* 1(5).

Matthes, F. E. (1939). Report of committee on glaciers, April 1939. *Eos, Transactions American Geophysical Union*, 20(4), 518– 523.

Matthews, J. A., and Briffa, K. R. (2005). The 'Little Ice Age': Re-evaluation of an evolving concept. *Geografiska Annaler: Series A, Physical Geography*, 87(1), 17– 36.

Mauquoy, D., Engelkes, T., Groot, M. H. M., Markesteijn, F., Oudejans, M. G., van Der Plicht, J., and van Geel, B. (2002). High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 186(3–4), 275– 310.

Mauquoy, D., Hughes, P. D. M., and van Geel, B. (2010). A protocol for plant macrofossil analysis of peat deposits. *Mires and Peat*, 7(6), 1– 5.

Mauquoy, D., and van Geel, B. (2007). Plant macrofossil methods and studies: Mire and peat macros. In: S. A. Elias (Ed.), *Encyclopedia of Quaternary Science* (2315– 2336). Elsevier Science.

Mauquoy, D., and Yeloff, D. (2008). Raised peat bog development and possible responses to environmental changes during the mid-to late-Holocene. Can the palaeoecological record be used to predict the nature and response of raised peat bogs to future climate change? *Biodiversity and Conservation*, 17(9), 2139– 2151.

Mazei, Y., and Tsyganov, A. N. (2006). *Freshwater testate amoebae*. KMK.

Metcalfe, D. B., Fisher, R. A., and Wardle, D. A. (2011). Plant communities as drivers of soil respiration: Pathways, mechanisms, and significance for global change. *Biogeosciences*, 8(8).

Mighall, T., Timberlake, S., Martínez-Cortizas, A., Silva-Sánchez, N., and Foster, I. D. L. (2017). Did prehistoric and Roman mining and metallurgy have a significant impact on vegetation? *Journal of Archaeological Science: Reports*, 11, 613– 625.

Mitchell, E. A., Charman, D. J., and Warner, B. G. (2008). Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present, and future. *Biodiversity and Conservation*, 17(9), 2115– 2137.

Moore, T. R., Roulet, N. T., and Waddington, J. M. (1998). Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change*, 40(2), 229– 245.

Murphy, M. T., McKinley, A., and Moore, T. R. (2009). Variations in above-and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. *Botany-Botanique*, 87(9), 845– 853.

Neukom, R., Steiger, N., Gómez-Navarro, J. J., Wang, J., and Werner, J. P. (2019). No evidence for globally coherent warm and cold periods over the preindustrial Common Era. *Nature*, 571(7766), 550– 554.

Noble, A., Palmer, S. M., Glaves, D. J., Crowle, A., Brown, L. E., & Holden, J. (2018). Prescribed burning, atmospheric pollution, and grazing effects on peatland vegetation composition. *Journal of Applied Ecology*, 55(2), 559-569.

Norby, R. J., Childs, J., Hanson, P. J., and Warren, J. M. (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, 9(22), 12571– 12585.

Olefeldt, D., Euskirchen, E. S., Harden, J., Kane, E., McGuire, A. D., Waldrop, M. P., & Turetsky, M. R. (2017). A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability. *Global Change Biology*, 23(6), 2428-2440.

Ordonez, A., Williams, J. W., and Svenning, J. C. (2016). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change*, 6(12), 1104– 1109.

Overpeck, J. T., Webb, T. I. I. I., and Prentice, I. C. (1985). Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogs. *Quaternary Research*, 23(1), 87– 108.

Page, S. E., & Baird, A. J. (2016). Peatlands and global change: response and resilience. *Annual Review of Environment and Resources, 41,* 35-57.

Page, N., Hughes, G., Jones, R., and Murphy, K. (2012). Excavations at Erglodd, Llangynfelyn, Ceredigion: Prehistoric/Roman lead smelting site and medieval trackway. *Archaeologia Cambrensis*, 161, 285– 356.

Pakarinen, P., & Tolonen, K. (1976). Regional survey of heavy metals in peat mosses (Sphagnum). *Ambio*, 38-40.

Payne, R. J. (2014). A natural experiment suggests little direct temperature forcing of the peatland palaeoclimate record. *Journal of Quaternary Science*, 29(6), 509– 514.

Payne, R. J., and Mitchell, E. A. (2007). Ecology of testate amoebae from mires in the Central Rhodope Mountains, Greece, and development of a transfer function for palaeohydrological reconstruction. *Protist*, 158(2), 159– 171.

Payne, R. J., and Mitchell, E. A. (2009). How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. *Journal of Paleolimnology*, 42(4), 483– 495.

Pellerin, S., and Lavoie, C. (2003). Reconstructing the recent dynamics of mires using a multitechnique approach. *Journal of Ecology*, 91(6), 1008– 1021.

Piotrowska, N., Blaauw, M., Mauquoy, D., and Chambers, F. M. (2011). Constructing deposition chronologies for peat deposits using radiocarbon dating. *Mires and Peat*, 7(10), 1– 14.

Poucher, P. (2009). *Wetland margins survey: Cors Fochno*. Dyfed Archaeological Trust.

Proctor, C. J., Baker, A., Barnes, W. L., and Gilmour, M. A. (2000). A thousand-year speleothem proxy record of North Atlantic climate from Scotland. *Climate Dynamics*, 16(10–11), 815– 820.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ramsey, C. B. (1995). Radiocarbon calibration and analysis of stratigraphy: the OxCal program. *Radiocarbon*, 37(2), 425– 430.

Reimer, P. J., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W., Muscheler, R., … Talamo, S. (2020). The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*, 62(4), 725– 757.

Rhodes, A. N. (1998). A method for the preparation and quantification of microscopic charcoal from terrestrial and lacustrine sediment cores. *The Holocene*, 8(1), 113– 117.

Richardson, S. J., Hartley, S. E., & Press, M. C. (2000). Climate warming experiments: are tents a potential barrier to interpretation?. *Ecological Entomology, 25*(3), 367-370.

Robroek, B. J. M., Limpens, J., Breeuwer, A., Crushell, P. H., and Schouten, M. G. C. (2007). Interspecific competition between *Sphagnum* mosses at different water tables. *Functional Ecology*, 21(4), 805– 812.

Rochefort, L., Isselin-Nondedeu, F., Boudreau, S., and Poulin, M. (2013). Comparing survey methods for monitoring vegetation change through time in a restored peatland. *Wetlands Ecology and Management*, 21(1), 71– 85.

Rodwell, J. S. (1991). *British plant communities: Volume 4, aquatic communities, swamps, and tall-herb fens* (Vol. 4). Cambridge University Press.

Rose, N. L. (2008). Quality control in the analysis of lake sediments for spheroidal carbonaceous particles. *Limnology and Oceanography: Methods*, 6(4), 172– 179.

Rose, N. L., and Appleby, P. G. (2005). Regional applications of lake sediment dating by spheroidal carbonaceous particle analysis I: United Kingdom. *Journal of Paleolimnology*, 34(3), 349– 361.

Rose, N. L., Harlock, S., Appleby, P. G., and Battarbee, R. W. (1995). Dating of recent lake sediments in the United Kingdom and Ireland using spheroidal carbonaceous particle (SCP) concentration profiles. *The Holocene*, 5(3), 328– 335.

Ross, H. B. (1987). Trace metals in precipitation in Sweden. *Water, Air, and Soil Pollution*, 36(3), 349-363.

Rouse, W. R., Douglas, M. S., Hecky, R. E., Hershey, A. E., Kling, G. W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B. J., Roulet, N. T., and Smol, J. P. (1997). Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes*, 11(8), 873– 902.

Rull, V. (2010). Ecology and palaeoecology: Two approaches, one objective. *The Open Ecology Journal*, 3(1).

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., Zielińska, M., Robroek, B. J., Jassey, V. E., Buttler, A., and Chojnicki, B. H. (2018). The impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in Northern Poland. *Wetlands*, 38(3), 551– 563.

Schlachter, K. J., and Horn, S. P. (2010). Sample preparation methods and replicability in macroscopic charcoal analysis. *Journal of Paleolimnology*, 44(2), 701– 708.

Schulz, J. (200). *Late-Holocene mire development of the lowland raised bogs Cors Caron and Cors Fochno: A palaeoecological approach using high resolution macrofossil analysis* [Unpublished Ph.D. thesis]. University of Southampton.

Seddon, A. W. R., Mackay, A. W., Baker, A. G., Birks, H. J. B., Breman, E., Buck, C. E., Ellis, E. C., Froyd, C. A., Gill, J. L., Gillson, L., Johnson, E. A., Jones, V. J., Juggins, S., Macias-Fauria, M., Mills, K., Morris, J. L., Nogués-Bravo, D., Punyasena, S. W., Roland, T. P., … Witkowski, A. (2014). Looking forward through the past: Identification of 50 priority research questions in palaeoecology. *Journal of Ecology*, 102(1), 256– 267.

Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. F., and Rustad, L. (2000). Global warming and terrestrial ecosystems: A conceptual framework for analysis. *BioScience*, 50(10), 871– 882.

Siemensma, F. (2019). *Microworld—World of amoeboid organisms*. [online source] Arcella.nl. https://www.arcella.nl/ [accessed 01/08/2019]

Simpson, G. L. (2007). Analogue methods in palaeoecology: Using the analogue package. *Journal of Statistical Software*, 22(2), 1– 29.

Smith, A. J. E. (2004). *The moss flora of Britain and Ireland*. Cambridge University Press.

Souto, M., Castro, D., Pontevedra-Pombal, X., Garcia-Rodeja, E., and Fraga, M. I. (2016). Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: Vascular plants. *Mires and Peat*, 18, 1– 21.

Souto, M., Castro, D., Pontevedra-Pombal, X., Garcia-Rodeja, E., and Fraga, M. I. (2017). Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: Bryophytes. *Mires and Peat*, 19.

Stace, C. (2010). *New flora of the British Isles*. Cambridge University Press.

Strack, M., Waddington, J. M., Rochefort, L., and Tuittila, E. S. (2006). Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research: Biogeosciences*, 111(G2).

Swindles, G. T. (2010). Dating recent peat profiles using spheroidal carbonaceous particles (SCPs). *Mires and Peat*, 7(03), 1– 5.

Swindles, G. T., Holden, J., Raby, C. L., Turner, T. E., Blundell, A., Charman, D. J., Menberu, M. W., and Kløve, B. (2015). Testing peatland water table depth transfer functions using high-resolution hydrological monitoring data. *Quaternary Science Reviews*, 120, 107– 117.

Swindles, G. T., Morris, P. J., Baird, A. J., Blaauw, M., and Plunkett, G. (2012). Ecohydrological feedbacks confound peat-based climate reconstructions. *Geophysical Research Letters*, 39(11).

Swindles, G. T., Morris, P. J., Mullan, D. J., Payne, R. J., Roland, T. P., Amesbury, M. J., Lamentowicz, M., Turner, T. E., Gallego-Sala, A., Sim, T., Barr, I. D., Blaauw, M., Blundell, A., Chambers, F. M., Charman, D. J., Feurdean, A., Galloway, J. M., Gałka, M., Green, S. M., … Warner, B. (2019). Widespread drying of European peatlands in recent centuries. *Nature Geoscience*, 12(11), 922– 928.

Swindles, G. T., Morris, P. J., Wheeler, J., Smith, M. W., Bacon, K. L., Edward Turner, T., Headley, A., and Galloway, J. M. (2016). Resilience of peatland ecosystem services over millennial timescales: Evidence from a degraded British bog. *Journal of Ecology*, 104(3), 621– 636.

Swindles, G. T., Roland, T. P., Amesbury, M. J., Lamentowicz, M., McKeown, M. M., Sim, T. G., Fewster, R. E., and Mitchell, E. A. (2020). Quantifying the effect of testate amoeba decomposition on peat-based water table reconstructions. *European Journal of Protistology*, 74, 125693.

Swindles, G. T., Turner, T. E., Roe, H. M., Hall, V. A., and Rea, H. A. (2015). Testing the cause of the *Sphagnum austinii* (Sull. Ex Aust.) decline: Multiproxy evidence from a raised bog in Northern Ireland. *Review of Palaeobotany and Palynology*, 213, 17– 26.

Talbot, J., Roulet, N. T., Sonnentag, O., and Moore, T. R. (2014). Increases in aboveground biomass and leaf area 85 years after drainage in a bog. *Botany-Botanique*, 92(10), 713– 721.

Totland, Ø., & Eide, W. (1999). Environmentally-dependent pollen limitation on seed production in alpine Ranunculus acris. *Ecoscience, 6*(2), 173-179.

Trinder, C. J., Artz, R. R., and Johnson, D. (2008). Contribution of plant photosynthate to soil respiration and dissolved organic carbon in a naturally recolonising cutover peatland. *Soil Biology and Biochemistry*, 40(7), 1622– 1628.

Trouet, V., Esper, J., Graham, N. E., Baker, A., Scourse, J. D., and Frank, D. C. (2009). Persistent positive North Atlantic Oscillation mode dominated the medieval climate anomaly. *Science*, 324(5923), 78– 80.

Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D., and Tuittila, E. S. (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, 196(1), 49– 67.

Turetsky, M., Wieder, K., Halsey, L. and Vitt, D., (2002). Current disturbance and the diminishing peatland carbon sink. *Geophysical Research Letters*, *29*(11), 21-1.

Turetsky, M. R., Manning, S. W., and Wieder, R. K. (2004). Dating recent peat deposits. *Wetlands*, 24(2), 324– 356.

Turner, T. E., Swindles, G. T., and Roucoux, K. H. (2014). Late Holocene ecohydrological and carbon dynamics of a UK raised bog: Impact of human activity and climate change. *Quaternary Science Reviews*, 84, 65– 85.

van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends in Ecology and Evolution*, 10(7), 270– 275.

van Loon, A. F. (2015). Hydrological drought explained. *Wiley Interdisciplinary Reviews: Water*, 2(4), 359– 392.

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H., Kattge, J., & Van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology*, 21(8), 3074-3086.

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., and Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8(1), 113– 127.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., and Epstein, H. E. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, 103(5), 1342– 1346.

Walker, T. N., Ward, S. E., Ostle, N. J., and Bardgett, R. D. (2015). Contrasting growth responses of dominant peatland plants to warming and vegetation composition. *Oecologia*, 178(1), 141– 151.

Wang, Y. I., Naumann, U., Wright, S. T., and Warton, D. I. (2012). mvabund–an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, 3(3), 471– 474.

Wang, Y., Naumann, U., Wright, S., Warton, D., Wang, M. Y., and Rcpp, I. (2020). *Package 'mvabund'.* CRAN-r project

Ward, S. E., Bardgett, R. D., McNamara, N. P., and Ostle, N. J. (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: Evidence from a plant removal experiment. *Functional Ecology*, 23(2), 454– 462.

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., and Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, 16(10), 1285– 1293.

Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J., and Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, 9(2), 141– 151.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., and Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water table manipulations. *Ecology*, 81(12), 3464– 3478.

Wilks, P. J. (1979). Mid-Holocene sea-level and sedimentation interactions in the Dovey Estuary area, Wales. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 26, 17– 36.

Willis, K. J., Bailey, R. M., Bhagwat, S. A., and Birks, H. J. B. (2010). Biodiversity baselines, thresholds, and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology and Evolution*, 25(10), 583– 591.

Xu, S., Liu, X., Li, X., & Tian, C. (2019). Soil organic carbon changes following wetland cultivation: a global meta-analysis. *Geoderma*, 347, 49-58.

Yavitt, J. B., Williams, C. J., and Wieder, R. K. (1997). Production of methane and carbon dioxide in peatland ecosystems across North America: Effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiology Journal*, 14(4), 299– 316.

Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: A review. *Biogeosciences*, 9(10), 4071.

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., and Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters*, 37(13). Zeh, L., Limpens, J., Erhagen, B., Bragazza, L., & Kalbitz, K. (2019). Plant functional types and temperature control carbon input via roots in peatland soils. *Plant and Soil, 438*(1), 19-38.

Chapter 4: Carbon cycle responses to experimental drought and warming in a Welsh ombrotrophic peatland in the context of late Holocene carbon accumulation

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4.1. Abstract

Peatlands are important sinks and stores of terrestrial carbon, but their future role in the global climate system under climate change is uncertain. Palaeoecological and experimental climate manipulation studies are commonly used to address these uncertainties, although their results often contradict each other. Furthermore, carbon accumulation rates estimated from both methods frequently fail to converge. We examine the effects of warming and episodic drought on carbon cycling from a long-term experimental site in an ombrotrophic peatland in Wales, simulating expected changes in temperature and drought frequency for the next c. 70 years. We compare carbon accumulation rates modelled from the 10-year experiment (2010 – 2020) with those derived from a peat core covering the past c. 1500 years. We partition components of the annual carbon budget for each experimental treatment and compare them with core-derived carbon accumulation rates. Significant differences in carbon accumulation occurred between experimental treatments, resulting from cumulative non-significant changes in decay rates and productivity, driven by differences in air temperature and water table depth. We identify a positive time-lagged relationship between carbon accumulation and reconstructed temperature anomalies in the long-term carbon accumulation record. Changes in carbon accumulation also correspond to vegetation changes. We suggest that palaeoecological studies should not consider changes in plant productivity to be the sole determinant controlling carbon accumulation rates and should acknowledge the role of changing decay rates following plant succession upon long-term carbon accumulation. Carbon accumulation rates estimated from both methods may converge, but often differ due to unquantifiable losses such as by reduced productivity, decay, or anthropogenic disturbances like fire.

We conclude that both methods are useful for discerning future peatland responses to climate change; however, core derived rates should be interpreted with consideration of all the contemporary mechanisms governing carbon accumulation. Based on these findings, we posit that the carbon sink function of existing peatlands will be weakened by increased warming and drought.

4.2. Introduction

Understanding how climate change will affect the carbon balance of terrestrial ecosystems is important because of their sensitivity to climatic conditions. Future changes in climate may drive ecological transformations that disrupt ecosystem functions such as carbon storage (Seddon *et al.,* 2014; Nolan *et al.,* 2018). Climate change is expected to substantially alter the ecology and ecosystem functioning of peatlands (Bu *et al.,* 2011), which are mostly located in the Northern Hemisphere where the greatest changes in climate are predicted, particularly in the northernmost latitudes (Hoegh-Guldberg *et al*., 2018; Lee *et al.,* 2021). Peatlands are important components of the global carbon system, containing at least 500 ± 100 billion tonnes (GT) of organic carbon in their soils (Gorham, 1991; Yu, 2012). They continuously cycle atmospheric and fluvial carbon as CO_2, CH_4 and dissolved organic carbon (DOC) (Blodau, 2002). When carbon accumulation exceeds decay, peatlands exert a negative climate feedback, cooling global temperatures over multi-centennial timescales. However, over shorter timescales, the relative contributions of CH_4 over CO_2 (CH_4 is a more potent greenhouse gas but has a shorter atmospheric residence time) means peatlands may contribute a net warming effect (Frolking and Roulet, 2007; Turetsky *et al.,* 2012).

How peatlands will respond to climate change is uncertain (Moore *et al.,* 1998; Loisel *et al.,* 2021). Warmer conditions and increased water table depths may accelerate CO_2 losses (Ise *et al.,* 2008; Bridgham *et al.,* 2008; Dorrepaal *et al.,* 2009; Huang *et al.,* 2021). Permafrost thaw may promote CH_4 releases in sub-arctic regions (Christensen *et al.,* 2004). Indirect impacts (e.g., increased drought and wildfires) may further amplify carbon loss (Turetsky *et al.,* 2011a; 2011b; Lee *et al.,* 2021). However, expansion of peatlands into northern territories beyond their current range could offset carbon losses (Limpens *et al.,* 2008; Frolking *et al.,* 2011; Dieleman *et al.,* 2015). Warmer, drier conditions may also reduce CH_4 emissions (Strack *et al.,* 2004; Huang *et al.,* 2021). While previous studies have suggested that reduced CH_4 emissions may offset the effects of increasing CO_2 emissions over 100 year timescales, (Frolking *et al.,* 2006), the methods used to calculate the CO_2 equivalent emissions of CH_4 and other greenhouse gases misrepresent the residency time of these gases in the atmosphere and how their concentrations change over time, instead only comparing instantaneous pulse emissions of gases, as opposed to cumulative emissions over time (Cain *et al.,* 2019). While, on balance, it is expected that peatlands will undergo net losses in carbon due to climate change, confidence in this projection is low (Loisel *et al.,* 2021). This uncertainty means peatlands are rarely included in global terrestrial models (Lee *et al.,* 2021) and are not yet incorporated in any Earth system models (Loisel *et al.,* 2021), despite their importance to the global carbon system.

The impact of climate change on peatlands is commonly investigated using either experimental or palaeoecological methods. Experimental studies artificially simulate environmental changes, allowing for the calculation of functional relationships between carbon fluxes and environmental variables (e.g., Updegraff *et al.,* 2001, Li *et al.,* 2021). These studies are limited by their short duration, making them unable to quantify long-term responses to climate change. They may also be affected by experimental artefacts. Carbon accumulated over a longer period may be inferred from peat cores (e.g., Clymo *et al.,* 1998; Ratcliffe *et al.,* 2018). When dated, these cores provide opportunities to estimate changes in carbon accumulation rates that can be related to proxy-based climate reconstructions or long-term instrumental datasets to identify drivers of change (Mauquoy *et al.,* 2002; 2004; Charman, 2007). This method permits comparison between carbon accumulation rates during periods of past climate change, such as the Medieval Climate Anomaly (MCA; c. 950 – 1250 CE) (Mann *et al.,* 2009) and the Little Ice Age (LIA; c. 1350 – 1850 CE) (Lamb, 1965), periods of relatively warmer and cooler conditions, respectively, in the Northern Hemisphere.

Integrating experimental and palaeoecological studies should improve our understanding of peatland responses to climate change (Frolking *et al.,* 2014; Lamentowicz *et al.,* 2016), but these methods often produce contradictory results. Most experimental studies suggest that warmer and drier conditions will enhance carbon losses (Dorrepaal *et al.,* 2009; Walker *et al.,* 2016) while many palaeoecological studies suggest the opposite, that carbon accumulation has increased during warmer periods relative to cooler periods (Charman *et al.,* 2013; van der Linden *et al.,* 2014).

Direct comparison of carbon accumulation rates derived from the two approaches is also complicated by artefacts inherent in core-derived estimates. Frolking *et al.* (2014) compared core-derived accumulation rates to net ecosystem carbon budgets using a process-based peatland model, finding that net ecosystem carbon budgets can differ from the past apparent carbon accumulation rates over short periods. Although these two estimates should converge, loss of carbon throughout the core (e.g., due to climatic perturbations, burning or drought) will reduce the apparent rate of carbon accumulation for older peat deposited prior to these events, limiting their comparability. Periods of carbon loss are reflected as a deceleration of carbon accumulation in palaeoecological studies, since core-derived values cannot be negative, providing no measure of carbon losses from the system (Yu, 2011; Young *et al.,* 2021). Carbon accumulation rates are therefore based on the amount of carbon retained throughout the profile, whereas contemporary carbon budgets can include all major carbon fluxes. In addition, peat core-derived accumulation rates in the acrotelm are inflated due to incomplete decomposition and decrease downcore due to continual carbon losses through time, meaning that carbon accumulation rates based on recently accumulated peats do not reflect later long-term storage (Clymo 1984; Yu, 2011; Young *et al.,* 2019, 2021).

In this study, we model annual carbon budgets for twelve experimental treatment plots (triplicates of: control, warmed, droughted and combined warmed and droughted treatments) from a ten-year climate manipulation experiment on an ombrotrophic peat bog in Wales. We test how increased warming and short-term, episodic drought affect the carbon sink functioning of peatlands. Drought in the context of this experimental study refers to sustained summer water table drawdown. We investigate any apparent disparities between palaeoecological and experimental approaches by partitioning different components of the annual carbon budget (CO_2 emissions and accumulation, CH_4 emissions, DOC fluxes) from our modelled budgets and comparing these with core-derived accumulation rates. We also compare dominant drivers of carbon accumulation in experimental plots with those in the long-term record.

The aim of this study is to understand this disparity in peatland carbon accumulation estimates between palaeoenvironmental and experimental methods, and to resolve differences between contemporary modelled annual carbon budgets and core-derived estimates. By corroborating the results of experimental and palaeoecological studies, we seek to reduce the uncertainty concerning the future effects of climate change on peatland carbon cycling.

4.3. Methods

4.3.1. Study site and coring location

Cors Fochno is a coastal lowland raised bog in Ceredigion, Wales (Figure 4.1). It is the largest expanse of primary surface lowland raised bog in both England and Wales. The central active zone comprises c. 2 km^2 of primary surface peat, surrounded by c. 4 km^2 of degraded peatland (Poucher, 2009). The vegetation is dominated by *Sphagnum pulchrum* lawns, with an undulating topography of hummocks (characterised mainly by *Sphagnum papillosum* and *Sphagnum medium*), and hollows (populated mainly by

Sphagnum cuspidatum). Other common species include *Rhynchospora alba, Eriophorum angustifolium, Calluna vulgaris, Erica tetralix* and *Myrica gale.* For a full list of plant species on the central portion of the site, refer to Andrews *et al*. (2021).

A single core (code BO17) was collected in September 2017 from a representative area of *Sphagnum pulchrum* carpet adjacent to the experimental site used in the study (Figure 4.1). The core was collected using a Russian peat sampler with a 5cm overlap between core sections. The top 50 cm was taken using a monolith tin. In addition to the data described in this paper, the core was analysed for plant macrofossils following adapted methods by Barber *et al.* (1994) and Mauquoy *et al.* (2010), and testate amoeba following methods by Hendon and Charman (1997). Full details and results of these analyses are provided in Andrews *et al*. (2021). In combination with these analyses, an age-depth model was generated using ^{14}C dates in addition to macrocharcoal and spheroidal carbonaceous particle (SCP) chronohorizons (Andrews *et al.,* 2021). In this study, we add new ^{210}Pb dates and tephrochronological markers and calculate apparent rates of carbon accumulation throughout the core (henceforth abbreviated to aCAR) based on an improved age-depth model for core BO17.

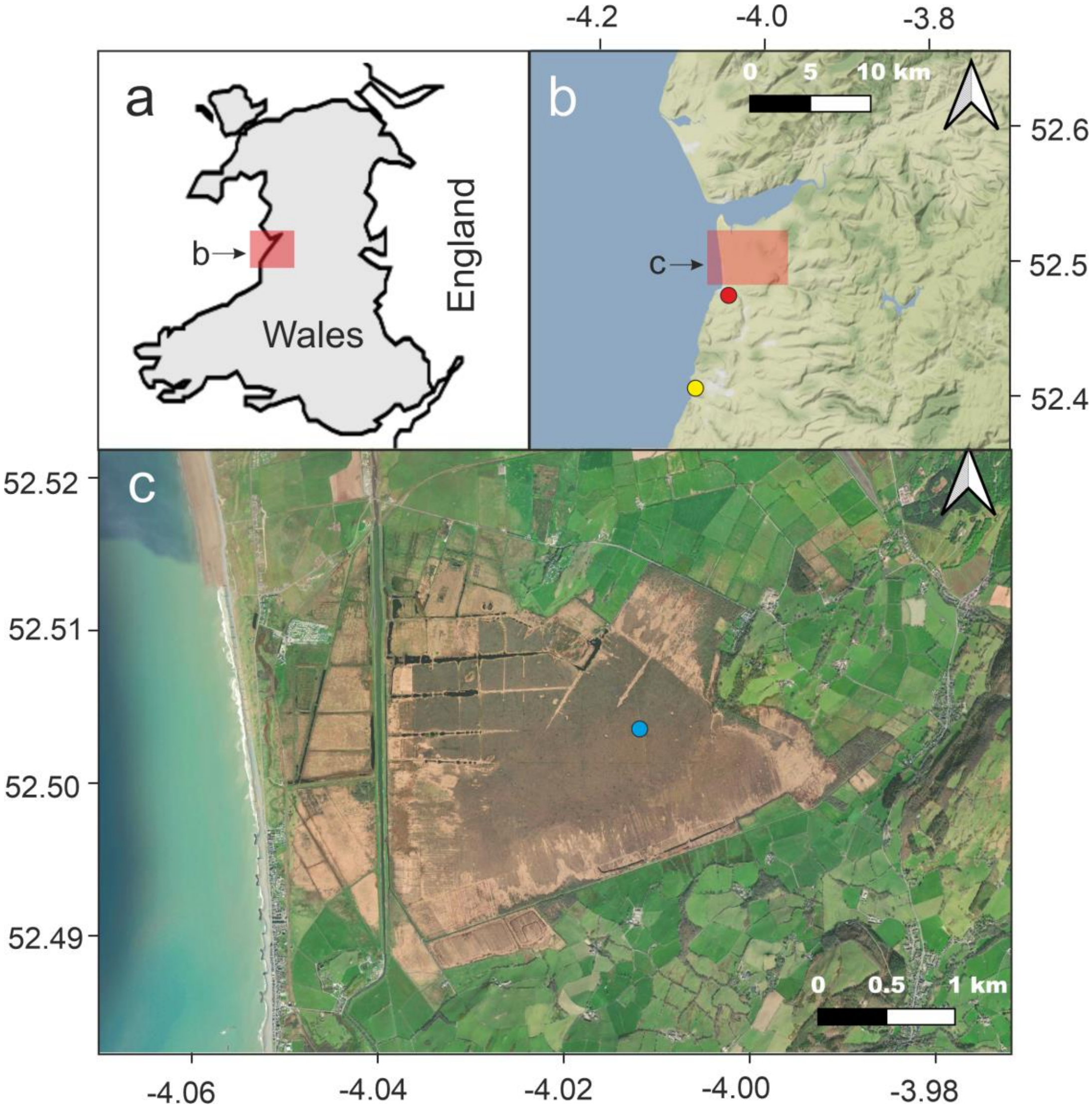

Figure 4.1. Location of the experimental site: a. Map of Wales. Red shaded areas show the area indicated by the following panel. b. topographic map showing the area from Machynlleth to Aberystwyth (Stamen terrain background). The location of Frondirion, where precipitation data were measured, is shown as a red dot. The location of Plas Gogerddan, where pan evapotranspiration rates were measured, is shown as a yellow dot. c. ESRI Satellite image Cors Fochno. showing the location of the experimental site and location of core BO17 (blue dot).

Three full-length cores (BO18 1-3) were taken along the length of our experimental transect (described below) at approximately equal distances also using the Russian peat sampler. These were used to calculate the long-term apparent rate of carbon accumulation (LORCA) (Clymo *et al.,* 1998).

4.3.2. Age-depth model improvement

4.3.2.1. ^{210}Pb dating

^{210}Pb dating is commonly used for dating recently accumulated peat in palaeoecological studies (Appleby, 1998; Turetsky *et al.,* 2004). To measure ^{210}Pb, 1 cm thick sub-samples were taken throughout core BO17. Bulk density was measured for each sample by dividing the volume of the wet peat sample by the sample weight after oven drying for 24 hours at <45°C (Chambers *et al.,* 2011). Samples were prepared following methods described by Appleby (1998). ^{210}Pb activity for each sample was measured by gamma spectroscopy using well detectors at the Consolidated Radio-Isotope Facility (CoRIF), University of Plymouth.

4.3.2.2. Tephrochronological analysis

We adopted the standard 'ashing' method (combustion of peat at 550°C) (Swindles *et al.,* 2010) to identify cryptotephra in core BO17 from contiguous 3 cm^3 samples taken throughout the core at 3 cm resolution. The remnant material was mounted on microscope slides using Histamount, and tephra identified at 400x magnification under cross-polarised light. Where tephra shards were identified, additional samples were taken at 1 cm resolution to determine a more precise position of the tephra horizon. Once precise horizons were identified, additional peat samples were extracted for geochemical analysis of cryptotephra shards by acid digestion using sulphuric and nitric acids, as detailed by Newton *et al.* (2007).

Geochemical ‘fingerprinting’ of identified tephra shards along with laboratory standards (BCR2g and Lipari) were carried out at the Edinburgh Tephra Analytical Unit (TAU) using a Cameca SX100 Electron Microprobe (Hayward, 2012; Hall and Hayward, 2015). A comparison with the Tephrabase database (Newton *et al.,* 2007) enabled identification of the volcanic eruptions from which tephras originated.

4.3.2.3. Age-depth modelling

^{210}Pb data were modelled within a Bayesian framework using the package ‘rplum’ (Aquino-López *et al.,* 2018; Blaauw *et al.,* 2021) along with the new tephra dates and the existing chronohorizons of Andrews *et al.* (2021). rplum generates a maximum age probability (MAP) at user-defined intervals (here every 1 cm), together with maximum and minimum ages, based upon the 95% confidence interval. This method improves on traditional techniques for modelling ^{210}Pb, allowing for the integration of ^{210}Pb dates with other dating methods in age-depth models without the need for re-modelling (Aquino-López *et al.,* 2018, 2020).

4.4. Core-derived carbon accumulation rates

4.4.1. Peat physical properties

We measured bulk density and total carbon content (%C) throughout each core. Contiguous 10 cm-thick sub-samples were taken from cores BO18 1 – 3 from the point of peat initiation to the top of the core. Bulk density was measured for each sample, and %C measured by analysing 55 ± 5 mg of milled material with a Vario Macro Carbon/Nitrogen Analyser.

The same procedures were carried out using material from core BO17, although samples were taken at contiguous 1 cm intervals. Carbon density was calculated by multiplying dry bulk density (g cm^3) by %C.

4.4.2. Long term apparent rate of carbon accumulation (LORCA)

Peat initiation dates were estimated using radiocarbon dating of samples from the point of peat initiation for each of the long cores (BO18 1 – 3). Subsamples of 1 cm^3 were extracted and washed through a 250 µm sieve. The fine particulate fraction (<250 µm) was retained for analysis following Piotrowska *et al.* (2011). Samples were cleaned by acid-alkali-acid washing and oven dried at < 45°C. Samples were analysed by accelerator mass spectrometry at DirectAMS (Washington, USA). Radiocarbon dates were calibrated using the IntCal20 radiocarbon calibration curve in OxCal version 4.4 (Bronk-Ramsey, 2017; Reimer *et al.,* 2020). We calculated LORCA by dividing the sum mass of accumulated carbon by the basal date for each core (Clymo *et al.,* 1998).

4.4.3. Apparent rates of carbon accumulation (aCAR)

We calculated aCAR following an adapted version of methods by Belshe *et al.* (2019). Sedimentation rates from the rplum model for core BO17 were converted from y cm^{-1} to cm y^{-1} by converting the posterior probability density functions of the accumulation times from Gamma to inverse Gamma distributions. We calculated carbon accumulation rates by multiplying the accumulation rate (in cm y^{-1}) by organic carbon density for each sampling interval. Mean and median aCAR rates and 95 % confidence intervals were then calculated from the cumulative density function.

4.4.4. Palaeoenvironmental reconstructions

Hydrological variability was reconstructed using a testate amoebae-based water table depth reconstruction and plant macrofossil analysis (Andrews *et al.,* 2021). Bog surface wetness (BSW) was reconstructed by applying Dupont's Hydrological Indices (DHI) to the plant macrofossil data (Dupont, 1986). Changes in BSW mostly reflect changes in precipitation, which is linked to temperature (Charman *et al.,* 2009). Each component of the peat was allocated a score relative to its hydrological preference (1= wettest and 8= driest). Species not assigned DHI scores (following indices by Mauquoy *et al.,* 2008, with the addition of *Sphagnum denticulatum*) were removed from the dataset and relative percentage abundances recalculated. Taxa scores are listed in the appendices (Supplementary Text 2.1).

4.5. Experimental analyses

4.5.1. Experimental design

The Cors Fochno experiment is a long term, fully factorial climate manipulation experiment started in the spring of 2010. This experiment simulates year-round climate warming and increased growing-season drought frequency by using open top chambers (OTCs) (Aronson and McNulty, 2009) and by drawdown of the water table in summer approximately every three years. The experimental setup is fully described by Andrews *et al*. (2021). Climatic conditions (measured by a weather station operated by Natural Resources Wales) for the period 2010 – 2019 are presented in Table 4.1.

Table 4.1. Maximum, minimum and average climatic conditions measured on Cors Fochno between 29/04/2010 and 28/01/2019.

	WIND SPEED (M/S)	AIR TEMP (°C)	SOIL TEMP (10CM) (°C)	SOIL TEMP (30CM) (°C)	PRECIPITATION (MM/H)
MAX	15.7	32.26	24.04	17.99	21.73
MIN	0	-10	1	3	0
AVERAGE	3.15	11.15	12.01	11.97	0.12

4.5.2. Greenhouse gas fluxes and dissolved organic carbon measurements

Surface exchanges of CO_2 and CH_4 were measured using the closed chamber method (Alm *et al.,* 2007; Rowson *et al.,* 2013). Gas flux measurements were made by placing a closed chamber system upon a PVC collar inserted in the soil within each plot. A fan circulated the air inside the chamber, and a rubber seal prevented the exchange of gases between the chamber and the atmosphere. Each measurement took a minimum of two minutes. Air was circulated from within the chamber into a factory-calibrated EGM-4 Infra-Red Gas Analyser (PP Systems, MA, USA), which was used to measure CO_2 fluxes between 2010 and 2016. Air temperatures and photosynthetically active radiation (PAR) within the chamber were measured at 1 second frequency and recorded by a Delta-T GP1 Irrigation Monitor data logger. From 2017 onwards, a factory-calibrated Ultra-Portable Los Gatos Greenhouse Gas Analyser (Los Gatos, California) was used to measure CO_2 and CH_4 fluxes as well as ambient air temperature.

We measured the net balance of CO_2 sequestration/efflux as Net Ecosystem Exchange (NEE) and greenhouse gas emissions as Net Ecosystem Respiration (NER). Gross Primary Productivity (GPP) was inferred from the difference between these measurements (NEE-

NER). From November 2017, we also measured the NEE of CH_4. We use the micro-meteorological sign convention in this study, with negative values indicating a carbon sink and positive values indicating a carbon source.

Sampling points were monitored at irregular intervals during field excursions that took place between 2010 and 2020, with more frequent sampling taking place during summer months (>50 % of the total number of measurements). The number of measurements, and the months of the year in which these took place are shown in Table 4.2. Throughout the 10 years of monitoring, measurements were taken at all months of the year with the exception of April. Gas flux measurements began in July 2010 and ended in September 2011, resuming again in December 2017 at the beginning of this project, with the most recent measurements taken in August 2020. Further sampling took place between 2014 – 2016, however these data were lost and therefore not included in this thesis.

Although each season is reasonably well represented in the dataset, there is a bias towards summertime measurements. This is largely due to the regular daily sampling that took place during the six-week drought experiments. This may bias the results of this study, potentially resulting in the overestimation of emissions and plant productivity rates (Byrne *et al*., 2004). In addition, all measurements were taken between the times of 09:00 and 16:30, when daily temperatures and light-levels are likely to be highest. As a result, differences in greenhouse gas fluxes at night are not represented by this dataset (Pavelka *et al*., 2018). Emissions of CH_4 from peatlands can be greater at night than day

(Dooling *et al.,* 2018), whereas rates of CO_2 uptake and emissions decline (Goulsbra *et al.,* 2016). This may result in our estimates of CO_2 fluxes being overestimated, while CH_4 fluxes may be underestimated in this study

Table 4.2. Total number of gas flux measurements (net ecosystem exchange, gross primary productivity and net ecosystem respiration of CO_2 taken throughout the study. Measurements of net ecosystem exchange of CH_4 measurements were taken from 2017 onwards.

	2010	2011	2017	2018	2019	2020	TOTAL
ALL:	768	821	24	110	418	60	2201
JAN	0	24	0	0	0	0	24
FEB	0	24	0	12	0	12	48
MAR	0	24	0	0	24	0	48
APR	0	0	0	0	0	0	0
MAY	0	48	0	14	22	0	84
JUN	0	24	0	24	0	0	48
JUL	120	120	0	24	0	0	264
AUG	480	528	0	12	240	48	1308
SEP	96	29	0	0	120	0	245
OCT	24	0	0	0	0	0	24
NOV	24	0	0	24	0	0	48
DEC	24	0	24	0	12	0	60

NER was measured beneath a light impermeable cover. NEE was measured under ambient light conditions. CH_4 fluxes were calculated from measurements taken without a cover (Hutchinson and Livingston, 1993) and all measurements lasted >120 seconds. Gas-flux calculation methods followed Alm *et al.* (2007) using the closed chamber method (Dossa *et al.,* 2015). Any fluxes with an r^2 <90 % were visually assessed for poor measurements, in which case they were discarded.

Pore-water DOC samples were taken by extracting c. 40ml of pore water from each plot using a 50ml syringe attached to a Rhizon sampler (pore size 1.5µm) inserted 10cm beneath the peat surface. Samples were taken at irregular intervals from 2018 until 2020 and stored in cool and dark conditions to avoid degradation prior to analysis. Each sample was filtered through a 0.45 µm filter to remove particulate organic matter and promptly analysed after sampling. Filters were flushed using a small amount of sample to remove possible contaminants (Norrman, 1993). In some cases, samples were frozen after filtering. DOC concentrations were calculated using an Elementar Vario TOC Select analyser. We sampled pore-water DOC from each plot on 17 occasions, taken at the end of each field excursion from 2018 to 2020 (Table 4.3) Two samples were excluded from the dataset due to potential contamination.

Table 4.3. Total number and timing of dissolved organic carbon measurements taken throughout the study period (2018 – 2020).

	2018	2019	2020	TOTAL
ALL:	6	9	2	17
JAN	0	0	0	0
FEB	1	0	1	2
MAR	0	1	0	1
APR	0	0	0	0
MAY	1	1	0	2
JUN	1	0	0	1
JUL	1	0	0	1
AUG	1	4	1	6
SEP	0	2	0	2
OCT	0	0	0	0
NOV	1	0	0	1
DEC	0	1	0	1

We tested for differences in measured carbon fluxes between treatments with mixed effects linear models using the ‘me4’ package in the statistical package ‘R’ (Bates *et al.,* 2012; R core team, 2021). Environmental variables were included as model covariates, determined by single-term deletions.

4.5.3. Flux modelling of greenhouse gases.

We generated multi-year carbon budgets for each experimental plot using interpolation and extrapolation techniques. Carbon budgets were generated for the years 2011 to 2018 using environmental variables measured from within each plot. Models for each flux were generated using data collected after 2017, since these models had the best predictive power (R^2) and the lowest sum of squared error (SSE).

Annual NER for each plot was modelled based on measured fluxes using the (2z + S) model (Rowson *et al.,* 2013), which expands upon the widely used Lloyd and Taylor (1994) model. The (2z + S) model links the Arrhenius relationship between soil temperature and measured NER to plant functioning, accounting for feedbacks between water tables, plant root exudates and seasonality. We fit the derived parameters of the modelled NER to temperature and water table depth data from each plot. Seven constants required for the Rowson *et al.* (2013) model was identified using the generalised reduced gradient (GRG2) nonlinear optimisation code in Excel (Lasdon *et al.,* 1978).

To model GPP and CH_4 emission rates, linear and non-linear relationships between these fluxes and measured environmental variables were investigated for each plot. From these relationships, a continuous time-series of estimated greenhouse gas fluxes was extrapolated using 6-hourly instrumental measurements measured from 2010 – 2019 from within each plot Due to instrumental malfunctioning that occurred between 2017 and 2019, PAR measurements for the site were deemed unreliable, and efforts to gap-fill using weather station data produced erroneous results. To account for dark-induced plant senescence during periods of low light, we followed similar methods to Creevy *et al.* (2020), using light intensity data to eliminate GPP fluxes in the absence of PAR, however Creevy *et al.* (2020) modelled GPP based upon a second order (quadratic) polynomial relationship.

In the absence of streamflow data for the site, a simple model proposed by Ridley (2014) was used to calculate annual DOC fluxes from Cors Fochno. Annual evapotranspiration rates were subtracted from net rainfall for Cors Fochno measured between 2010-2019. The remaining value was multiplied by the mean pore-water DOC concentration for each plot, arriving at an annual estimate for DOC flux. Net annual rainfall from the site was calculated from continuous measurements taken from 2010 to 2019 from a location near Borth (Frondirion) (Figure 4.1b) (Justin Lyons, pers. comm.). Average pan evaporation rates from Plas Gogerddan, Aberystwyth (Figure 4.1b) (600 mm m^{-2} y^{-1}) were adjusted by a conversion factor of 0.7, accounting for the water-holding capacity of *Sphagnum,* giving an annual evaporation rate of 420 mm m^{-2} yr^{-1} (Ridley, 2014). This model assumes a bulk lateral sub-surface movement of rainfall throughout the peat and plug-flow of DOC throughout the system. It is assumed that all water not returned to the atmosphere by evapotranspiration is lost rapidly via overland flow. All water released from the site contains the same amount of DOC as was measured within the plots, and no mixing of water occurred. These assumptions are doubtful since mixing is likely to occur within Cors Fochno. Between 8 – 9.5 % of the water lost from the site is estimated to have moved through the catotelm (Baird *et al.,* 2006). Furthermore, while the majority of precipitation is likely to be quickly lost from the system via overland flow when the water table is high (Waddington and Roulet, 1997), lowering of the water-table may increase the water-holding capacity of the site, allowing more water to be retained (Holden, 2005). DOC production is also likely to exhibit high spatial variability due to differences in peat macroforms and vegetation, with areas dominated by grasses or sedges experiencing a greater supply of root exudates than areas dominated by *Sphagnum* or *Calluna vulgaris* (Ritson *et al*., 2017). These assumptions mean that the DOC fluxes estimated for this study are likely to have been overestimated.

Although not directly quantified in this study, dissolved inorganic carbon (DIC) and particulate organic carbon (POC) can also contribute significantly to the hydrological carbon budgets of peatlands (Rowson *et al*., 2010). Concentrations of POC have been shown to occur relative to those of DOC at a ratio of 1:10 in stream water draining from upland peat in the UK (Hope *et al.,* 1997; Heinemeyer *et al*., 2019). Dawson *et al.* (2002) found that POC constituted 22.7% of the total hydrological carbon flux from a Welsh peat-fed upland catchment, relative to 69% DOC. In relatively undisturbed ombrotrophic peatlands, POC fluxes are considered to be low and are generally not included in carbon budget studies (Lindsay, 2010). Here, we assume that the 1:10 ratio applies to Cors Fochno and estimate POC as being 10 % of annual estimated DOC fluxes.

Contributions of DIC are also likely to be small from Cors Fochno, due to the acidic nature of the peat pore-water at the site. In low pH waters that characterise ombrotrophic peatlands, DIC only occurs as dissolved free CO_2 and HCO_3^- ions (Neal and Hill, 1994) and there is likely to be little to no DIC input from groundwater or weathering within the central dome due to the ombrotrophic nature of this portion of the site (Reid *et al.,* 1981). Dawson *et al*. (2002) estimated that DIC from streams draining from two acidic peat-fed catchments in Scotland and Wales represented 2.1 % and 8.3 % of total hydrological fluxes, respectively. For both sites, average DIC concentrations were c. 3.0

mg l^{-1}. This average value was used to estimate annual DIC fluxes for the site, using the same model as was used to estimate DOC fluxes for each year. As these estimates for both POC and DIC are based upon the same model used to estimate DOC fluxes, they are subject to the same uncertainties, meaning estimates of both fluxes are likely to be overestimated in this study.

Annual budgets for each component of the carbon cycle were calculated for the years 2011 - 2018 by summing the modelled GPP, NER, CH_4, and DOC values for each year and plot. The modelled annual estimates for each carbon flux were multiplied by 6 to account for the 6-hourly intervals between measurements of environmental variables inside each plot The mass of each flux in terms of carbon (reported in units of g C m^{-2} y^{-1}) was calculated for each plot and year..

CH_4 is an important greenhouse gas with a global warming potential (GWP) c. 28 times that of CO_2*,* owing to its enhanced infrared absorptivity, and a shorter residence time in the atmosphere (Whiting and Chanton, 2001; Myhre *et al.,* 2011). We calculated the GWP for CH_4 to convert this gas to its CO_2 equivalent for 100 years by multiplying the total annual modelled CH_4 flux estimates by 28, following the GWP100 protocol (Myhre *et al.,* 2011). This was summed with NEE to calculate the total CO_2-equivalent emissions. We tested for significant differences of annual carbon budgets between treatments using generalised linear mixed effects models (GLMMs). Plots nested in blocks and year were included as random factors and treatments were set as fixed factors.

4.5.4. Environmental controls affecting aCAR

We compared core-derived aCAR throughout the whole core and in catotelmic peats against testate amoebae-derived water table depths and a qualitative measure for 'bog surface wetness' (BSW) using the DHI index by comparing the model fit of the data with a suite of linear and non-linear regressions. BSW is a qualitative measure of past hydroclimatic conditions at the peatland surface and is driven mostly by changes in precipitation reinforced by temperature (Charman *et al.,* 2009). The influence of climate was tested by comparing aCAR with a 1000 year-long reconstruction of mean annual temperature anomalies for the Northern Hemisphere (Mann *et al.,* 1999) and the Central England Temperature (CET) dataset (Manley, 1953; 1974; Parker *et al.,* 1992; Parker and Horton, 2005) using cross-correlation analysis ('BINCOR' package, Polanco-Martínez *et al.,* 2019). This approach, proposed by Mudelsee (2010), calculates correlations between values obtained on different time points.

4.6. Results

4.6.1. Tephrochronology, ^{210}Pb and improved age-depth model

We identified three tephra layers in core BO17, at 13 cm (BO17-1), 27cm (BO17-2) and 37 cm (BO17-3). Identified shards possessed similar geochemistry to layers previously identified in Cors Fochno by Watson *et al.* (2017). Tephra are identified by comparing the geochemical data generated in this study with the results of previous studies (Swindles *et al.,* 2010). We compared the geochemistry of these shards with tephra shard geochemistry profiles from Britain, the Republic of Ireland, Northern Ireland, and

Iceland (Figure 4.2) and concluded that sherds derived most likely from the eruptions of Hekla in 1947 (tephra BO17-1), 1845 (BO17-2) and 1510 CE (BO17-3). These age assignments are consistent with the ^{210}Pb, SCP, charcoal and ^{14}C chronologies. (Supplementary Figure 2.2)

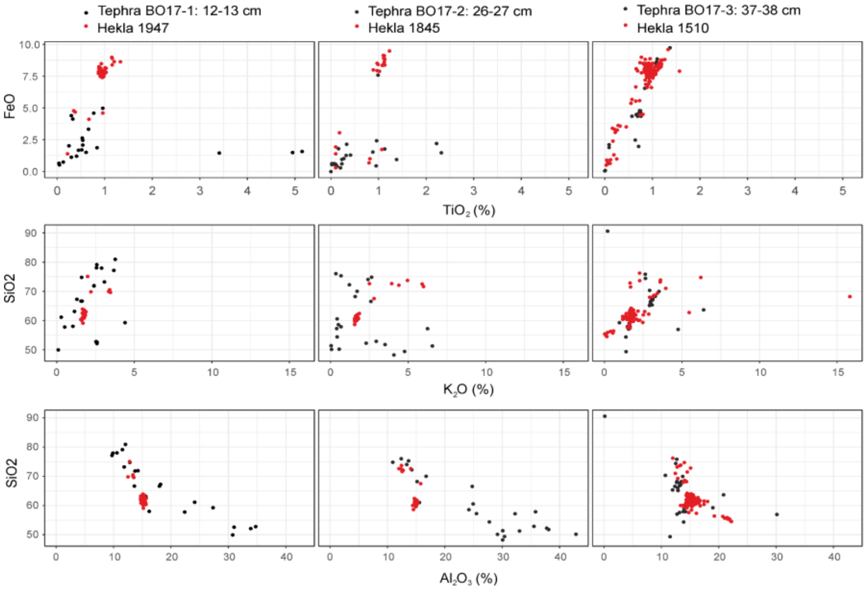

Figure 4.2. Major element bi-plots showing tephra shard glass chemistry from the BO17-1, BO17-2 and BO17-3 layers detected from core BO17 at Cors Fochno (shown as black points) contrasted with the glass geochemistry of known tephras based on type data (Swindles, 2006; Pilcher *et al.,* 1996; Watson *et al.,* 2015; Matthews, 2008; Housley *et al.,* 2010; Cole and Mitchel, 2003; Rea *et al.,* 2012; Dugmore *et al.,* 1995 and Larsen *et al.,* 1999) shown as red points.

The three new tephra dates and ^{210}Pb data were added to the previous age-depth model for core BO17 generated by spheroidal carbonaceous particles, microcharcoal and radiocarbon dates (Andrews *et al.,* 2021). The position of these dates within the ^{210}Pb profile generated in this study are illustrated in Supplementary Figure 2.2. The new Bayesian age-depth model generated in rplum, incorporating former and newly generated dates, is shown in Figure 4.3. Accumulation rates notably slow down between the Hekla 1845 and the Hekla 1510 tephra-horizons, suggesting that peat accumulation rates were exceptionally low between these dates.

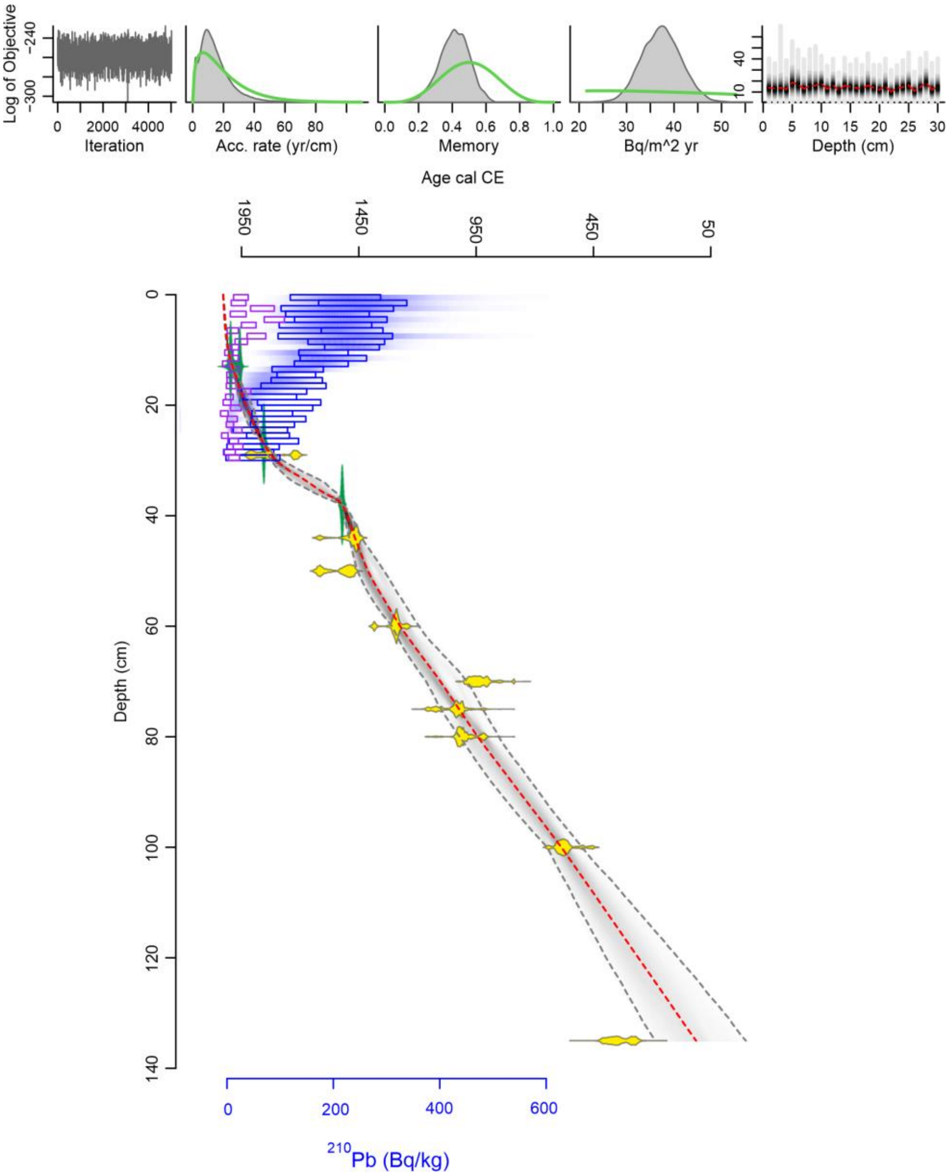

Figure 4.3. Age-depth model for core BO17 plotted using rplum (Aquino-López *et al.,* 2018; 2020). Dark blue shapes indicate posterior distributions of ^{14}C dates, green shapes indicate calendar dates (tephra horizons, charcoal, or spheroidal carbonaceous particle dates). Yellow shapes within the plot reflect the probability density functions for ^{14}C dates. The shaded bars towards the top of the profile show the supported (purple) and unsupported (light blue) ^{210}Pb activity and their uncertainties. The plots on the top of the figure show model performance and parameters, illustrating (from left to right) 1: the MCMC iterations 2: the prior (green) and posterior (grey) distributions for the accumulation rate α, 3: memory ω, 4: ^{210}Pb supply and 5: the supply of supported ^{210}Pb.

4.6.2. Long term apparent rate of carbon accumulation (LORCA)

LORCA estimates for all three cores showed good agreement. Mean LORCA values were 31.3 ± 2.1 g C m^{-2} y^{-1} (2σ). The basal date for BO18-1 was younger than BO18-2 and BO18-3 by c. 300 years. Details of the carbon content carbon throughout each core and their basal ages are provided in Supplementary Figure 2.3 and Supplementary Tables 2.8 – 2.9.

4.6.3. aCAR and palaeoenvironmental reconstruction

Reconstructed aCAR, along with changes in bog surface wetness, inferred water table depth, macrocharcoal and changes in vegetation throughout core BO17 are shown in Figure 4.4. The median aCAR for the whole of core BO17 was 45 (40 - 52) g C m^{-2} y^{-1}. High aCAR occurs in the acrotelm above 12cm, following c. 1985 CE. Median aCAR for this period was 127 (105 - 157) g C m^{-2} y^{-1}. For catotelmic peat (beneath 12cm) median aCAR was 34 (30 - 42) g C m^{-2} y^{-1}. For the time-periods encompassing the Medieval Climate Anomaly (c. 950 – 1250 yrs. CE) and LIA (c.1300 – 1850 yrs. CE) aCAR was 33 (26 – 43) and 34 (27 – 5 0) g C m^{-2} y^{-1} respectively; however, aCAR rates throughout the Little Ice Age varied substantially.

The Dupont Hydrological Index and water table depth reconstructions show good agreement, with major trends in reconstructed water table depth being reflected by simultaneous shifts in the same direction in the DHI curve. For example, increasing water tables coincide with increased bog surface wetness between c. 1600 – 1800 CE (Figure 4.4). Bog surface wetness fluctuates between the periods c. 590 – 740 CE and c. 1320 –

1460 CE, with a general trend towards reduced BSW coinciding with macrocharcoal peaks; however, this is not reflected by the reconstructed water table. This is likely an artefact of the effect of the burning event upon plant community composition resulting in a shift in the botanical composition of the peat currently. DHI values were inflated owing to the low relative abundance of *Sphagnum* and other wet indicator species during this time, with the peat being composed mostly of ericaceous rootlets during this period inflating the DHI value (Andrews, 2021).

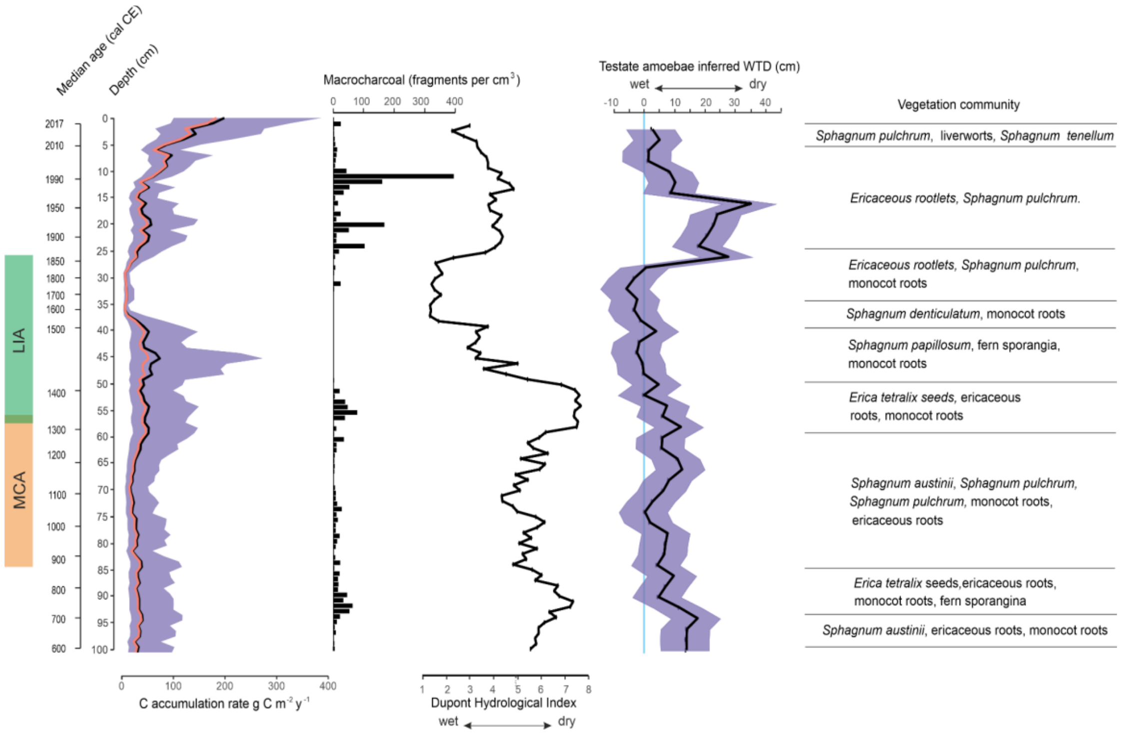

Figure 4.4. Apparent rate of carbon accumulation (aCAR) from core BO17, estimated using methods outlined by Belshe *et al*. (2019). The red line is the mean, the black line signifies the median aCAR and the purple shading is the 95% probability distribution function for each depth. This is plotted against (from left to right) the macrocharcoal, Dupont Hydrological Index and testate amoebae-derived water table depth reconstruction for core BO17 (Andrews *et al.,* 2021). The light blue horizontal bar running through the testate amoebae water table depth reconstruction indicates the position of the water table. The horizontal bars on the far left of the figure show the time envelope (minimum and maximum age range) of the Medieval Climate Anomaly (MCA; orange) and the Little Ice Age (LIA; green).

4.6.4. Correlation with environmental conditions

No significant cross correlation occurred between aCAR and the CET temperature record (Figure 4.5a). A significant negative time-lagged correlation was identified between reconstructed Northern Hemisphere temperature anomalies and aCAR (CCF; $r_{x,y}$ =0.454 at 95 % C.I., lag=14), indicating that temperature increases are preceded by reduced aCAR by 129 – 164 years (Figure 4.5b). The direction of this relationship is reversed when acrotelm aCAR is excluded (Figure 4.5c): increased temperatures precede increased aCAR by c. 51 years (CCF; $r_{x,y}$ =0.369 at 95 % C.I., lag=-5).

To handle negative values, a constant (+10) was added to the reconstructed water table depths to plot these values on a negative axis. We found that the relationship between the palaeoecological proxies and carbon accumulation rates were best explained with logarithmic models. This may relate to the logarithmic relationship between average annual temperatures and peat decomposition rates commonly seen in peatlands (Clymo *et al*., 1998). Weak but highly significant relationships were identified between aCAR and both reconstructed water table depths ($p = <0.001$; $R^2 = 0.17$) and BSW ($p = <0.001$; $R^2 = 0.31$) (Figure 4.6a-b) for the catotelmic portion of the core. These relationships remained significant when aCAR for the whole core (including the acrotelm) were included between reconstructed water table depths ($p = <0.01$; $R^2 = 0.17$) and BSW ($p = <0.02$; $R^2 = 0.06$) (Figure 4.6c-d).

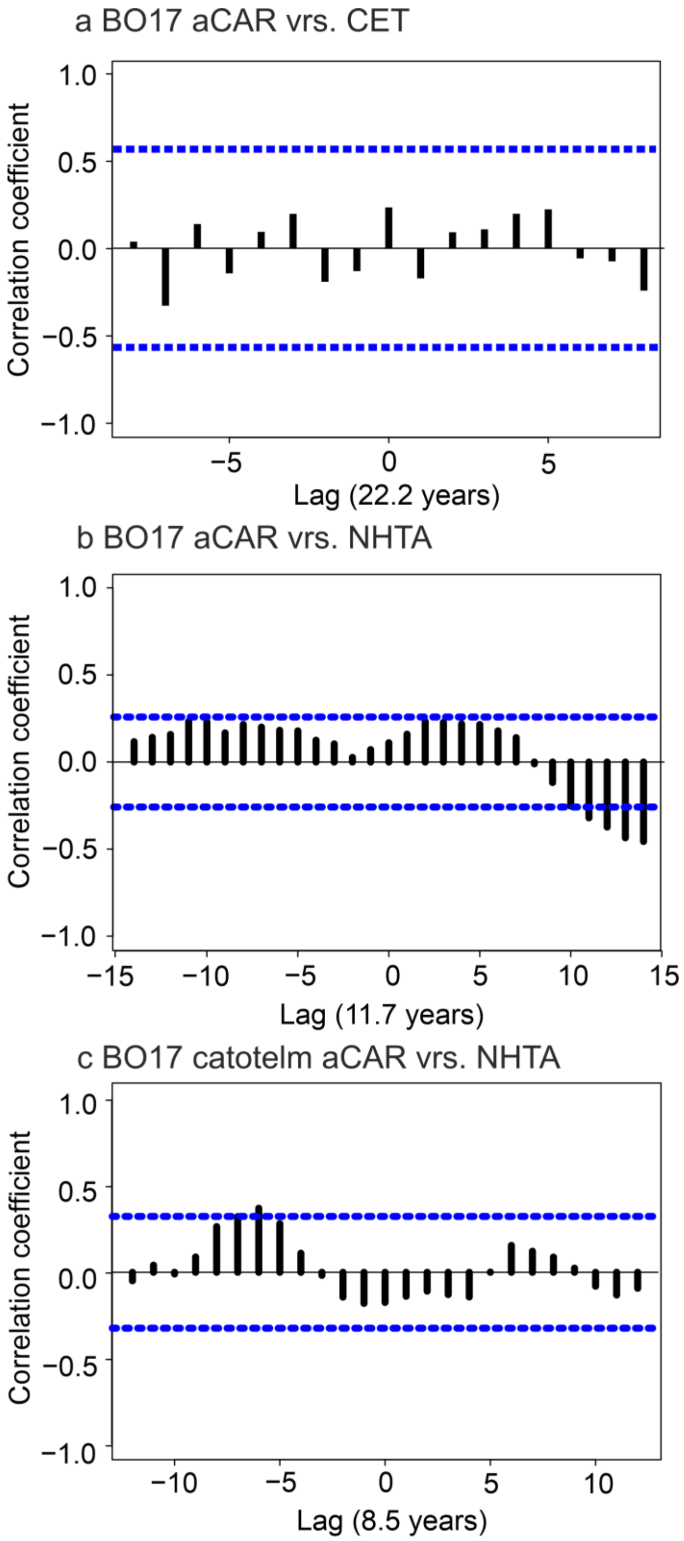

Figure 4.5. Cross correlation functions showing time-lagged correlations between a: apparent rates of carbon accumulation (aCAR) throughout core BO17 and the central England Temperature (CET) series; b: aCAR and reconstructed temperature anomalies for the Northern Hemisphere (NHTA) and c: aCAR beneath the catotelm and Northern Hemisphere temperature anomaly reconstruction.

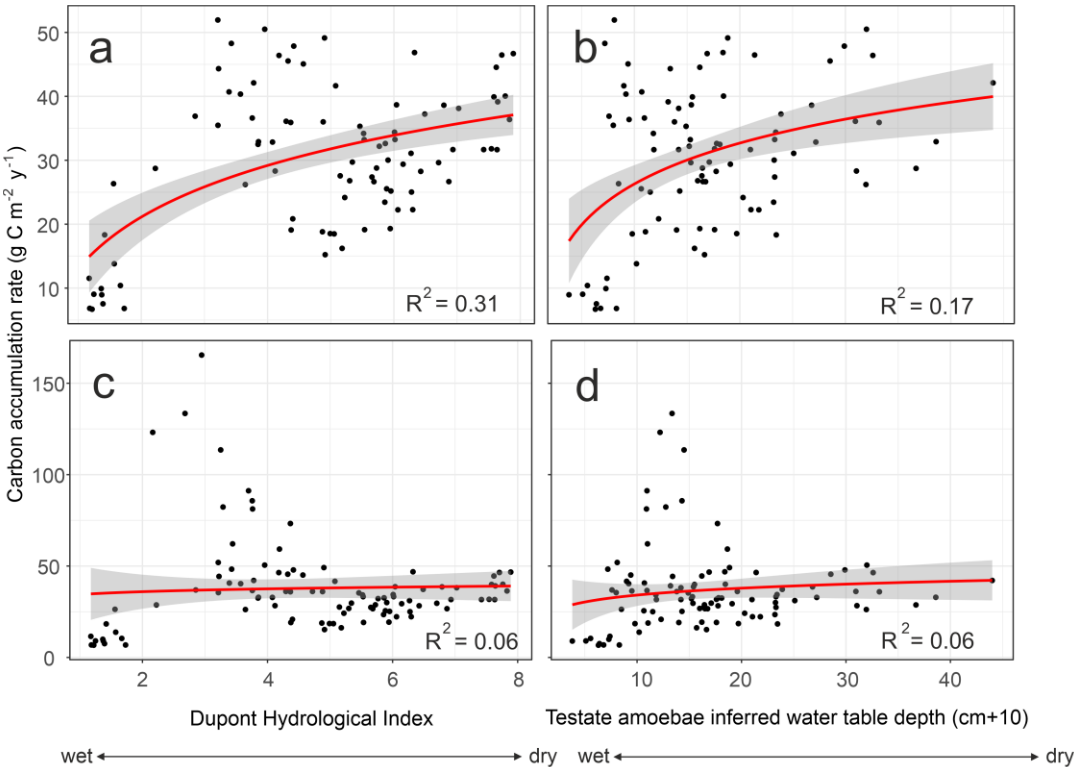

Figure 4.6. Logarithmic models showing the relationships between hydrological proxies (a and c: Dupont Hydrological Index; b and c: Testate amoebae derived water table reconstructions) for core BO17 and apparent rates of carbon accumulation throughout the core. Plots a and b are for the catotelmic peats, whereas plots c and d are for the whole core. Grey shaded areas show the 95% confidence interval for each regression model.

4.6.5. Environmental variables and experimental treatment effects

Continuous six-hourly time series for temperature (air and soil at 10 cm depth) and water table depth were measured between 27/08/2010 and 06/08/2019 for each plot. This allowed the calculation of annual net ecosystem carbon budgets (NECB) for each plot for the years 2011 to 2018 (the years for which full annual temperature records were available). The results of the generalised linear models are provided in Table 4.4. Average six-hourly time series data across all plots for all measured climatic variables are given in Supplementary Figure 2.1.

Table 4.4. Summary of generalised mixed effects linear models testing for treatment effects upon environmental conditions (air and soil temperature at 10cm depth, water table depth), for the years 2011-2018. Values for Gross Primary Productivity (GPP), Net Ecosystem Exchange (NEE), Net Ecosystem Respiration (NER) are g CO_2 M^{-2} h^{-1}. CH_4 values are g CH_4 M^{-2} h^{-1}. Dissolved Organic Carbon (DOC) concentration values are g/l^{-3}. Fixed factor (treatment) estimates are the mean effect of the fixed factor upon the measured variable, with CI showing the 95% confidence interval for this estimate.

	Air temperature °C				**10cm depth soil temperature °C**				**Water table depth (cm)**			
Treatment	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**P**	**Estimates**	**CI**	**Statistic**	**P**
Controls (Intercept)	11	10.6 – 11.5	47.4	**<0.001**	11.4	10.9 – 11.9	41.9	**<0.001**	8.2	5.2 – 11.2	5.3	0.001
Warmed	0.8	0.1 – 1.4	2.4	**0.042**	0.2	-0.5 – 0.9	0.6	0.571	-1	-4.8 – 2.9	-0.5	0.641
Drought	0.1	-0.5 – 0.7	0.2	0.837	-0.5	-1.2 – 0.2	-1.4	0.197	1	-2.9 – 4.8	0.5	0.636
Combined	0.1	-0.5 – 0.7	0.4	0.688	0.6	-0.2 – 1.3	1.5	0.169	1.9	-1.9 – 5.8	1	0.361
Warming	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**P**	**Estimates**	**CI**	**Statistic**	**P**
Controls (Intercept)	11.1	10.7 – 11.4	59.3	**<0.001**	11.1	10.7 – 11.5	54	**<0.001**	8.7	6.4 – 11.0	7.3	**0.001**
All warmed	0.4	-0.1 – 0.9	1.7	0.123	0.6	0.1 – 1.2	2.4	**0.038**	0	-2.8 – 2.8	0	0.999
Drought	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**P**	**Estimates**	**CI**	**Statistic**	**P**
Controls (Intercept)	11.4	11.0 – 11.8	57.6	**<0.001**	11.5	11.0 – 12.0	45.7	**<0.001**	7.7	5.5 – 9.9	6.8	**0.003**
Drought	-0.3	-0.8 – 0.2	-1.1	0.31	-0.1	-0.8 – 0.6	-0.3	0.797	1.9	-0.5 – 4.4	1.6	0.159

Average annual air temperatures varied by less than 2°C between years, with the warmest year being 2017. Average air temperature in the warmed treatment plots was significantly higher than controls by c. 0.8°C, however there was no significant difference in air temperature between the combined (warmed and droughted) plots and controls. Mean soil temperatures varied little by year, ranging between 11 and 12°C. Soil temperature was significantly higher in both the warmed and the combined (warmed plus droughted) plots than those plots without OTCs, by c. 0.6°C, indicative of a warming effect owing to the presence of OTCs.

Mean water table depths varied between years, with water table declines occurring during (natural) drought years in 2014 and 2018. During these years, mean water table depths were c. 11 cm deeper than average. Over the ten years of the study, mean water table level fell by 5 cm, indicating that the site is becoming drier, possibly due to ongoing reductions in summer precipitation rates and increased temperatures for the region (Compo *et al.,* 2011; Swindles *et al.,* 2019). There was no significant effect of the four experimental summer droughts on the average water table over the seven-year period, suggesting that, although groundwater pumping significantly changed water table depths in the droughted plots (Andrews *et al.,* 2021), simulated droughts did not have a long-term effect upon water table depths.

4.6.6. Measured components of the peatland carbon budget

The results of the generalised linear mixed effects models on the measured components of the peatland carbon budgets are shown in Supplementary Table 2.7. Significant differences in net ecosystem exchange were identified in all warmed plots. This effect was the same between warmed and combined treatment plots, with a mean reduction of c. 0.07 g CO_2 m^{-2} h^{-1} across both treatments relative to controls. We also found that CH_4 efflux was significantly reduced with warming, by 0.36 mg CH_4 m^{-2} h^{-1} relative to controls.

4.6.7. Modelling of CO_2 and CH_4 fluxes

Use of the (2z + S) model to estimate NER of CO_2 improved the average R^2 of each plot from 0.29 to 0.49 compared with the Lloyd and Taylor (1994) model and reduced the SSE from 0.37 to 0.20. Therefore, the Rowson *et al.* (2013) model was used since it provided a more robust estimate of annual NER due to the improvements in fit and error terms compared to the Lloyd and Taylor model. This model reduces the probability that

NER emissions will be underestimated during the summer months and overestimated in the winter (Rowson *et al.,* 2013). However, model improvements were modest, and the models only explain ~ 50 % of the variance in the data on average, therefore our confidence in these model projections is relatively low.

The models used in this study to estimate annual fluxes of NER, GPP and CH_4 showed relatively poor agreement with the measured data, although the degree of this agreement varied between each plot and for each flux. In general, the disagreement was highest during warmer periods. For NER of CO_2, the modelled coefficient of determination varied between plots (range $R^2 = 0.28 – 0.76$). The relationship between observed and predicted NER is illustrated by Figure 4.7.

CH_4 fluxes were extrapolated based upon their exponential relationship with soil temperature, shown in Figure 4.8. A similar exponential response of CH_4 to soil temperature was found by Zhu *et al.* (2020), relating to the temperature dependence of processes that govern the production and oxidation of CH_4. Water table level and soil temperature are usually the dominant controls of methane fluxes in peatlands, due to soil temperatures influencing the rate of microbial processes and water tables governing the depth of the area where methanogenesis can take place (Ma *et al.*, 2017). However, including water table depth in the models resulted in unrealistic estimates of methane emissions rates in this study. Large uncertainties are common in models of CH_4 emissions from peatlands (Ma *et al.,* 2017). In the case of this study, the model shows relatively poor predictive ability where temperatures and fluxes of CH_4 are highest. This is possibly due to large increases in CH_4 emission that were seen during the start of the 2019 drought period. The poor model fits may relate to ebullition events following the rapid removal of pore-water from the plots.

In the absence of a reliable time series of PAR data, GPP were modelled based upon the exponential relationship between GPP and soil temperature (Figure 4.8). The modelled coefficient of determination varied between plots (range R^2 = 0.11 – 0.59, mean= 0.32). The R^2 for all models used are shown in Table 4.5. The applicability of an exponential model to explain temperature sensitivity of GPP is supported by Zhang *et al.* (2017), where an exponential model was used to fit respiration rates with temperature for temperate terrestrial non-forest ecosystems, including permanent wetlands. This exponential relationship may relate to the temperature dependence of photosynthesis. Zheng *et al*. (2016) state that conceptually, GPP may decrease were a temperature threshold to be crossed. Therefore, this exponential model is dependable only within the normal range of temperatures experienced at the site. The use of this model may have resulted in an overestimation of GPP rates during extreme heatwave events (e.g., the summer of 2018), which may explain the larger residuals that occur under warmer conditions (Figure 4.8).

Comparisons between modelled and measured fluxes are shown in figures 4.9 – 4.11 for CH_4 efflux, GPP and NER respectively. These show that the modelled data were in general agreement with the measured data, although large departures occur for all, particularly for certain plots during the summer months.

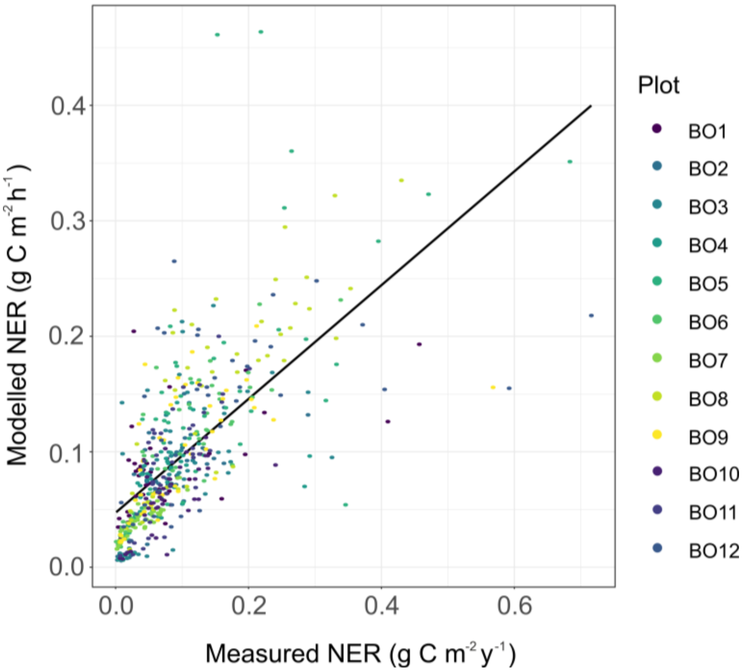

Figure 4.7. Biplot of observed and predicted net ecosystem respiration rates for the (2z + S) model (Rowson *et al.*, 2013). The black line shows the line of best fit for all modelled values.

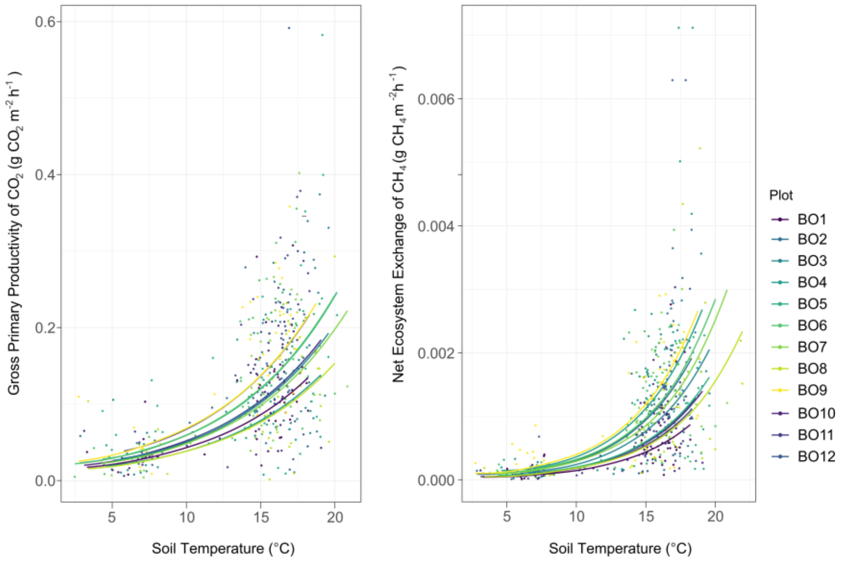

Figure 4.8. Exponential models used to estimate gross primary productivity of CO_2 and net ecosystem exchange of CH_4 using continuous measurements of soil temperature taken from within each plot. The points show the measured values for each flux while the lines show the exponential line of best fit used to estimate these fluxes.

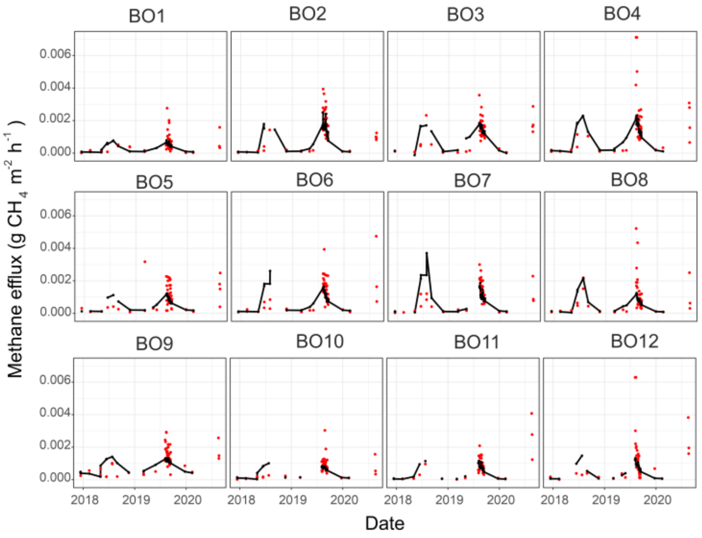

Figure 4.9. Timeline comparisons of predicted (black dots and lines) and measured (red dots) methane efflux rates for each plot from November 2017 - August 2020. The black line shows the trend between adjacent points in the predicted data.

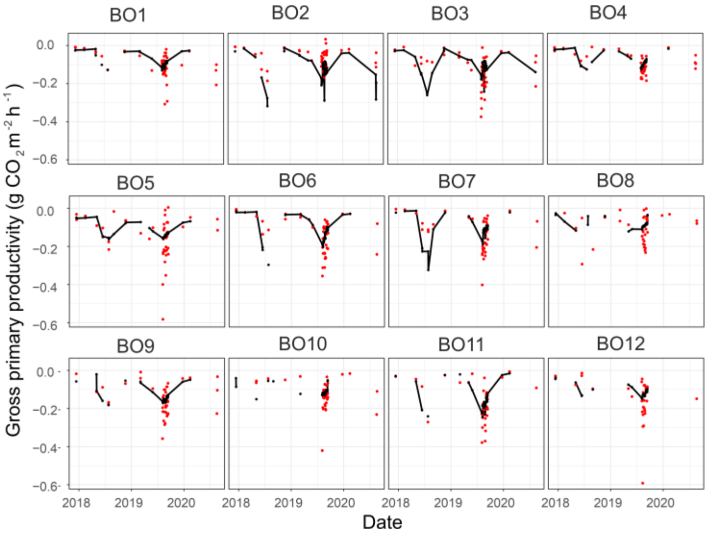

Figure 4.10. Timeline comparisons of predicted (black dots and lines) and measured (red dots) gross primary productivity rates for each plot from November 2017 - August 2020. The black line shows the trend between adjacent points in the predicted data.

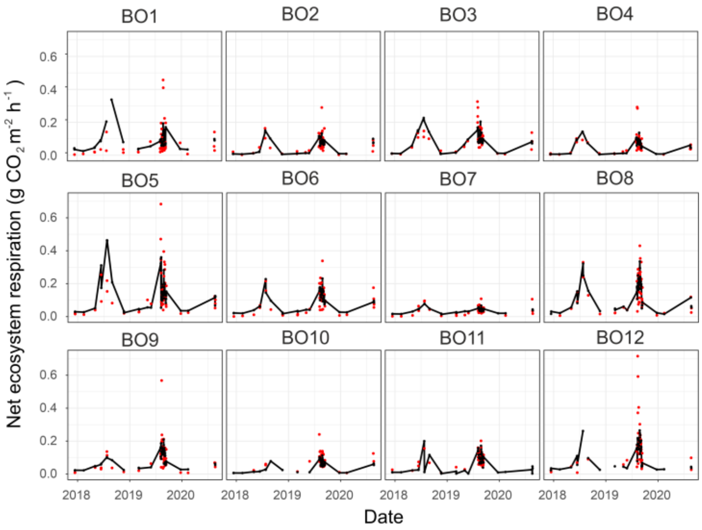

Figure 4.11. Timeline comparisons of predicted (black dots and lines) and measured (red dots) net ecosystem respiration rates for each plot from November 2017 - August 2020. The black line shows the trend between adjacent points in the predicted data.

Table 4.5. R^2 values for models chosen for NER and GPP of CO_2 and CH_4 fluxes.

NER (CO_2)	**R^2**	**GPP (CO_2)**	**R^2**	**CH_4**	**R^2**
BO1	0.31	BO1	0.26	BO1	0.29
BO2	0.51	BO2	0.56	BO2	0.63
BO3	0.52	BO3	0.29	BO3	0.36
BO4	0.32	BO4	0.38	BO4	0.31
BO5	0.38	BO5	0.26	BO5	0.25
BO6	0.68	BO6	0.33	BO6	0.25
BO7	0.76	BO7	0.19	BO7	0.25
BO8	0.71	BO8	0.26	BO8	0.27
BO9	0.35	BO9	0.33	BO9	0.32
BO10	0.50	BO10	0.35	BO10	0.29
BO11	0.59	BO11	0.59	BO11	0.42
BO12	0.27	BO12	0.12	BO12	0.27

4.6.8. Modelled greenhouse gas fluxes and annual budgets

Modelled annual carbon fluxes are illustrated as box plots in Figure 4.12. The results of the generalised linear mixed effects models on the modelled components of the greenhouse gas budget are given in Supplementary Table 2.8. We identify a significant treatment effect upon modelled net ecosystem exchange. Pairwise comparisons identified significant differences between control and warmed plots, combined and control, and combined and drought plots, with differences being mostly due to a significant effect of experimental warming (Supplementary Table 2.7). Control and drought treatment plots were consistent sinks of CO_2, sequestering 221.5 ± 111.6 and 162.6 ± 62.2 g CO_2 m^{-2} $y^{-1,}$ respectively. These are within the range of annual net ecosystem exchange rates of CO_2 reported by Roulet *et al*. (2007) from raised bogs in Canada (7 to 411 g CO_2 m^{-2} y^{-1}) and by Arneth *et al*. (2002) of 179 to 223 g CO_2 m^{-2} y^{-1} from raised bogs in Siberia. Combined treatment plots were a consistent source of $CO_{2,}$ emitting at a rate of 14.3 ± 88.0 g CO_2 m^{-2} y^{-1}, an increase of c. 106 % while treatment plots subjected to warming alone were small sinks of carbon, sequestering 97.9 g CO2: 56 % less than controls.

Modelled annual CO_2 respiration was on average 256.1 ± 120.6 g CO_2 m^{-2} y^{-1} across all plots. Control plots were the lowest emitters of CO_2, averaging 163.7 ± 21.7 g CO_2 m^{-2} y^{-1}. Net ecosystem respiration significantly increased both due to combined warming and drought, as well as due to the presence of OTCs Warming and drought increased CO_2 emissions by c. 205 CO_2 m^{-2} y^{-1} relative to controls, while annual respiration rates increased by c. 139 CO_2 m^{-2} y^{-1} relative to controls across all plots with OTCs (Supplementary Table 2.7).

We identified no significant effects of treatment upon gross primary productivity, which was on average -373.1 ± 90.3 g CO_2 m^{-2} y^{-1} across all plots. Estimated annual dissolved organic carbon fluxes were on average 25.0 ± 5.9 g C m^{-2} y^{-1} between all plots across all measurement years and did not differ significantly due to the treatments. Although no significant changes occurred in DOC due to the treatments, slight differences in the median values suggest that drought had a slight positive effect upon DOC production. This may relate to changes in the physical and chemical structure of the peat following drying, resulting in increased DOC production rates (Holden and Burt, 2002; Holden, 2005). DOC constituted a significant carbon flux in our experimental plots, representing an average of 27.5 ± 8.8 % of all modelled annual carbon fluxes. Our DOC flux estimates are relatively high compared to ranges reported from other studies of raised bogs. For example, in Canada DOC fluxes rates ranged between 13 – 21 g C m^{-2} y^{-1} and in Sweden they were much lower, between 4.2 – 6.7 g C m^{-2} y^{-1} (Waddington and Roulet, 2000; Roulet *et al.*, 2007). The estimates reported here exceed those reported from a UK upland peat complex (Dawson *et al.*, 2002). This suggests that the DOC fluxes predicted in this study using the plug flow model of Ridley (2014) were overestimated.

Estimated POC and DIC fluxes were very low for the site. If the 1:10 ratio for POC:DOC concentration is assumed to hold true for Cors Fochno, then POC is released from the site at an average rate of 2.5 ± 0.5 g C m^{-2} y^{-1} across all treatment plots. Estimated annual DIC fluxes were roughly equal to POC fluxes, at 2.6 ± 0.5 g C m^{-2} y^{-1}. Together, we estimate that POC and DOC represent c. 20 % the total hydrological carbon flux. As with DOC, this value may be an overestimation, however these estimates do not consider the increasing effects that drought and storm events may have upon these fluxes (Hope *et al.*, 1994).

4.6.9. Methane, methane-CO_2 equivalent emissions and annual net carbon budgets

Annual estimated methane fluxes were on average 4.89 ± 1.3 g CH_4 m^{-2} yr^{-1} between all experimental plots. This is within the range of 4 – 6 g CH_4 m^{-2} yr^{-1} reported from raised bogs in Canada (Roulet *et al*., 2007) and is close to a reported average of 5 g CH_4 m^{-2} yr^{-1} from a Swedish raised bog (Waddington and Roulet, 2000). Net ecosystem respiration of CH_4 was 5.3 ± 0.9 g CH_4 m^{-2} y^{-1} in the control plots and 6.4 ± 1.0 g CH_4 m^{-2}. Emissions were significantly lower in the combined warmed and drought plot, which emitted CH_4 at a rate of 3.8 ± 0.9 g CH_4 m^{-2} y^{-1}. The presence of OTCs significantly reduced CH_4 emissions from an average of 5.9 ± 0.9 g CH_4 m^{-2} y^{-1} to 4.1 ± 0.9 g CH_4 m^{-2} y^{-1}, a reduction of c. 1.7 g CH_4 m^{-2} y^{-1}, a change of c. 29 %. Annual estimates for carbon dioxide equivalent CH_4 emissions varied widely across all plots (22.9 ± 127.5 g C m^{-2} y^{-1}), with significant differences identified between treatments.

Total estimated annual carbon budgets differed significantly between treatments. The control plots had the highest carbon accumulation rates, with average annual accumulation budgets of 56.4 ± 30.4 g C m^{-2} y^{-1}. This estimate is within the estimated range for the annual carbon budgets of two UK blanket bog sites (56 – 72 g C m^{-2} y^{-1}) (Billet *et al.,* 2010), although it is greater than estimates by Dinsmore *et al.* (2009) for Auchencorth Moss (30.7 g C m^{-2} y^{-1}), an ombrotrophic bog in Scotland. The combined warming and drought treatments had the lowest overall carbon accumulation rates, which we estimated to be losing carbon at a rate of 34.6 ± 23.3 g C m^{-2} y^{-1}. Warming alone also significantly reduced annual carbon sequestration by 40.3 ± 13.4 g C m^{-2} y^{-1} in comparison to control plots, although these plots were still on average weak sinks of carbon, accumulating 0.6 ± 37.9 g C m^{-2} y^{-1}.

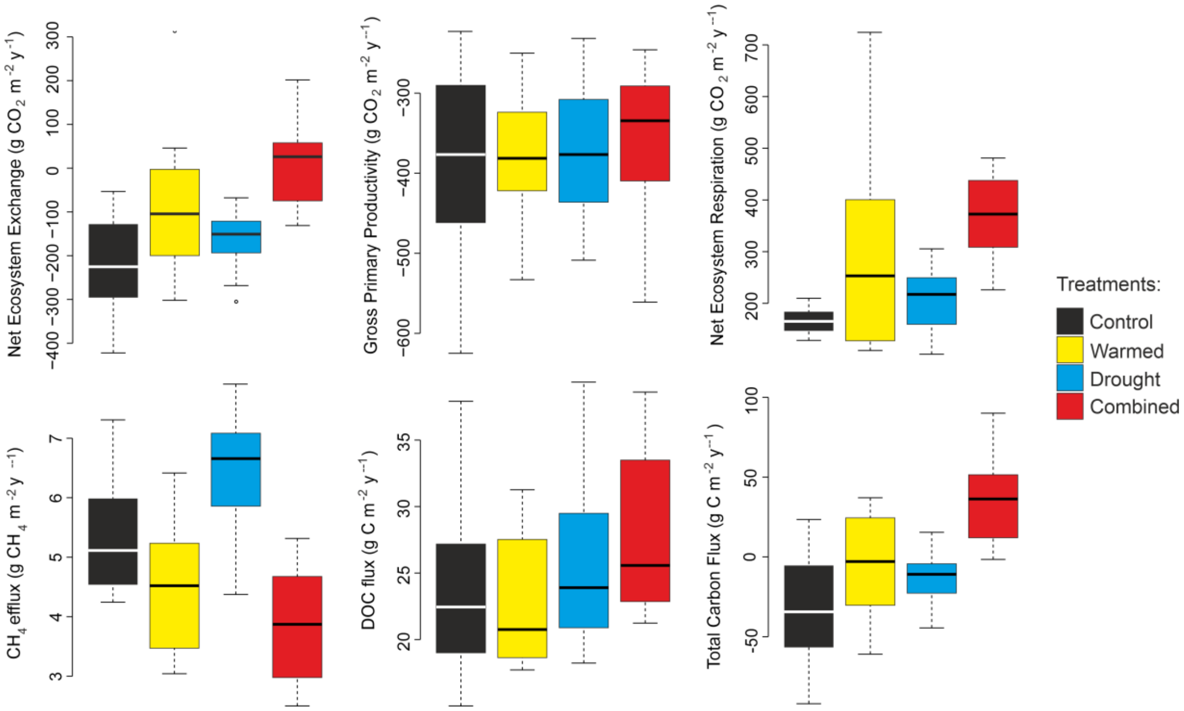

Figure 4.12. Box plots of modelled annual carbon budget flux components, displaying differences by treatment, from the Cors Fochno experimental site. Years modelled were 2011-2018.

4.7. Discussion

4.7.1. Explaining the discrepancy between contemporary and core derived carbon accumulation

We find that the inferred environmental variables governing carbon accumulation rates differ between the experimental study and the long-term record. In the experimental study, carbon accumulation rate (NEE) is driven mostly by water table depth and the availability of photosynthetically active radiation (PAR). Respiration (NER) increases with increased air temperature, reflecting increased decomposition rates in the acrotelm with warming (Bu *et al.,* 2011). Primary productivity is mainly governed by air temperature and photosynthetically active radiation, likely reflecting increased productivity during the summer. Including aCAR from surface peats appears to produce weaker correlations when compared with past changes in hydrology or temperature (Figure 4.6). This likely relates to the known 'acrotelm effect,' occurring due to the incomplete decomposition of organic material above the catotelm causing apparently high carbon accumulation rates in this section of the core (Young *et al.,* 2019).

No significant relationship was found between carbon accumulation rates and the Central England Temperature record. This likely relates to the low number of binned data points (n = 14) for this analysis using the BINCOR method, highlighting the difficulty of correlating palaeoecological data with even relatively long instrumental datasets. We caution against interpreting changes in aCAR in recently accumulated peats in relation to changes in climate or any other environmental variable, since the increased aCAR in acrotelmic peats are the result of incomplete decomposition and therefore do not realistically reflect long-term carbon accumulation rates (Young *et al.,* 2019).

When acrotelmic peats are excluded from the analysis, we report a positive time-lagged relationship with air temperature anomalies, with increases in aCAR appearing to occur prior to temperature increases by 52 years. This lag may reflect the amount of time organic material spends in the aerobic acrotelm before it is incorporated into the anaerobic catotelm, as peat humification is often considered to be a measure of this initial period of decay (Chambers *et al.,* 2011) . This suggests that warming may benefit long term carbon retention in sub-surface peat (Clymo, 1984; Frolking *et al.,* 2014). However, chronological uncertainty increases in the lower sections of the core, due to a paucity of additional dating methods other than ^{14}C for these sections. Therefore, this time lag may simply be the result of chronological uncertainty in our age-depth model (Polanco-Martinez *et al.,* 2019).

It is important to note that the analyses here are based upon measurements from a single core. These carbon accumulation rates may not be representative for the site as a whole. Within-site comparisons of carbon accumulation rates derived from cores can show considerable variation, relating to spatial differences in vegetation community composition and macroforms (Turunen *et al.*, 2004; Loisel and Garneau, 2010). Furthermore, the effects of temperature upon carbon accumulation at Cors Fochno are likely to differ from the hemispheric average calculated by Mann *et al.* (1999). While there is greater legitimacy in making a geographical teleconnection with the Central England Temperature Record, this record proved too short for correlations to be made. This highlights the difficulty of correlating peatland long-term palaeoecological records with meteorological datasets.

Despite the results of these correlations, there are notable exceptions within the palaeoecological record where carbon accumulation rates increase during relatively wetter/cooler periods. Carbon accumulation rates were more variable during the Little Ice Age than during the Medieval Climate Anomaly, despite no significant overall differences in mean aCAR during these periods. In core BO17, between c. 1150 and 1450 CE, aCAR showed an increase. This followed a shift in the botanical composition of the peat, characterised by a transition from *Sphagnum austinii/Sphagnum pulchrum* to *Erica tetralix* and monocot-dominated communities. Accumulation rates increased again following a shift towards *Sphagnum papillosum* dominance between c. 1410 and 1460 CE. As water tables continued to increase throughout this period, aCAR rates rapidly declined until reaching their lowest values c. 1600 CE, coincident with the development of bog pool conditions dominated by *Sphagnum denticulatum* remains (Andrews *et al.,* 2021). During this time, there is an apparent reduction in peat accumulation in the age-depth model. Carbon accumulation rates fell as the site became increasingly wet, and aquatic conditions persisted at the coring location until the development of the modern-day vegetation community around c. 1850 CE, coincident with a period of abrupt water table drawdown attributed to drainage activity (Poucher, 2009; Andrews *et al.,* 2021). In contrast with the LIA, during the MCA carbon accumulation rates, hydrological conditions and peat botanical composition were relatively stable, with vegetation dominated by *Sphagnum austinii*. Other studies report similar patterns of stability in water table and vegetation during the MCA and instability during the LIA (e.g., Klein *et al.,* 2013; Magnan *et al.,* 2019). This suggests that these changes in aCAR are determined by changes in the botanical composition of the peat, as well as the degree of waterlogging occurring during this time. Certain vegetation produces more readily decomposed litter than other types (Bengtsson *et al.,* 2016; Bell *et al.,* 2018). Species that grow in wetter conditions on peatlands typically decompose more readily, but are also often more productive, than those associated with drier conditions (Mauquoy *et al.,* 2002). For example, hummock-forming species such as the *Sphagnum* sect. *Sphagnum* species (e.g., *Sphagnum papillosum, Sphagnum austinii*) produce more recalcitrant litter than *Sphagnum* sect. *Cuspidatum* type species which are usually associated with hollows or bog pools (e.g., *Sphagnum cuspidatum, Sphagnum pulchrum*) (Bengtsson *et al.,* 2016) and grow closer to the water table. An imbalance between GPP and NER resulting from highly labile material and low productivity during the LIA may explain the very low carbon accumulation rates during the bog pool period in core BO17.

Similar changes in vegetation with increasingly wet conditions as are seen in core BO17 during the LIA are frequently reported in palaeoecological studies (Blackford and Chambers, 1993; Mauquoy *et al.,* 2002; Magnan *et al.,* 2019). A study from subarctic Quebec, Canada, found reduced precipitation during this time resulted in drier conditions, which drove an increase in aCAR (Loisel and Garneau, 2010), suggesting that precipitation is more important than changes in temperature in driving these shifts. In contemporary gas flux studies, bog pools are consistent sources of carbon (McEnroe *et al.,* 2009). This would be reflected in the long-term carbon accumulation record as a decline in aCAR, as occurs during the end of the LIA. We cannot corroborate this with our experimental findings, however, since the vegetation within our experimental plots are not analogous with those found in areas of prolonged standing water. This suggests that changes in aCAR reflect the relative recalcitrance of organic carbon in the acrotelm, governed by the characteristics of the plant material (Loisel and Garneau, 2010). Vegetation community composition in peatlands is itself controlled by hydroclimatic conditions (Breeuwer *et al.,* 2008), with non-linear, abrupt changes often occurring in response to sustained changes in water table depth (Belyea, 2009), as seen in the botanical composition of the peat in core BO17.

Some palaeoecological studies have interpreted differences in aCAR between the MCA and the LIA as the result of changes in light availability and growing season length affecting plant productivity, with increased cloudiness during the LIA and increased growing season length during the MCA given as primary causes for these differences (Charman *et al.,* 2013; van der Linden *et al.,* 2014). However, this interpretation downplays the importance of decomposition processes. Whilst these are controlled by hydroclimatic conditions (Belyea, 2009; Breeuwer *et al.,* 2008), botanical characteristics of the peat are likely to govern carbon accumulation rates over longer time periods. Our experimental measurements show that soil respiration rates are governed mainly by air temperature, with measured NER reflecting net carbon losses in the acrotelm due to aerobic respiration (Yu *et al.,* 2001). This may be due to the mostly non-limiting moisture conditions that characterise wet sites such as Cors Fochno during non-drought periods, where temperature is the dominant controlling variable (Steinweg *et al.,* 2012). In contrast, the amount of carbon retained within specific sections throughout the peat column depends upon the recalcitrance of the plant remains in the peat. Similar conclusions were reached by Mauquoy *et al.* (2002) and Loisel and Garneau (2010) when comparing differences in carbon accumulation rates between the MCA and the LIA in peatland palaeoecological records. We argue that the results of experimental manipulation studies, which show that warmer climatic conditions weaken carbon accumulation rates, are not in dispute with palaeoecological studies. Since it is not possible to quantify whether changes in carbon accumulation rates inferred from peat cores are due to changes in productivity or decomposition, a single climatic driver should not be used to explain differences in carbon accumulation between time periods. However, understanding how decomposition varies between vegetation communities may aid interpretation of such changes, leading to ecologically informed interpretations of changes in decomposition and accumulation rates through time.

Experimental studies indicate that, in the future, increased temperature and reduced water tables will drive increases in ericaceous shrub cover in peatlands (Weltzin *et al.,* 2003; Buttler *et al.,* 2015; Malhotra *et al.,* 2020; Andrews *et al.,* 2021). This may coincide with a reduction in *Sphagnum* cover (Norby *et al.,* 2019). Such a change may initially increase productivity rates (Ward *et al.,* 2013) but may be offset by accelerated decomposition due to increased root exudate supply, a loss of inhibitory polyphenols associated with *Sphagnum* and a decline in recalcitrant litter (Weltzin *et al.,* 2000; Norby *et al.,* 2019). This suggests that while short-term carbon accumulation rates may increase with increased ericaceous cover, this will be reflected by increased soil respiration and over the long-term lead to an overall reduction in carbon accumulation rates.

Periods of burning are indicated throughout the palaeoecological record of Cors Fochno. These do not appear to coincide with periods of reduced aCAR. This may be due to the addition of charcoal into the soil, derived from the carbonisation of the above-ground biomass during the fire events. Charcoal is largely biologically unavailable and can form a recalcitrant layer of rapidly deposited carbon in peatlands. This influx of carbon may cause an apparent increase of aCAR rates following fires. Similar findings were found by Heinemeyer *et al*. (2018), where increased charcoal inputs derived from managed burning of the above-ground biomass correlated with aCAR from three UK blanket bog sites. However, the relative amount of carbon released into the atmosphere due to burning was not quantified (Young *et al.,* 2019).

4.7.2. Comparing aCAR and net ecosystem carbon budgets

We partitioned the modelled annual carbon budgets for each treatment to compare with the long term aCAR record from core BO17. In this section, carbon uptake is presented as positive values to facilitate comparison with core-derived estimates (Figure 4.13a). The partitioned components of the net ecosystem carbon budgets for all modelled years are shown in Figure 4.13b.

From the top of the core and through the acrotelm, we see that aCAR overlaps with the average annual rate of carbon uptake (GPP) for all plots (101 ± 24 g C m^{-2} y^{-1}) and all treatments. In this layer, little to no decomposition has taken place, therefore aCAR mostly reflects carbon accumulated by the surface vegetation, which does not differ significantly between treatments. When carbon losses following ecosystem respiration are accounted for, average modelled carbon accumulation rates fall to 31 ± 36.8 g C m^{-2} y^{-1} for all plots. While the range of carbon accumulation rates between treatments still overlap with the 95% uncertainty of the aCAR record, there are clear differences that reflect the significant effect of experimental warming upon modelled NER rates. Mean annual carbon budgets indicate control plots remain carbon sinks, sequestering 32.6 ± 32.5 g C m^{-2} y^{-1}, overlapping with aCAR following the development of the present-day vegetation community after c. 1850 CE and with increased rates during the early LIA between c. 1200 – 1450 CE. Mean annual carbon budgets indicate the drought treatment plots are also still net sinks, sequestering carbon at a rate of 13.9 ± 15.6 g C

m^{-2} y^{-1} and still overlap with these periods where aCAR is highest. For control and drought plots, mean annual carbon budgets are above the average LORCA for Cors Fochno, whereas aCAR rates the warmed plots are lower than the average LORCA. Mean annual carbon accumulation rates from warmed plots remain weak sinks, sequestering carbon at 0.6 ± 37.9 g C m^{-2} y^{-1}, which overlaps with aCAR throughout the MCA period. The greatest difference between aCAR and modelled annual budgets are seen within the combined warming and drought plots. These plots become net carbon sources due to CO_2 emissions alone, losing 34.6 ± 23.2 g C m^{-2} y^{-1}.

Carbon losses due to CH_4 efflux have little effect upon reducing total carbon accumulation rates, reflecting the slow decomposition of material stored throughout the entire depth of the catotelm (Clymo, 1984). Therefore, the reduction in CH_4 emission seen with warming is unlikely to have a substantial effect upon aCAR rates. This effect contrasts with most studies that report a positive relationship between CH_4 production and temperature (e.g., Granberg *et al.,* 2001; Updegraff *et al.,* 2001; Lai, 2009; Zhang *et al.,* 2021). Other studies have shown reductions in CH_4 emissions due to reduced soil moisture and lower water tables (e.g., Strack *et al.,* 2004; Turetsky *et al.,* 2008; Eriksson *et al.,* 2010). While no significant effects upon water table depth occurred due to warming, increased temperatures may have reduced soil moisture in the aerobic levels sufficiently to alter soil decay processes. Alternative explanations may relate to the effect of experimental warming upon soil microbial communities, which may favour bacteria over methanogens (Kim *et al.,* 2012). However, other studies have found that warming changes methanogens abundance, community structure and type (Kim *et* al., 2012; Turetsky *et al.,* 2008). The effects of climate change upon microbial communities and decay are poorly understood but have been shown to vary by site. These differential effects may result in variation in changes in the relative emissions of greenhouse gases with changes in climate (Kolton *et al.,* 2019). Such changes may also drive a shift in methane oxidation activity with warming, favouring increased methane oxidation due to methanotrophy (Kip *et al.,* 2010). However, increased temperatures have been shown exert a greater influence upon methanogenesis than CH_4 oxidation (Dunfield *et al.,* 1993).

By accounting for DOC fluxes out of the bog, average carbon accumulation rates fall further, with the control plots accumulating carbon at a rate of 32.4 ± 32.5 g C m^{-2} y^{-1}. While median carbon accumulation rates in the control plots remain within the range of aCAR in the catotelm (29.8 – 41.5 g C m^{-2} y^{-1}) and the average LORCA measurements (31.6 ± 2.2 g C m^{-2} y^{-1}), mean carbon budgets are much lower than mean aCAR, since these quantify periods of carbon loss, which cannot be accounted for in core-derived estimates (Young *et al.,* 2019). Prolonged carbon losses would be reflected as a slowing down of aCAR, as occurs between c. 1600 – 1800 CE during the latter half of the LIA in the BO17 record. Including our estimated annual POC and DIC fluxes into this calculation reduces the average carbon accumulation rates further, with carbon accumulation rates within the control plots falling to c. 27.4 g C m^{-2} y^{-1}, slightly below the range of aCAR estimated for the catotelm. While relatively small, POC and DIC fluxes combined are equal to c. 16 % of the estimated carbon accumulation rates within the control plots. However, the hydrological fluxes estimated by this study are highly uncertain and are likely to be significantly overestimated.

There is a need for POC and DIC to be measured and modelled more accurately in peatland net ecosystem carbon budget studies, as these fluxes may be more important pathways for carbon loss from peatlands then they are generally assumed to be. This may be particularly true under climate change, as increasing drought frequency and severity may cause POC fluxes from peatlands to be greater due increased peat erosion following physical and biogeochemical changes in peat due to drying (Evans *et al*., 2005).

In addition to drought, storm events can also increase hydrological fluxes from peatlands and are also projected to increase in frequency and severity in some regions (Clark *et al.,* 2007; Austnes *et al.,* 2010). Most of the DOC (31 – 66 % of total annual DOC export) exported in rivers draining from peatland catchments is released following storm events (Hinton *et al*., 1997; Clark *et al*, 2007). Incorporating accurate assessments of hydrological fluxes during storm events requires high resolution, long-term monitoring that was beyond the scope of this study (Clark *et al*., 2007), however we acknowledge that not accounting for these fluxes increases the uncertainty of our hydrological flux estimates (Clark *et al*., 2007; Austnes *et al*., 2010).

Our results suggest that carbon accumulation rates between palaeoecological and modelled net ecosystem carbon budgets can overlap. There are many instances where this occurs in other studies. For example, Roulet *et al*. (2007) compared multi-year annual carbon balances (CO_2, CH_4 and DOC) from the Mer Bleue peatland in Ottawa, Canada, calculating a mean carbon balance of -21.5 ± 39.0 g Cm^{-2} y^{-1}. This was comparable with LORCA from two cores from the same site (21.9 ± 2.8 and 14.0 ± 37.6

g C m^{-2} y^{-1}). Our results demonstrate the importance of including hydrological carbon fluxes in NECB estimates, despite often being poorly understood (Blodau, 2002). These fluxes are often important components of the carbon cycle in peatlands and their inclusion provides more accurate estimates of carbon accumulation, comparable with core derived estimates (Webb *et al.,* 2019).

While it is unclear why the NECB is greater than the LORCA from the same sites in some studies (e.g., Ratcliffe *et al.,* 2018; Yu, 2012), this likely relates to unquantifiable carbon losses resulting from disturbance episodes (e.g., burning, drought) potentially removing large quantities of organic carbon from the peat column over time, compromising comparison between the two records (Frolking *et al.,* 2014; Ratcliffe *et al.,* 2018). These losses will have a greater influence upon LORCA in heavily disturbed sites relative to others, the relatively pristine conditions of Cors Fochno possibly explaining the relatively good comparability between modelled and core-derived carbon accumulation rates in this study. Despite a few instances of apparent *in-situ* wildfires affecting Cors Fochno in the palaeoecological record and extensive drainage from c. 1850 until the mid-20th century (Andrews *et al.,* 2021), the central portion of Cors Fochno is relatively pristine compared with many other sites. These effects limit the applicability of joint experimental and palaeoenvironmental studies in heavily disturbed sites for inferring functional relationships between carbon accumulation and climate over differing timescales.

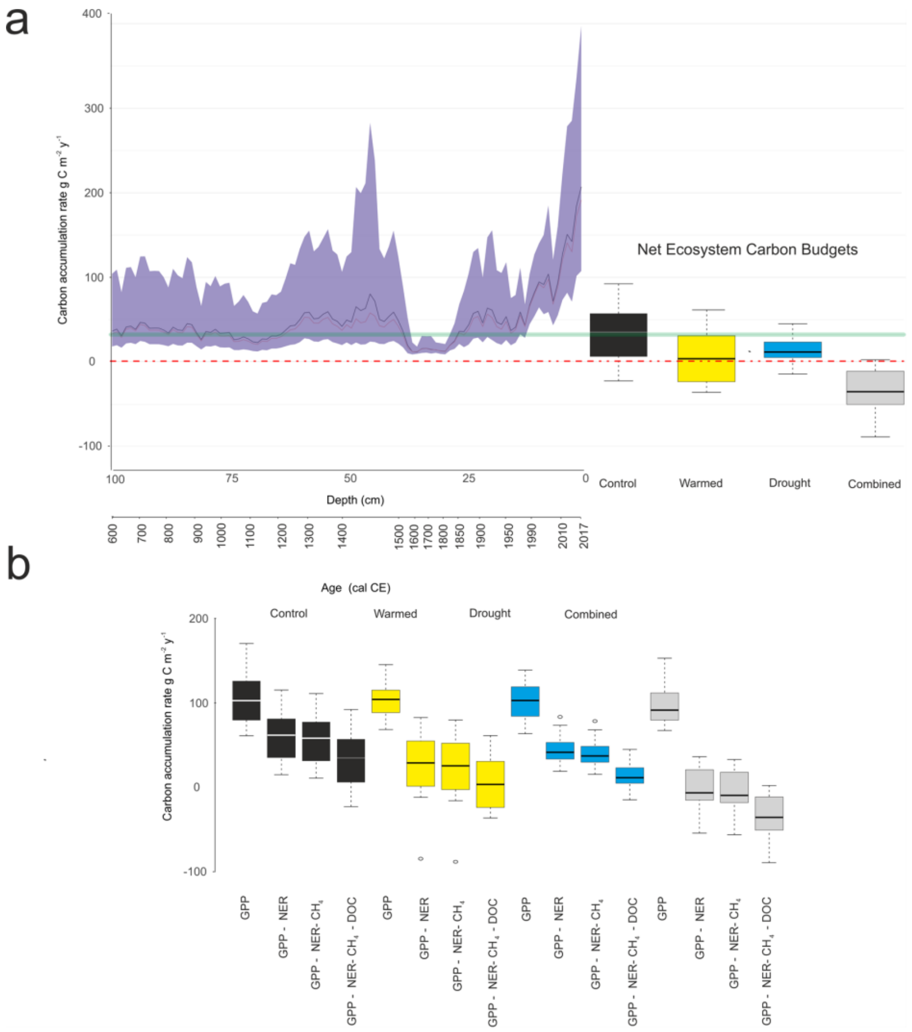

Figure 4.13. a: Apparent rates of carbon accumulation for core BO17 compared with modelled net ecosystem carbon budgets for all treatments (control, warmed, drought and combined warming and drought). The purple shade represents the 95% confidence interval for carbon accumulation rates, based upon age uncertainty. The green bar represents the average long-term rate of carbon accumulation (LORCA) and its uncertainty. The red dashed line indicates the level of zero carbon accumulation; values above this line represent carbon sinks and below carbon sources. Age is given as the median age probability from the age-depth model for core BO17. b. Partitioned components of the net ecosystem carbon budget, showing the contributions of each carbon source into the final net carbon budget.

4.7.3. Future carbon dynamics with climate change

We find that experimental warming combined with increased drought frequency (four x 4-week-long droughts) over the course of ten years reduced the carbon sink capacity of the experimental treatment plots on Cors Fochno. Annual carbon budgets from control plots suggest that the site is a net carbon sink for most years, sequestering carbon at an annual average rate of 32.6 ± 32.5 g C m^{-2} y^{-1}. For the combined treatment plots, the site is a net carbon source, losing carbon at an average rate of 34.6 ± 23.2 g C m^{-2} y^{-1}, an almost exact carbon loss as the normal carbon sink for the bog. We cannot corroborate this finding with the palaeoecological record since climate changes during the MCA were variable and not associated with sustained warming or increased drought. The palaeoecological record is not sufficiently detailed to provide evidence for individual drought events (Andrews *et al.,* 2021). While mean aCAR were lower during the MCA than during the early part of the LIA, we cannot discern whether this resulted from a change in NER or GPP, or simply relates to differences in the decomposability in the two different *Sphagnum* species that characterise these periods.

Warming is often the strongest factor influencing carbon dynamics in experimental studies (Weltzin *et al.,* 2000; Breeuwer *et al.,* 2008; Heijmans *et al.,* 2013; Dieleman *et al.,* 2015). Our experiment exerted an average range of warming of 0.1 – 0.9 °C upon air temperature, relevant to climate projections for the region for the next c. 40 years (Lowe *et al.,* 2018). Results from other studies reporting similar increases in air temperatures vary. Some report no changes in NEE (e.g., Chivers *et al.,* 2009) while others report increased carbon accumulation (e.g., Munir *et al.,* 2014). For measured fluxes, we find no significant differences in GPP or NER between treatments, although annual modelled NER is significantly higher in warmed plots. While some studies report increased GPP with warming (Chivers *et al.,* 2009; Munir *et al.,* 2014) many report no changes (e.g., Johnson *et al.,* 2013; Laine *et al.,* 2019). Increased NER is frequently reported with warming (e.g., Updegraff *et al.,* 2001; Chivers *et al.,* 2009; Voigt *et al.,* 2017; Samson *et al.,* 2018) but sites with higher water tables report less sensitivity to temperature (Laine *et al.,* 2019), as is the case for Cors Fochno.

Lund *et al*. (2012) state that the response of GPP to drought depends upon the timing, severity, and duration of a drought. Drought events during periods of vegetation development can severely reduce GPP rates in peatlands. A study by Rinne *et al.* (2020) analysed how the 2018 drought in Europe affected CH_4 and CO_2 exchange in five peatlands from Finland and Sweden, finding that drought reduced summertime CO_2 uptake and CH_4 emissions for four of the five sites. The outlier site experienced increased temperatures but not reduced precipitation, resulting in an increase in GPP and no change in CH_4 emissions.

Field measurements of carbon emissions from longer actual droughts exceed our estimates (Lund *et al.,* 2012; Rinne *et al.,* 2020). For example, emissions of 220 g C m^{-2} y^{-2} were reported between 2013 and 2014 from the La Guette peatland in France following a drought year (D'Angelo *et al.,* 2021). At Cors Fochno, average modelled emissions during the year 2018, a period of (natural) hydrological drought affecting much of Europe, were -31.4 ± 41.9 g C m^{-2} y^{-2} across all plots. The difference between real drought events and our estimates likely relate to the timing and relatively low severity of our simulated droughts. Our manipulated droughts were relatively short-lived (four weeks long) and took place towards the end of the peak growing season (August to September). Our experimental design did not allow for consistent increases in air temperatures as could occur during real drought events, and we could not prevent precipitation from entering the plots. These factors in combination minimise the impact of our simulated droughts upon vegetation and are likely to make our estimates relatively conservative.

We record a significant reduction in CH_4 emissions with warming. Such a change has been reported in some studies (e.g., Lund *et al.,* 2020) while most studies report an increase (Yang *et al.,* 2014) or no change in CH_4 emissions (Li *et al.,* 2021). Similar findings have been found for estimates of the net climatic effect of water table drawdown in peatlands upon global climate (Huang *et al.,* 2021), with soil drying significantly reducing methane emissions in some studies (Yang *et al.,* 2014). It is possible that increased temperatures within the plots with OTCs reduced soil moisture, reducing CH_4 emissions. Despite the reductions in emissions due to warming, when expressed as their CO_2 equivalents, only control plots remained net greenhouse gas sinks. Estimated CO_2 + CH_4 CO_2-eq emissions from combined treatments were 193.7 ± 51.9 g C m^{-2} y^{-1} greater than controls. Reduced CH_4 emissions do not offset the effects of CO_2 increases, according to the GWP100 protocol, however this protocol only considers the difference between pulse emissions of greenhouse gases (Allen *et al*., 2016; Lynch *et al*., 2020). The cumulative effect of reduced CH_4 emissions over time may have a significant effect upon the global warming potential of the site, as shown by Lynch *et al*. (2020).

Although the effects of climate warming and drying upon northern peatlands remain uncertain, it is not contested that warming will increase the rate of peat decomposition

(Clymo *et al*., 1998; Dorrepaal *et al*., 2009). How this will affect peatlands across the Northern Hemisphere is likely to vary depending upon differences in vegetation, peatland type and the differences in warming and drought frequency experienced in different regions (Bu *et al*., 2011). For example, in the northernmost latitudes, permafrost peatlands have become net carbon sources due to increased peat decay following permafrost thaw (Malmer *et al*., 2005). Net primary productivity may also increase in these regions in response to warming, potentially offsetting the effects of increased decay and maintaining carbon sink functioning (Vitt *et al*., 2000; Camill *et al.,* 2001; Flanagan *et al*., 2011). Some studies have indicated that peatlands in sub arctic regions have become net sources of carbon due to recent warming (Salm *et al.,* 2009; 2012; Backstrand *et al*., 2010). While peatlands exhibit autogenic hydrological feedbacks that counter the effects of gradual, long-term warming and drying upon ecosystem function (Waddington *et al*., 2015), they are less resilient to rapid changes in climate, and anthropogenic perturbations may further weaken peatland resilience to climate change (Page and Baird, 2016).

4.8. Conclusions

This study investigates the apparent disparity between the results of palaeoecological and experimental studies when assessing future peatland climate change responses by reproducing both studies in tandem on the same site. To our knowledge, this is the first time that modelled annual carbon budgets from a climate manipulation experiment have been contextualised with carbon accumulation rates from the past c. 1500 years from the same site.

Intermediate IPCC scenarios predict that terrestrial ecosystems will accumulate less carbon by the later 21st century (Lee *et al.,* 2021). Consideration of experimental and palaeoecological lines of evidence suggest that even with modest changes in temperature and episodic drought severity, existing peatlands will shift from net sinks to net sources of carbon, except in cases where plant succession results in the development of plant communities that produce litter that is less prone to decay. In the palaeoecological record, long-term changes in carbon accumulation rates occur in response to shifts in vegetation resulting from climate change or human activity. This change likely reflects differences in species-specific decomposability, which is generally lower for species that prefer drier conditions. Since the palaeoecological record cannot identify carbon losses, determining whether a period of increased carbon accumulation is a period of increased respiration relative to productivity, or vice versa, is impossible. However, plant physiology and decomposition studies may be useful to assist in interpreting these records. We conclude that core-derived carbon accumulation rates in peatland studies are often lower during cooler periods such as the Little Ice Age due to increased decomposition resulting from the development of more aquatic vegetation that store carbon less readily. Experimental studies are often too short to capture shifts in vegetation of this magnitude.

The results of this study show that warming and combined warming and increased drought frequency will increase carbon emissions from the experimental site at Cors Fochno. However, the experimental site is not representative of the entire peatland, neither is it representative of all peatlands in the UK or across the Northern Hemisphere. Given that peatland plant community responses to changes in water tables are abrupt and often non-linear (Belyea, 2009), vegetation changes characterised by increased shrub dominance and a reduction in *Sphagnum* may drive increases in decay due to an increase of labile soil litter supply. Palaeoecological studies may provide important context for how such changes may affect long-term carbon storage. Presently, peatland responses to warming are not fully included in climate models despite being important terrestrial stores of carbon (Lee *et al.,* 2021). Future climate models should account for changes in peatland vegetation with climate, and its respective impact upon carbon accumulation and emissions.

We demonstrate that aCAR can converge with net ecosystem carbon budgets when important carbon fluxes (e.g., DOC) are considered, and the sites have lost relatively little carbon through time. However, since core-derived estimates cannot quantify carbon losses, aCAR will always remain above zero, whilst NECB measurements can be negative. Whilst others advise against comparison between aCAR and NECB (Young *et al.,* 2021) we demonstrate that aCAR can provide useful insights into past changes in carbon dynamics that may be placed in context with contemporary carbon budgets (Frolking *et al.,* 2014). However, these should be interpreted carefully and combined with plant macrofossil and other palaeo-proxy analyses wherever possible. Furthermore, they should be considered with reference to known processes that affect carbon accumulation rates in contemporary experimental studies, which are multi-directional and governed by a range of climatic and environmental factors.

We find a significant weakening of the carbon sink capacity of our site with annual air warming of between 0.1 – 0.9 °C, resulting from subtle changes in plant productivity and soil respiration, with carbon being released mainly in the form of CO_2. This effect is amplified with increased drought frequency, to the extent that Cors Fochno becomes a net carbon source, warming global climate. Reductions in CH_4 due to warming or surface peat drying do not compensate for increases in CO_2 over 100-year timescales, although this may not be the case were we to consider cumulative emissions as opposed to pulse emissions as per the GWP100 protocol. Coupled with increased shrub dominance, potential reductions in *Sphagnum* productivity and abundance with enhanced warming, existing peatlands may become a significant carbon source with future warming, although the severity of this change will differ between sites and regions due to differences between peatlands, anthropogenic disturbances and regional differences in the severity of climate changes experienced

This has important implications for future climate feedbacks, since the temperature and drought effects imparted during our experimental are relatively small, in line with changes anticipated during the next c. 40 years for this region (Lowe *et al.,* 2018). However, this is lower than IPCC predictions for global temperatures by 2100 even from the lowest emission scenarios, particularly for the higher latitudes where the most profound changes in temperature and precipitation are projected to occur (Lee *et al.,* 2021). Projected temperature changes for the Northern Hemisphere are greater than the warming imparted by our experiment. We predict that even minor warming and increased droughts will weaken peatland carbon sink functioning, with areas affected by increased drought potentially becoming net carbon sources. Peatlands are large carbon stores, and loss of their carbon sink function could drive a positive climate feedback, warming global climate, and potentially destabilise their vast carbon stores (Joosten *et al.,* 2016). Halting any further degradation of peatlands is the most effective way to minimise future positive climate feedbacks.

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Data availability:

All data used in this study is publicly available from 10.6084/m9.figshare.17041364. Plant macrofossil and testate amoebae data are available from https://doi.org/10.6084/m9.figshare.15395199.v1.

Conflict of interest

The authors declare no conflict of interest.

4.10. References

Allen, M. R., Fuglestvedt, J. S., Shine, K. P., Reisinger, A., Pierrehumbert, R. T., & Forster, P. M. (2016). New use of global warming potentials to compare cumulative and short-lived climate pollutants. *Nature Climate Change*, 6(8), 773-776.

Alm, J., Shurpali, N.J., Minkkinen, K., Aro, L., Hytanen, J., Lauriia, T., Lohila, A., Maijanen, M., Martikainen, P.J., Mäkiranta, P. and Penttilä, T., (2007). Emission factors and their uncertainty for the exchange of CO2, CH4 and N2O in Finnish managed peatlands. *Boreal Environment Research*, *12*(2).

Andrews, L.O., Rowson, J.G., Caporn, S.J., Dise, N.B., Barton, E., Garrett, E., Roland. Gehrels, W., Gehrels, M., Kay, M. and Payne, R.J., (2021). Plant community responses to experimental climate manipulation in a Welsh ombrotrophic peatland and their palaeoenvironmental context. *Global Change Biology.*

Appleby, P.G., (1998). *Dating recent sediments by 210 Pb: Problems and solutions* (No. STUK-A--145).

Aquino-López, M.A., Blaauw, M., Christen, J.A., and Sanderson, N.K., (2018). Bayesian Analysis of ^{210}Pb Dating. *Journal of Agricultural, Biological and Environmental Statistics*, *23*(3), 317-333.

Aquino-López, M.A., Ruiz-Fernández, A.C., Blaauw, M. and Sanchez-Cabeza, J.A., (2020). Comparing classical and Bayesian 210Pb dating models in human-impacted aquatic environments. *Quaternary Geochronology*, *60*, p.101106.

Arneth, A., Kurbatova, J., Kolle, O., Shibistova, O. B., Lloyd, J., Vygodskaya, N. N., & Schulze, E. D. (2002). Comparative ecosystem–atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO2 fluxes. Tellus B: *Chemical and Physical Meteorology,* 54(5), 514-530.

Aronson, E.L. and McNulty, S.G., (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, *149*(11), 1791-1799.

Austnes, K., Evans, C. D., Eliot-Laize, C., Naden, P. S., & Old, G. H. (2010). Effects of storm events on mobilisation and in-stream processing of dissolved organic matter (DOM) in a Welsh peatland catchment. *Biogeochemistry*, 99(1), 157-173.

Bäckstrand, K., Crill, P. M., Jackowicz-Korczynski, M., Mastepanov, M., Christensen, T. R., & Bastviken, D. (2010). Annual carbon gas budget for a subarctic peatland, Northern Sweden. *Biogeosciences*, 7(1), 95-108.

Baird, A. J., Eades, P. A., and Surridge, B. W. (2008). The hydraulic structure of a raised bog and its implications for ecohydrological modelling of bog development. Ecohydrology: Ecosystems, Land and Water Process Interactions, *Ecohydrogeomorphology*, 1(4), 289-298.

Barber, K.E., Chambers, F.M., Maddy, D., Stoneman, R., and Brew, J.S., (1994). A sensitive high-resolution record of late Holocene climatic change from a raised bog in northern England. *The Holocene*, *4*(2), 198-205.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F. and Grothendieck, G., (2012). Package 'lme4'. *CRAN. R Foundation for Statistical Computing, Vienna, Austria*.

Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J., Freeman, C., and Clark, J.M., (2018). Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma*, *331*, 29-37.

Belshe, E.F., Sanjuan, J., Leiva-Dueñas, C., Piñeiro-Juncal, N., Serrano, O., Lavery, P. and Mateo, M.A., (2019). Modelling organic carbon accumulation rates and residence times in coastal vegetated ecosystems. *Journal of Geophysical Research: Biogeosciences*, *124*(11), 3652-3671.

Belyea, L.R., (2009). Nonlinear dynamics of peatlands and potential feedbacks on the climate system. *Carbon cycling in northern peatlands*, *184*, 5-18.

Bengtsson, F., Granath, G. and Rydin, H., (2016). Photosynthesis, growth, and decay traits in Sphagnum–a multispecies comparison. *Ecology and Evolution*, *6*(10), 3325-3341.

Billett, M.F., Charman, D.J., Clark, J.M., Evans, C.D., Evans, M.G., Ostle, N.J., Worrall, F., Burden, A., Dinsmore, K.J., Jones, T., and McNamara, N.P., (2010). Carbon balance of UK peatlands: current state of knowledge and future research challenges. *Climate Research*, *45*, 13-29.

Blaauw, M., Christen, J. A and Aquino-López, M. A. (2021). rplum: Bayesian Age-Depth Modelling of Cores Dated by Pb-210. R package version 0.2.2.

Blackford, J.J. and Chambers, F.M., (1993). Determining the degree of peat decomposition for peat-based paleoclimatic studies. *International Peat Journal;*(*Finland)*, *8*(5).

Blodau, C., (2002). Carbon cycling in peatlands A review of processes and controls. *Environmental Reviews*, *10*(2), 111-134.

Breeuwer, A., Heijmans, M., Robroek, B.J., Limpens, J. and Berendse, F., (2008). The effect of increased temperature and nitrogen deposition on decomposition in bogs. *Oikos*, *117*(8), 1258-1268.

Bridgham, S.D., Pastor, J., Dewey, B., Weltzin, J.F. and Updegraff, K., (2008). Rapid carbon response of peatlands to climate change. *Ecology*, *89*(11), 3041-3048.

Bronk-Ramsey, C., (2017). Methods for summarizing radiocarbon datasets. *Radiocarbon*, *59*(6), 1809-1833.

Bu, Z., Hans, J., Li, H., Zhao, G., Zheng, X., Ma, J. and Zeng, J., (2011). The response of peatlands to climate warming: A review. *Acta Ecologica Sinica*, *31*(3), 157-162.

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A. and Bragazza, L., (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science*, *26*(5), 964-974.

Byrne, K.A., Chojnicki, B., Christensen, T.R., Drosler, M., Frolking, S., Lindroth, A., Mailhammer, J., Malmer, N., Selin, P., Turunen, J. and Valentini, R., (2004). *EU peatlands: Current carbon stocks and trace gas fluxes.*

Cain, M., Lynch, J., Allen, M. R., Fuglestvedt, J. S., Frame, D. J., & Macey, A. H. (2019). Improved calculation of warming-equivalent emissions for short-lived climate pollutants. *NPJ climate and atmospheric science,* 2(1), 1-7.

Camill, P., Lynch, J. A., Clark, J. S., Adams, J. B., & Jordan, B. (2001). Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems*, 4(5), 461-478.

Chambers, F.M., Beilman, D.W. and Yu, Z., (2011). Methods for determining peat humification and for quantifying peat bulk density, organic matter, and carbon content for palaeostudies of climate and peatland carbon dynamics. *Mires and Peat*, *7*(7), 1-10.

Charman, D.J., (2007). Summer water deficit variability controls on peatland water table changes: implications for Holocene palaeoclimate reconstructions. *The Holocene*, *17*(2), 217-227.

Charman, D.J., Barber, K.E., Blaauw, M., Langdon, P.G., Mauquoy, D., Daley, T.J., Hughes, P.D. and Karofeld, E., (2009). Climate drivers for peatland palaeoclimate records. *Quaternary Science Reviews*, *28*(19-20), 1811-1819.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D. and Jackson, S.T., (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, *10*(2), 929-944.

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W. and McGuire, A.D., (2009). Effects of experimental water table and temperature manipulations on ecosystem CO 2 fluxes in an Alaskan rich fen. *Ecosystems*, *12*(8), 1329-1342

Christensen, T.R., Johansson, T., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P. and Svensson, B.H., (2004). Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophysical Research Letters*, *31*(4).

Clark, J. M., Lane, S. N., Chapman, P. J., & Adamson, J. K. (2007). Export of dissolved organic carbon from an upland peatland during storm events: Implications for flux estimates. *Journal of Hydrology*, 347(3-4), 438-447.

Clymo, R.S., (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *303*(1117), 605-654.

Clymo, R.S., Turunen, J. and Tolonen, K., (1998). Carbon accumulation in peatland. *Oikos*, 368-388.

Cole, E.E. and Mitchel, F.J.G. (2003). Human impact on the Irish landscape during the late Holocene inferred from palynological studies at three peatland sites. *The Holocene 13*(4)**,** 507-515.

Compo, G.P., Whitaker, J.S., Sardeshmukh, P.D., Matsui, N., Allan, R.J., Yin, X., Gleason, B.E., Vose, R.S., Rutledge, G., Bessemoulin, P. and Brönnimann, S., (2011). The twentieth century reanalysis project. *Quarterly Journal of the Royal Meteorological Society*, *137*(654), 1-28.

Creevy, A.L., Payne, R.J., Andersen, R. and Rowson, J.G., (2020). Annual gaseous carbon budgets of forest-to-bog restoration sites are strongly determined by vegetation composition. *Science of the Total Environment*, *705*, p.135863.

D'Angelo, B., Leroy, F., Guimbaud, C., Jacotot, A., Zocatelli, R., Gogo, S. and Laggoun-Défarge, F., (2021). Carbon Balance and Spatial Variability of CO 2 and CH 4 Fluxes in a Sphagnum-Dominated Peatland in a Temperate Climate. *Wetlands*, *41*(1), 1-12.

Dawson, J. J. C., Billett, M. F., Neal, C., and Hill, S. (2002). A comparison of particulate, dissolved and gaseous carbon in two contrasting upland streams in the UK. *Journal of Hydrology*, *257*(1-4), 226-246.

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W. and Lindo, Z., (2015). Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability. *Global Change Biology*, *21*(1), 388-395.

Dinsmore, K. J., Skiba, U. M., Billett, M. F., Rees, R. M., & Drewer, J. (2009). Spatial and temporal variability in CH4 and N2O fluxes from a Scottish ombrotrophic peatland: Implications for modelling and up-scaling. *Soil Biology and Biochemistry*, 41(6), 1315-1323.

Dooling, G. P., Chapman, P. J., Baird, A. J., Shepherd, M. J., and Kohler, T. (2018). Daytime-only measurements underestimate CH_4 emissions from a restored bog. *Ecoscience*, *25*(3), 259-270.

Dorrepaal, E., Toet, S., van Logtestijn, R.S., Swart, E., van De Weg, M.J., Callaghan, T.V. and Aerts, R., (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, *460*(7255), 616-619.

Dossa, G.G., Paudel, E., Wang, H., Cao, K., Schaefer, D. and Harrison, R.D.,(2015). Correct calculation of CO 2 efflux using a closed chamber linked to a non-dispersive infrared gas analyzer. *Methods in Ecology and Evolution*, *6*(12), 1435-1442.

Dugmore, A.J., Larsen, G, and Newton, A.J. (1995). Seven tephra isochrones in Scotland. *The Holocene 5*/3**,** 257-266.

Dunfield, P., Dumont, R., and Moore, T.R., (1993). Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biology and Biochemistry*, *25*(3), 321-326.

Dupont, L.M., (1986). Temperature and rainfall variation in the Holocene based on comparative palaeoecology and isotope geology of a hummock and a hollow (Bourtangerveen, The Netherlands). *Review of Palaeobotany and Palynology*, *48*(1-3), 71-159.

Eddy, J.A., (1976). The maunder minimum. *Science*, *192*(4245), 1189-1202.

Eriksson, T., Öquist, M.G. and Nilsson, M.B., (2010). Effects of decadal deposition of nitrogen and sulphur, and increased temperature, on methane emissions from a boreal peatland. *Journal of Geophysical Research: Biogeosciences*, *115*(G4).

Evans, C.D., Monteith, D.T. and Cooper, D.M., (2005). Long-term increases in surface water dissolved organic carbon: observations, possible causes and environmental impacts. *Environmental Pollution*, *137*(1), 55-71.

Fenner, N., Freeman, C., Lock, M.A., Harmens, H., Reynolds, B. and Sparks, T., (2007). Interactions between elevated CO2 and warming could amplify DOC exports from peatland catchments. *Environmental Science and Technology*, *41*(9), 3146-3152.

Flanagan, L. B., & Syed, K. H. (2011). Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Global Change Biology*, 17(7), 2271-2287.

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B. and Fenner, N., (2001). Export of organic carbon from peat soils. *Nature*, *412*(6849), 785-785.

Frolking, S. and Roulet, N.T., (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, *13*(5), 1079-1088.

Frolking, S., Roulet, N. and Fuglestvedt, J., (2006). How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research: Biogeosciences*, *111*(G1).

Frolking, S., Talbot, J., and Subin, Z.M., (2014). Exploring the relationship between peatland net carbon balance and apparent carbon accumulation rate at century to millennial time scales. *The Holocene*, *24*(9), 1167-1173.

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S. and Roulet, N., (2011). Peatlands in the Earth's 21st century climate system. *Environmental Reviews*, *19*(NA), 371-396.

Glatzel, S., Lemke, S. and Gerold, G., (2006). Short-term effects of an exceptionally hot and dry summer on decomposition of surface peat in a restored temperate bog. *European Journal of Soil Biology*, *42*(4), 219-229.

Gorham, E., (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, *1*(2), 182-195.

Goulsbra, C., Rickards, N., Brown, S., Evans, M., Boult, S., and Alderson, D. (2016). Diurnal variations in CO2 flux from peatland floodplains: Implications for models of ecosystem respiration. *Aquatic Sciences, 78*(3), 477-489.

Granberg, G., Sundh, I., Svensson, B.H. and Nilsson, M., (2001). Effects of temperature, and nitrogen and sulfur deposition, on methane emission from a boreal mire. *Ecology*, *82*(7), 1982-1998.

Hall, M. and Hayward, C., (2014). Preparation of micro-and crypto-tephras for quantitative microbeam analysis. *Geological Society, London, Special Publications*, *398*(1), 21-28.

Hayward, C., (2012). High spatial resolution electron probe microanalysis of tephras and melt inclusions without beam-induced chemical modification. *The Holocene*, *22*(1), 119-125.

Heijmans, M.M., van der Knaap, Y.A., Holmgren, M. and Limpens, J., (2013). Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Global Change Biology*, *19*(7), 2240-2250.

Heinemeyer, A., Asena, Q., Burn, W. L., & Jones, A. L. (2018). Peatland carbon stocks and burn history: Blanket bog peat core evidence highlights charcoal impacts on peat physical properties and long-term carbon storage. *Geography and Environment*, 5(2), e00063.

Heinemeyer A., Vallack H.W., Morton P.A., Pateman R., Dytham C., Ineson P., McClean C., Bristow C., and Pearce-Higgins J.W. (2019) *Restoration of heather-dominated blanket bog vegetation on grouse moors for biodiversity, carbon storage, greenhouse gas emissions and water regulation: comparing burning to alternative mowing and uncut management*. Final Report to Defra on Project BD5104, Stockholm Environment Institute at the University of York, York, UK.

Hendon, D., and Charman, D. J. (1997). The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, *7*(2), 199-205.

Hinton, M. J., Schiff, S. L., & English, M. C. (1997). The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. *Biogeochemistry, 36*(1), 67-88.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F. and Guiot, J., (2018). Impacts of 1.5° C Global Warming on Natural and Human Systems. In: *Global warming of 1.5° C. An IPCC Special Report on the impacts of global warming of 1.5° C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. World Meteorological Organization Technical Document.Holden, J., & Burt, T. P. (2002). Laboratory experiments on drought and runoff in blanket peat. *European Journal of Soil Science*, 53(4), 675-690.

Hope, D., Billett, M. F., and Cresser, M. S. (1994). A review of the export of carbon in river water: fluxes and processes. *Environmental pollution*, 84(3), 301-324.

Hope, D., Billett, M. F., Milne, R., & Brown, T. A. (1997). Exports of organic carbon in British rivers. *Hydrological Processes*, 11(3), 325-344.

Housley, R.A., Blockley, S. P. E., Matthews, I. P., MacLeod, A., Lowe, J. J., Ramsay, S., Miller, J. J. and Campbell, E.N (2010). Late Holocene vegetation and palaeoenvironmental history of the Dunadd area, Argyll, Scotland: chronology of events. *Journal of Archaeological Science 37*, 577-593.

Huang, Y., Ciais, P., Luo, Y., Zhu, D., Wang, Y., Qiu, C., Goll, D.S., Guenet, B., Makowski, D., De Graaf, I. and Leifeld, J., (2021). Tradeoff of CO2 and CH4 emissions from global peatlands under water table drawdown. *Nature Climate Change*, 1-5.

Hutchinson, G.L. and Livingston, G.P., (1993). Use of chamber systems to measure trace gas fluxes. *Agricultural ecosystem effects on trace gases and global climate change*, *55*, 63-78.

Ise, T., Dunn, A.L., Wofsy, S.C. and Moorcroft, P.R., (2008). High sensitivity of peat decomposition to climate change through water table feedback. *Nature Geoscience*, *1*(11), 763-766.

Johnson, C.P., Pypker, T.G., Hribljan, J.A. and Chimner, R.A., (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO 2/CH 4 dynamics in a northern Michigan peatland. *Ecosystems*, *16*(5), 736-748.

Joosten, H. A. J. J. P. A., Sirin, A., Couwenberg, J., Laine, J., and Smith, P. (2016). The role of peatlands in climate regulation. In: *Peatland restoration and ecosystem services: science, policy, and practice*, 66. Cambridge University Press.

Kim, S.Y., Freeman, C., Fenner, N. and Kang, H., (2012). Functional and structural responses of bacterial and methanogen communities to 3-year warming incubation in different depths of peat mire. *Applied Soil Ecology*, *57*, 23-30.

Kip, N., van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.J., Smolders, A.J., Jetten, M.S., Damsté, J.S.S. and Den Camp, H.J.O., (2010). Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nature Geoscience*, *3*(9), 617-621.

Klein, E.S., Booth, R.K., Yu, Z., Mark, B.G. and Stansell, N.D., (2013). Hydrology-mediated differential response of carbon accumulation to late Holocene climate change at two peatlands in Southcentral Alaska. *Quaternary Science Reviews*, *64*, 61-75.

Kolton, M., Marks, A., Wilson, R.M., Chanton, J.P. and Kostka, J.E., (2019). Impact of warming on greenhouse gas production and microbial diversity in anoxic peat from a Sphagnum-dominated bog (Grand Rapids, Minnesota, United States). *Frontiers in Microbiology*, *10*, 870.

Lai, D.Y.F., (2009). Methane dynamics in northern peatlands: a review. *Pedosphere*, *19*(4), 409-421.

Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H. and Tuittila, E.S., (2019). Warming impacts on boreal fen CO2 exchange under wet and dry conditions. *Global Change Biology*, *25*(6), 1995-2008.

Lamb, H.H., (1965). The early medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *1*, 13-37.

Lamentowicz, M., Słowińska, S., Słowiński, M., Jassey, V., Chojnicki, B., Reczuga, M., Zielińska, M., Marcisz, K., Barabach, J., Samson, M. and Kołaczek, P., (2016). Combining short-term manipulative experiments with long-term palaeoecological investigations at high resolution to assess the response of Sphagnum peatlands to drought, fire and warming. *Mires and Peat*, *18*, p.20.

Larsen, G., Dugmore, A., J., and Newton, A.J. (1999). Geochemistry of historic silicic tephras in Iceland. *The Holocene 9*(4)**,** 463-471.

Lasdon, L.S., Waren, A.D., Jain, A. and Ratner, M., (1978). Design and testing of a generalized reduced gradient code for nonlinear programming. *ACM Transactions on Mathematical Software* (*TOMS)*, *4*(1), 34-50.

Lee, J. Y., J. Marotzke, G. Bala, L. Cao, S. Corti, J. P. Dunne, F. Engelbrecht, E. Fischer, J. C. Fyfe, C. Jones, A. Maycock, J. Mutemi, O. Ndiaye, S. Panickal, T. Zhou, (2021). Future Global Climate: Scenario Based Projections and Near-Term Information. In: *Climate Change 2021: The Physical Science Basis.* Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Li, Q., Gogo, S., Leroy, F., Guimbaud, C. and Laggoun-Défarge, F., (2021). Response of peatland CO2 and CH4 fluxes to experimental warming and the carbon balance. *Frontiers in Earth Science*, *9*, p.471.

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H. and Schaepman-Strub, G., (2008). Peatlands and the carbon cycle: from local processes to global implications–a synthesis. *Biogeosciences*, *5*(5), 1475-1491.

Lindsay, R. (2010). *Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change*. University of East London, Environmental Research Group.

Lloyd, J. and Taylor, J.A., (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 315-323.

Loisel, J. and Garneau, M., (2010). Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*(3-4), 493-533.

Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W., Benavides, J.C., Blewett, J., Camill, P., Charman, D.J. and Chawchai, S., (2021). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*(1), 70-77.

Lowe, J.A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G. and Fung, F., (2018). UKCP18 science overview report. *Met Office Hadley Centre: Exeter, UK*.

Lund, M., Christensen, T.R., Lindroth, A. and Schubert, P., (2012). Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. *Environmental Research Letters*, *7*(4), p.045704.

Lynch, J., Cain, M., Pierrehumbert, R., and Allen, M. (2020). Demonstrating GWP*: a means of reporting warming-equivalent emissions that captures the contrasting impacts of short-and long-lived climate pollutants. *Environmental Research Letters*, *15*(4), 044023.

Ma, S., Jiang, J., Huang, Y., Shi, Z., Wilson, R.M., Ricciuto, D., Sebestyen, S.D., Hanson, P.J. and Luo, Y., (2017). Data-constrained projections of methane fluxes in a northern Minnesota peatland in response to elevated CO2 and warming. Journal of Geophysical Research: *Biogeosciences*, 122(11), 2841-2861.

Magnan, G., Le Stum-Boivin, É., Garneau, M., Grondin, P., Fenton, N. and Bergeron, Y., (2019). Holocene vegetation dynamics and hydrological variability in forested peatlands of the Clay Belt, eastern Canada, reconstructed using a palaeoecological approach. *Boreas*, *48*(1), 131-146.

Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Vander Stel, H., Feron, S.C., Hanson, P.J. and Iversen, C.M., (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences*, *117*(30), 17627-17634.

Malmer, N., Johansson, T., Olsrud, M., & Christensen, T. R. (2005). Vegetation, climatic changes, and net carbon sequestration in a North-Scandinavian subarctic mire over 30 years. *Global Change Biology, 11*(11), 1895-1909.

Manley, G., (1953). The mean temperature of central England, 1698–1952. *Quarterly Journal of the Royal Meteorological Society*, *79*(340), 242-261.

Manley, G., (1974). Central England temperatures: monthly means 1659 to 1973. *Quarterly Journal of the Royal Meteorological Society*, *100*(425), 389-405.

Mann, M. E., Bradley, R. S., & Hughes, M. K. (1999). Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical research letters*, 26(6), 759-762.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. and Ni, F., (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, *326*(5957), 1256-1260.

Matthews, I. (2008) Roman Lode, Exmoor, Devon: Tephrochronology Scientific Dating Report Scientific Dating Report. *English Heritage Research Department Report Series 26*-2008, 16.

Mauquoy, D, T. Engelkes, M. H. M. Groot, F. Markesteijn, M. G. Oudejans, J. van Der Plicht, and B. van Geel. (2002) High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 186, no. 3-4 275-310.

Mauquoy, D., Blaauw, M., van Geel, B., Borromei, A., Quattrocchio, M., Chambers, F.M. and Possnert, G., (2004). Late Holocene climatic changes in Tierra del Fuego based on multiproxy analyses of peat deposits. *Quaternary Research*, *61*(2), 148-158.

Mauquoy, D., Hughes, P.D.M. and van Geel, B., (2010). A protocol for plant macrofossil analysis of peat deposits. *Mires and Peat*, *7*(6), 1-5.

Mauquoy, D., Yeloff, D., van Geel, B., Charman, D.J. and Blundell, A., (2008). Two decadally resolved records from north-west European peat bogs show rapid climate changes associated with solar variability during the mid–late Holocene. *Journal of Quaternary Science: Published for the Quaternary Research Association*, *23*(8), 745-763.

McEnroe, N.A., Roulet, N.T., Moore, T.R. and Garneau, M., (2009). Do pool surface area and depth control CO2 and CH4 fluxes from an ombrotrophic raised bog, James Bay, Canada? *Journal of Geophysical Research: Biogeosciences*, *114*(G1).

Moore, T.R., Roulet, N.T. and Waddington, J.M., (1998). Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change*, *40*(2), 229-245.

Mudelsee, M., (2013). *Climate time series analysis* (Vol. 30). Heidelberg: Springer.

Munir, T.M., Perkins, M., Kaing, E. and Strack, M., (2015). Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water table-lowering simulations of climate change. *Biogeosciences*, *12*(4), 1091-1111.

Myhre, G., Bréon, F.M. and Granier, C., (2011). Anthropogenic and Natural Radiative Forcing 2. *Notes*, *16*.

Neal, C., & Hill, S. (1994). Dissolved inorganic and organic carbon in moorland and forest streams: Plynlimon, Mid-Wales. *Journal of Hydrology*, 153(1-4), 231-243.

Newton, A.J., Dugmore, A.J. and Gittings, B.M., (2007). Tephrabase: tephrochronology and the development of a centralised European database. *Journal of Quaternary Science*, *22*(7), 737-743.

Nolan, C., Overpeck, J.T., Allen, J.R., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R. and Djamali, M., (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, *361*(6405), 920-923.

Norby, R.J., Childs, J., Hanson, P.J. and Warren, J.M., (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, *9*(22), 12571-12585.

Norrman, B., (1993). Filtration of water samples for DOC studies. *Marine Chemistry*, 41(1-3), 239-242.

Page, S.E., and Baird, A.J., (2016). Peatlands and global change: response and resilience. *Annual Review of Environment and Resources*, 41, 35-57.

Parker, D. and Horton, B., (2005). Uncertainties in central England temperature 1878–2003 and some improvements to the maximum and minimum series. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *25*(9), 1173-1188.

Parker, D.E., Legg, T.P. and Folland, C.K., (1992). A new daily central England temperature series, 1772–1991. *International Journal of Climatology*, 12(4), 317-342.

Pavelka, M., Acosta, M., Kiese, R., Altimir, N., Brümmer, C., Crill, P., Darenova, E., Fuß, R., Gielen, B., Graf, A. and Klemedtsson, L., (2018). Standardisation of chamber technique for CO2, N2O and CH4 fluxes measurements from terrestrial ecosystems. *International Agrophysics*, 32(4).

Pilcher, J.R., Hall, V.A. and McCormac, F.G. (1996). An outline tephrochronology for the Holocene of the north of Ireland. *Journal of Quaternary Science,* 11 (6)**,** 485-494.

Piotrowska, N., Blaauw, M., Mauquoy, D. and Chambers, F.M., (2011). Constructing deposition chronologies for peat deposits using radiocarbon dating. *Mires and Peat*, *7*(10), 1-14.

Polanco-Martinez, J.M., Medina-Elizalde, M.A., Sanchez, G. and Mudelsee, M., (2019). BINCOR: an R package for estimating the correlation between two unevenly spaced time series.

Poucher P. (2009). *Wetland Margins Survey: Cors Fochno*. Dyfed Archaeological Trust

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ratcliffe, J., Andersen, R., Anderson, R., Newton, A., Campbell, D., Mauquoy, D. and Payne, R., (2018). Contemporary carbon fluxes do not reflect the long-term carbon balance for an Atlantic blanket bog. *The Holocene*, *28*(1), 140-149.

Rea, HA, Swindles, G. T. and Roe, H. M. (2012). The Hekla 1947 tephra in the north of Ireland: regional distribution, concentration, and geochemistry. *Journal of Quaternary Science 27***,** 425-431.

Reid, J. M., MacLeod, D. A., & Cresser, M. S. (1981). Factors affecting the chemistry of precipitation and river water in an upland catchment. *Journal of Hydrology*, 50, 129-145.

Reimer, P.J., Austin, W.E., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M. and Grootes, P.M., (2020). The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon,* 62(4), 725-757.

Ridley, L.M., (2014). *Study of dissolved organic matter in peatlands: molecular characterisation of a dynamic carbon reservoir*. (PhD thesis), University of Edinburgh.

Rinne, J., Tuovinen, J.P., Klemedtsson, L., Aurela, M., Holst, J., Lohila, A., Weslien, P., Vestin, P., Łakomiec, P., Peichl, M. and Tuittila, E.S., (2020). Effect of the 2018 European drought on methane and carbon dioxide exchange of northern mire ecosystems. *Philosophical Transactions of the Royal Society B*, *375*(1810), p.20190517.

Ritson, J. P., Brazier, R. E., Graham, N. J., Freeman, C., Templeton, M. R., & Clark, J. M. (2017). The effect of drought on dissolved organic carbon (DOC) release from peatland soil and vegetation sources. *Biogeosciences*, 14(11), 2891-2902.

Roulet, N.T., Lafleur, P.M., Richard, P.J., Moore, T.R., Humphreys, E.R. and Bubier, J.I.L.L., (2007). Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, *13*(2), 397-411.

Rowson, J.G., Worrall, F., and Evans, M.G., (2013). Predicting soil respiration from peatlands. *Science of the Total Environment*, *442*, 397-404.

Rowson, J. G., Gibson, H. S., Worrall, F., Ostle, N., Burt, T. P., & Adamson, J. K. (2010). The complete carbon budget of a drained peat catchment. *Soil Use and Management, 26*(3), 261-273.

Salm, J. O., Kimmel, K., Uri, V., & Mander, Ü. (2009). Global warming potential of drained and undrained peatlands in Estonia: a synthesis. *Wetlands, 29*(4), 1081-1092.

Salm, J. O., Maddison, M., Tammik, S., Soosaar, K., Truu, J., & Mander, Ü. (2012). Emissions of CO2, CH4 and N2O from undisturbed, drained, and mined peatlands in Estonia. *Hydrobiologia,* 692(1), 41-55.

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., Zielińska, M., Robroek, B.J., Jassey, V.E., Buttler, A. and Chojnicki, B.H., (2018). The impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in Northern Poland. *Wetlands*, *38*(3), 551-563.

Seddon, A.W., Mackay, A.W., Baker, A.G., Birks, H.J.B., Breman, E., Buck, C.E., Ellis, E.C., Froyd, C.A., Gill, J.L., Gillson, L. and Johnson, E.A., (2014). Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology*, *102*(1), 256-267.

Sim, T.G., Swindles, G.T., Morris, P.J., Baird, A.J., Cooper, C.L., Gallego-Sala, A.V., Charman, D.J., Roland, T.P., Borken, W., Mullan, D.J. and Aquino-López, M.A., (2021). Divergent responses of permafrost peatlands to recent climate change. *Environmental Research Letters*, *16*(3), p.034001.

Steinweg, J.M., Dukes, J.S. and Wallenstein, M.D., (2012). Modeling the effects of temperature and moisture on soil enzyme activity: linking laboratory assays to continuous field data. *Soil Biology and Biochemistry*, *55*, 85-92.

Strack, M., Waddington, J.M. and Tuittila, E.S., (2004). Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. *Global Biogeochemical Cycles*, *18*(4).

Swindles, G. (2006). *Reconstructions of Holocene climate change from peatland in the north of Ireland*. Unpublished PhD thesis, Queen's University, Belfast,

Swindles, G.T., De Vleeschouwer, F. and Plunkett, G., (2010). Dating peat profiles using tephra: stratigraphy, geochemistry, and chronology. *Mires and Peat*, *7*.

Troels-Smith, J., (1955). Karakterisering af løse jordarter. *Danmarks Geologiske Undersøgelse* IV. Række, 3(10), 1-73.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D. and Tuittila, E.S., (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, *196*(1), 49-67.

Turetsky, M.R., Donahue, W. and Benscoter, B.W., (2011b). Experimental drying intensifies burning and carbon losses in a northern peatland. *Nature Communications*, *2*(1), 1-5.

Turetsky, M.R., Kane, E.S., Harden, J.W., Ottmar, R.D., Manies, K.L., Hoy, E., and Kasischke, E.S., (2011a). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, *4*(1), 27-31.

Turetsky, M.R., Manning, S.W., and Wieder, R.K., (2004). Dating recent peat deposits. *Wetlands*, *24*(2), 324-356.

Turetsky, M.R., Treat, C.C., Waldrop, M.P., Waddington, J.M., Harden, J.W. and McGuire, A.D., (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. Journal of Geophysical Research: *Biogeosciences*, 113(G3).

Turunen, J., Roulet, N. T., Moore, T. R., & Richard, P. J. (2004). Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. *Global Biogeochemical Cycles,* 18(3).

Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P. and Harth, C., (2001). Response of CO2 and CH4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, *11*(2), 311-326.

Usoskin, I.G., Arlt, R., Asvestari, E., Hawkins, E., Käpylä, M., Kovaltsov, G.A., Krivova, N., Lockwood, M., Mursula, K., O'Reilly, J. and Owens, M., (2015). The Maunder minimum (1645–1715) was indeed a grand minimum: A reassessment of multiple datasets. *Astronomy and Astrophysics*, *581*, p.A95.

van der Linden, M., Heijmans, M.M. and van Geel, B., (2014). Carbon accumulation in peat deposits from northern Sweden to northern Germany during the last millennium. *The Holocene*, *24*(9), 1117-1125.

Vitt, D. H., Halsey, L. A., & Zoltai, S. C. (2000). The changing landscape of Canada's western boreal forest: the current dynamics of permafrost. *Canadian Journal of Forest Research,* 30(2), 283-287.

Voigt, C., Lamprecht, R.E., Marushchak, M.E., Lind, S.E., Novakovskiy, A., Aurela, M., Martikainen, P.J. and Biasi, C., (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases–carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, *23*(8), 3121-3138.

Waddington, J. M., & Roulet, N. T. (2000). Carbon balance of a boreal patterned peatland. *Global Change Biology, 6*(1), 87-97.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K. and Moore, P.A., (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, *8*(1), 113-127.

Walker, T.N., Garnett, M.H., Ward, S.E., Oakley, S., Bardgett, R.D. and Ostle, N.J., (2016). Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology*, *22*(5), 1880-1889.

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A. and Bardgett, R.D., (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, *16*(10), 1285-1293.

Watson, E.J., Swindles, G.T., Lawson, I.T. and Savov, I.P. (2015). Spatial variability of tephra and carbon accumulation in a Holocene peatland. *Quaternary Science Reviews,* 124**,** 248-264

Watson, E.J., Swindles, G.T., Lawson, I.T., Savov, I.P. and Wastegård, S., (2017). The presence of Holocene cryptotephra in Wales and southern England. *Journal of Quaternary Science*, *32*(4), 493-500.

Webb, J.R., Santos, I.R., Maher, D.T. and Finlay, K., (2019). The importance of aquatic carbon fluxes in net ecosystem carbon budgets: a catchment-scale review. *Ecosystems*, *22*(3), 508-527.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G. and Pockman, W.T., (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, *53*(10), 941-952.

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K. and Chapin, C.T., (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, *81*(12), 3464-3478.

Whiting, G.J. and Chanton, J.P., (2001). Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus B*, *53*(5), 521-528.

Worrall, F., and Burt, T.P., (2007). Trends in DOC concentration in Great Britain. *Journal of Hydrology*, *346*(3-4), 81-92.

Worrall, F., Burt, T.P. and Adamson, J.K., (2006). Trends in drought frequency–the fate of DOC export from British peatlands. *Climatic Change*, *76*(3), 339-359.

Yang, G., Chen, H., Wu, N., Tian, J., Peng, C., Zhu, Q., Zhu, D., He, Y., Zheng, Q. and Zhang, C., (2014). Effects of soil warming rainfall reduction and water table level on CH4 emissions from the Zoige peatland in China. *Soil Biology and Biochemistry*, *78*, 83-89.

Young, D.M., Baird, A.J., Charman, D.J., Evans, C.D., Gallego-Sala, A.V., Gill, P.J., Hughes, P.D., Morris, P.J. and Swindles, G.T., (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific reports*, *9*(1), 1-8.

Young, D.M., Baird, A.J., Gallego-Sala, A.V. and Loisel, J., (2021). A cautionary tale about using the apparent carbon accumulation rate (aCAR) obtained from peat cores. *Scientific Reports*, *11*(1), 1-12.

Yu, Z., (2011). Holocene carbon flux histories of the world's peatlands: Global carbon-cycle implications. *The Holocene*, *21*(5), 761-774.

Yu, Z., Turetsky, M.R., Campbell, I.D. and Vitt, D.H., (2001). Modelling long-term peatland dynamics. II. Processes and rates as inferred from litter and peat-core data. *Ecological Modelling*, *145*(2-3), 159-173.

Yu, Z.C., (2012). Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, *9*(10), 4071-4085.Zhang, Z., Zhang, R., Cescatti, A., Wohlfahrt, G., Buchmann, N., Zhu, J., Chen, G., Moyano, F., Pumpanen, J., Hirano, T. and Takagi, K., (2017). Effect of climate warming on the annual terrestrial net ecosystem CO2 exchange globally in the boreal and temperate regions*. Scientific reports*, 7(1), 1-11.

Zhang, H., Tuittila, E.S., Korrensalo, A., Laine, A.M., Uljas, S., Welti, N., Kerttula, J., Maljanen, M., Elliott, D., Vesala, T. and Lohila, A., (2021). Methane production and oxidation potentials along a fen-bog gradient from southern boreal to subarctic peatlands in Finland. *Global Change Biology*.

Zhu, D., Wu, N., Bhattarai, N., Oli, K.P., Chen, H., Rawat, G.S., Rashid, I., Dhakal, M., Joshi, S., Tian, J., and Zhu, Q.A., 2021. Methane emissions respond to soil temperature in convergent patterns but divergent sensitivities across wetlands along altitude. *Global Change Biology*, 27(4), 941-955.

Chapter 5: Testing the sensitivity of palaeoecological decay proxies and litter decomposition to experimental warming and drought in a Welsh ombrotrophic peatland: Implications for peatland palaeoecological studies.

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5.1. Summary

Decomposition of organic matter is an important component of the peatland carbon balance. In this study we investigated how decomposition is affected by climate change by testing the sensitivity to simulated warming and drought of the Tea Bag Index (TBI) and three paleoenvironmental proxies for decay: loss on ignition (LOI); C/N ratios and peat humification. Above- and below ground samples were analysed following 92 days of incubation in a field experiment on a Welsh raised bog. Results were compared with the long-term palaeoecological record for the past c. 1500 years. Despite a significant mean annual 10 cm soil temperature increase of ~0.5°C during the incubation period, no treatment affected the TBI parameters or the palaeo-proxies. Warming increased the stabilisation of below-ground organic matter relative to the peat surface, while under drought conditions the opposite occurred. Buried tea bags lost less organic matter than surface bags. In the palaeoecological record, each proxy exhibited distinct trends, with variation above the range seen in our experimental treatments, indicative that the botanical composition of the peat controls degrees of decomposition, rather than climate. While humification and LOI may be sensitive to changes in decomposition, they appear insensitive to relatively small shifts in climate.

5.2. Introduction

Northern peatlands represent the largest terrestrial store of organic soil carbon (Gorham, 1991; Yu, 2012). They act as net carbon sinks, owing to the imbalance between production and decay resulting from cool, waterlogged conditions that inhibit microbial activity (Freeman *et al.,* 1996; Clymo *et al.,* 1998; Bragazza *et al.,* 2016). This net accumulation has led to an estimated c. 550 Gt C being stored in boreal peatlands since their initiation (Yu *et al.,* 2010), despite representing only c. 3% of terrestrial land area (Gorham, 1991, Xu *et al.,* 2018). Most peatlands occur in the Northern Hemisphere (Xu *et al.,* 2018) where the greatest changes in temperature and precipitation due to anthropogenic climate change (Lee *et al.,* 2021) are projected to occur.

In addition to warmer temperatures, extreme weather events are expected to increase, including more frequent summer droughts (Lee *et al.,* 2021). Lowered water levels expose formerly waterlogged peats to aerobic conditions (Bragazza *et al.,* 2016). This may alter peatland productivity and remove the constraints that inhibit decay, stimulating decomposition (Fenner and Freeman, 2001; Freeman *et al.,* 2004). Such changes may alter the peatland carbon balance, affecting climate feedbacks of greenhouse gas emissions to the atmosphere (Heimann and Reichstein, 2008; Charman *et al.,* 2013; Waddington *et al.,* 2015; Gallego-Sala *et al.,* 2018). Assessing how organic matter decomposition will respond to climate change is important for understanding how peatlands will influence the global climate system under future warming conditions.

Peatlands preserve an archive of past environmental change within their stratigraphy (Chambers and Charman, 2004). Numerous palaeoecological studies have reconstructed past environmental conditions from peatlands, ascribed to both natural (climate) and anthropogenic drivers (e.g., Chambers *et al.,* 2011; Turner *et al.,* 2014). For more than a century (Barber, 1981) these studies have relied upon identification and quantification of biological proxies such as pollen and plant macrofossils (Barber *et al.,* 2003; Sillasoo *et al.,* 2007) and quantitative or semi-quantitative assessment of the physical or chemical properties of the peat (Blackford and Chambers 1991; 1993; 1995). In the past few decades, developments in numerical methods have allowed quantitative reconstructions of past environmental change by applying contemporary species - environment relationships to fossil assemblages (Imbrie and Kipp, 1971; Woodland *et al.,* 1998). In particular, testate amoebae have been widely applied in quantitative palaeohydrological reconstructions in peatland studies (Charman, 2001; Mitchell *et al.,* 2008). While transfer function-based reconstructions have specific limitations, their usefulness has been validated and tested by numerous experimental and comparative studies, allowing for refinement of these methods (e.g., Payne, 2007; Charman *et al.,* 2009; Payne *et al.,* 2011; Swindles *et al.,* 2015; Swindles *et al.,* 2020). Many older proxies (e.g., colorimetric peat humification; C/N ratios) are also still frequently used in peatland palaeoclimate studies (e.g., Zhang *et al.,* 2021; Tsyganov *et al.,* 2021). The semi-quantitative nature of changes inferred by these methods can make them difficult to interpret in terms of actual changes in climate (Woodland *et al.,* 1998).

Decomposition proxies are rarely tested experimentally. While some studies have found good correlations between proxies and decomposition indices or meteorological climate records (Blackford and Chambers 1991; 1995; Tfaily *et al.,* 2014), others have not (Mauquoy *et al.,* 2002; Blundell and Barber, 2005). For example, Borgmark and Schoning (2006) compared humification and C/N records with reconstructed water levels from two Swedish peat bogs and correlated these records with meteorological data. They found that C/N ratios and humification indices were strongly correlated and exhibited similar trends between sites, but that correlations between these decomposition proxies and reconstructed water table depths were weak. Increased decomposition appeared to precede drier climatic conditions, reflecting renewed decomposition of previously deposited, older peat. Payne and Blackford (2008) compared humification records with testate amoebae-inferred water table depth reconstructions from multiple cores from south-east Alaska, finding little coherence between sites or between proxies. Zaccone *et al.* (2018) tested several physical, chemical, and spectroscopic approaches from nine peatlands across four continents to identify which methods for determining humification were most effective. They found that C/N ratios correlated poorly with most other proxies, and that the supply of inorganic wind-blown material was mainly responsible for variations in LOI. Spectroscopic indices (including alkali-extracted humic acids) showed good correlations between sites. Zaccone *et al.* (2018) recommended the ratios of hydrogen and carbon (H/C) as the proxy most representative of peat humification, whilst being cost-effective and removing the need for chemical dissolution that may introduce artefacts. Understanding whether these proxies preserve palaeoenvironmental decay signals relevant to past climate changes is fundamental to their continued use in peatland studies and is essential for their use in testing climate models (Swindles *et al.,* 2012).

This study explores the effects of simulated warming and drought on surface and subsoil decomposition and labile organic matter stabilisation using the tea bag index (TBI) method (Keuskamp *et al.,* 2013). Remaining litter from the tea bag experiment is used to test the sensitivity of three palaeoecological proxies for decomposition: peat humification (Aaby and Tauber, 1975; Blackford and Chambers, 1993); C/N ratios (Malmer and Holm, 1984; Kuhry and Vitt, 1996) and loss on ignition (LOI) (Bouyoucos, 1934; Leifield *et al.,* 2011). Finally, we compare the results to changes in these proxies throughout a peat core spanning the past c. 1500 years from the same site. We hypothesise that increased temperatures and drought frequency increase decay rates and that the magnitude and direction of these changes will be reflected in the palaeoecological proxies.

5.3. Methods

5.3.1. Experimental site.

Cors Fochno (Lat: 52.50°N, Long: 4.01°W) (Figure 5.1a – c) is a *Sphagnum*-dominated raised bog in Ceredigion, Wales. It has a central zone comprising c. 2 km^2 of actively accumulating primary surface peat, surrounded by c. 4 km^2 of degraded peatland (Poucher, 2009). Dominant vegetation includes *Sphagnum pulchrum, Rhynchospora alba* and *Calluna vulgaris*.

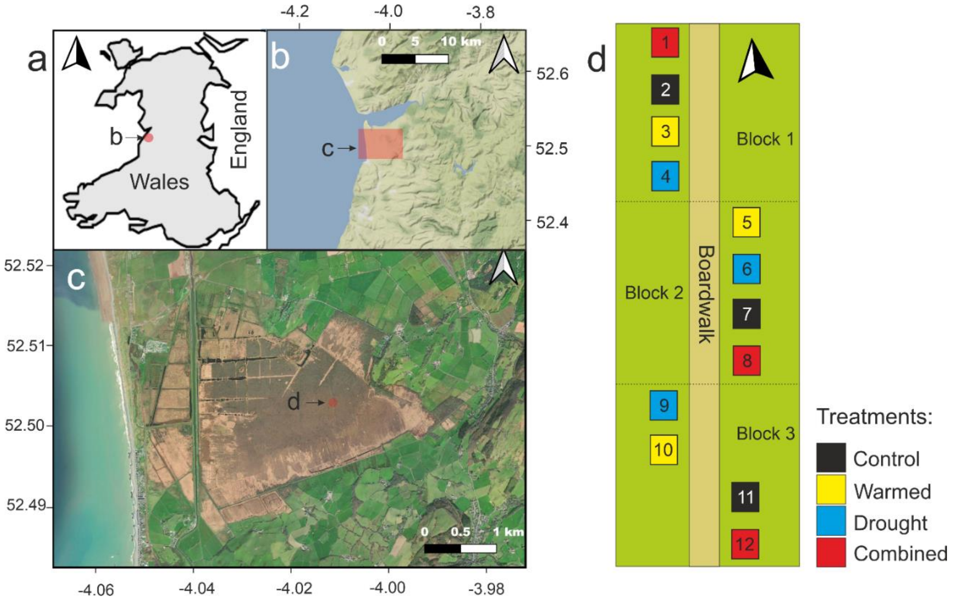

Figure 5.1. Location of the experimental site: a. Map of Wales. Red shaded areas show the area indicated by the following panel. b. topographic map showing the area from Machynlleth to Aberystwyth (Stamen terrain background). c. ESRI Satellite image Cors Fochno. showing the location of the experimental site and location of core BO17 (red dot). d. Schematic (not to scale) showing the design of the Cors Fochno experimental climate manipulation site along the boardwalk.

5.3.2. Experimental design

The Cors Fochno experiment is a long-term fully factorial *in-situ* climate manipulation study that was established in 2010. Twelve experimental plots were subjected to one of three experimental treatments, arranged in three blocks along a transect running through the intact, raised portion of the site (Figure 5.1d). The experiment is intended to determine the long-term effects of future projected changes in climate warming and drought upon ecosystem functioning, reflecting the predicted range for the region from the present until c. 2070 (Lowe *et al.,* 2018). The experiment simulates climate warming using open top chambers (OTCs), and increased drought frequency by seasonal pumping of groundwater from within the plots (Figure 5.2). The treatments are 1. Control (no treatment), 2. *In-situ* passive warming, 3. Seasonal summer drought manipulation and 4. Combined warming and drought. Four experimental droughts were carried out in

2010, 2011, 2014 and 2019. Drought events are simulated during the summer months (typically between July to September), generating an average water table drawdown of c. 16 cm over four weeks, while the OTCs warm air temperatures within the treatment plots all year by 0.3 – 0.7°C relative to ambient (control) temperatures. The experimental setup is fully described by Andrews *et al.* (2021). The incubation period of litter bags in this study began one week after the end of the last drought experiment in 2019.

Air and soil (10 cm depth) temperatures were initially measured using HOBO Onset U10 Temperature loggers (Onset Computer Corporation; Massachusetts USA) within each plot; in 2018 they were replaced with HOBO U23 Pro v2 temperature sensors. TruTrack WT-HR 2000 water height data loggers (Trutrack, Christchurch, New Zealand) recorded changes in water levels, converted to water table depths by calibration with manual water table depth measurements. Air, soil (10 cm depth) and water table depths were recorded at six-hourly intervals. Data gaps in the water table records were gap-filled by linear interpolation with an adjacent dip-well operated by Natural Resources Wales.

Vegetation community composition was measured for 2019 as part of a long-term study investigating the effects of the experimental treatments upon vegetation community change (methods described in Andrews *et al.* 2021). Vegetation communities (expressed as species percentage relative abundance) were ordered into sub-groups using hierarchical clustering, and differences in decomposition between each group were tested to assess how vegetation community composition influences decay. Ward's minimum variance method was used to identify clustering structures. The number of clusters was determined using the average silhouette approach. All analyses were performed using the package ‘cluster’ using the statistical package ‘R’ version 4.0.5 (R Core Team, 2010; Maechler *et al.,* 2021).

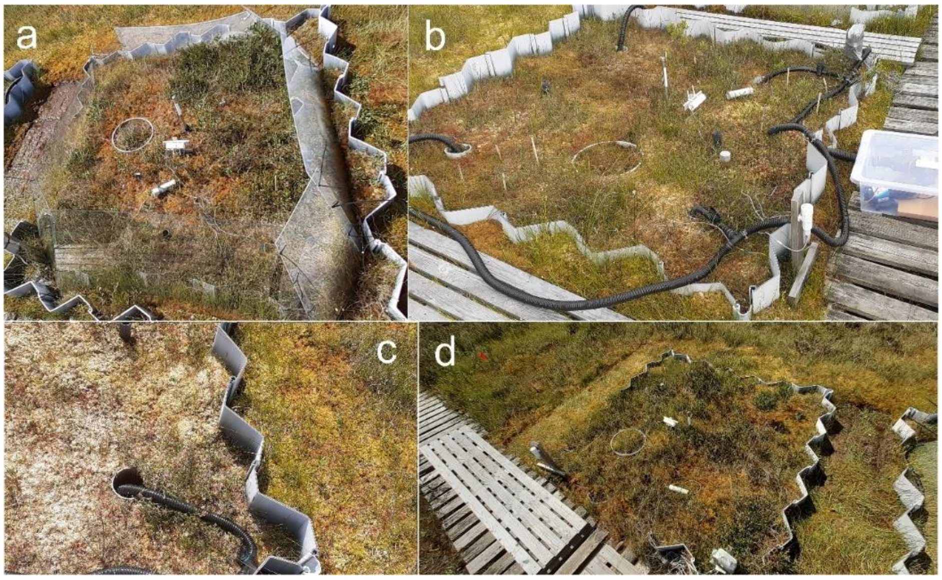

Figure 5.2. Photographs of the treatment plots in Cors Fochno. a. Warmed plot with open top chamber (OTC) b. Drought plot showing the pumping infrastructure used during the episodic seasonal drought simulation, c. Plot showing the pumping wells within the plot (left side of figure) and the effect of drought simulation upon *Sphagnum* compared with the site (right side of figure) d. Control plot. Photos by Luke Andrews.

5.3.3. Tea Bag Index

The Tea Bag Index (TBI) method (Keuskamp *et al.,* 2013) was used to measure the effects of warming and drought upon decay. This method utilises two litter types of varying resistance to decay: Lipton green tea (*Camellia sinensis*; EAN: 8714100770542) represents readily decomposed (labile) material and rooibos tea (*Aspalanthus linearis*; EAN: 8711327514348) represents decay resistant (recalcitrant) material. The TBI method calculates two decay parameters: Stabilisation (*S)* represents the transformation of labile organic matter into more recalcitrant compounds by microbial activity and environmental conditions. Higher *S* indicates a greater potential for long-term carbon storage (Keuskamp *et al.,* 2013). Decomposition rate (*k*) reflects microbial decay and short-term carbon dynamics (Prescott, 2010; Keuskamp *et al.,* 2013). Keuskamp *et al.* (2013) originally recommended the use of tea bags using synthetic, woven tetrahedron bags, however non-woven tetrahedron bags were used in our study since woven mesh bags were discontinued in 2017. This may affect comparison between the results of this study and others using woven bags, due to the differences in mesh sizes between these two types of material (Teatime4Science, 2021).

The woven mesh bags were preferred by Keuskamp *et al*., (2013) due to the consistent mesh size of the bags. Mesh size in litterbag studies can determine the amount of mass lost and gained by the bags, with smaller mesh sizes potentially interfering with decomposition processes and excluding larger-bodied decomposers (Lecerf, 2017). The non-woven mesh bags do not have a standardised mesh size; therefore their use may reduce the reproducibility of this study.

A few studies have assessed the TBI method to see how well tea performs as an alternative for peatland vegetation in litter decomposition studies, and whether the results of the TBI method are comparable to traditional litterbag decomposition studies. Blume-Werry *et al*. (2021) compared the degree of leaching between the two types of tea used by this method and the leaves and roots of various temperate peatland plant species. They found that while green tea lost more mass by leaching than the other leaves tested, rooibos tea leached less, potentially offsetting this difference. Duddigan *et al*. (2000) incubated samples of both tea types and analysed the remains to assess how changes in the stoichiometry of carbon and nitrogen compared with other plant litters. Both studies concluded that tea was a suitable proxy for other vegetation types.

MacDonald *et al.*, (2018) and Didion *et al*. (2016) compared the mass lost and decomposition rates from traditional litter bag studies on peatlands to those derived from the TBI method. The TBI method observed similar responses to environmental variables and trends between wet and dry sites, indicating that the TBI reflects the same spatial patterns in decomposition.

Each bag was oven-dried at <45°C for 48 hours prior to weighing. The mass of tea per bag was calculated by subtracting the weight of each bag from the average empty bag weight (mean bag weights ± 1 sd: green= 1.88 ± 0.06 g; rooibos= 2.16 ± 0.05 g, n= 5). Five replicate pairs of green tea and rooibos bags were placed onto the surface of each plot. Another five replicate pairs were buried beneath the peat surface to a depth of 8cm._While tea bags are sometimes leached by flushing with water prior to incubation to remove water soluble compounds that may influence results (Seelen *et al.,* 2019), findings by Blume-Werry *et al.* (2021) show that this modification is unnecessary. Experimental field incubation began on the 12th of September 2019. Tea bags were retrieved after 92 days on the 13th of December 2019. These dates were chosen to capture the time of year where litterfall from ericaceous plants was highest at the site (Ritson *et al.,* 2016). During the autumn and spring, the contribution of surface litter and heterotrophic respiration towards net ecosystem respiration in terrestrial ecosystems is highest, in accordance with the increased rates of litterfall (Luo and Zhou, 2010; Bonnett *et al.,* 2006; Jovani-Sancho *et al*., 2021). The short nature and timing of this experimental incubation means that we might expect decomposition rates to be lower than they would be during the summer, as decomposition rates are reduced under colder conditions. However, in a litter bag experiment conducted in northern Quebec over the course of a full year, between 59 – 65 % of the decomposition took place during the winter months (Bartsch and Moore, 1985).

Recovered bags were dried at <45°C for 48 hours after retrieval. Unfortunately, all surface sample replicates from plot 9 (drought) and a buried tea bag from plot 8 (combined treatment) were lost during incubation. Following drying, each bag was opened. Foreign particles (rootlets, sphagnum leaves) were carefully removed, and the bag contents re-weighed. Mass loss (%) was calculated for each bag. TBI parameters *S* and *k* were calculated for each replicate using equations detailed in Keuskamp *et al.* (2013). After analysis, remaining green tea from each tea bag was homogenised using a ball mill, and each sample was analysed for colorimetric light absorbance (as a measure of humification), LOI and C/N ratios following standard methods. Green tea was analysed since it was viewed that the labile green tea would better reflect changes due to decomposition than rooibos tea during the short incubation time.

5.3.4. Decomposition proxies

5.3.4.1. Colorimetric % light transmittance (humification analysis)

Humification is one of the most frequently used proxies for climate-driven decomposition in peatland studies (de Jong *et al.,* 2010). Peat humification reflects the extent of peat decomposition in the acrotelm, the oxic layer above the water table, prior to its incorporation into the permanently saturated catotelm, where decay rates are much slower (Clymo, 1984; Blackford and Chambers, 1993; de Jong, 2010; Chambers *et al.,* 2011; 2012). Humic acids concentrate in peat as by-products of organic matter decay and are dark brown in colour. Darkly coloured peat is assumed to indicate high degrees of humification, indicating drier or warmer conditions that promoted increased decomposition rates and reduced peat accumulation rates (de Jong *et al.,* 2010). By chemically extracting humic acids from peat, their concentrations can be determined from the optical absorption of the resulting solution using colorimetric procedures (light spectroscopy) (Aaby, 1976; Blackford and Chambers, 1993).

Humification is determined in this study following methods outlined by Roos-Barraclough *et al.* (2004). Sub-samples of green tea weighing 0.02g were placed into a 50ml centrifuge tube containing 8% sodium hydrochloride solution and stirred using a vortex mixer for ten seconds. Samples were heated for 60 minutes in a water bath at 95°C before filtering through Whatman type '0' qualitative paper filters. Filtered samples were then diluted to 20 ml with deionised water and centrifuged at 3000 rpm for five minutes, to remove remnants of inorganic material (Blackford and Chambers, 1993). Humification was measured as percentage light transmission using a spectrophotometer at 550 µm (Aaby and Tauber, 1975; de Jong *et al.,* 2010). Each measurement was repeated three times to ensure analytical precision. To prevent colour loss during analysis, samples were prepared in batches of 20, initial measurements were repeated at the end of each batch to ensure no colour loss had occurred, and batches were analysed following a strict time schedule.

5.3.4.2. C/N ratio

Carbon (C) is preferentially lost over nitrogen (N) during peat decay, therefore increases in the ratio between total C and N in peat is considered to reflect the degree of decomposition that has taken place over time (Malmer and Holm, 1984; Leifeld *et al.,* 2020). Total C and N content were measured by analysing 55 ± 5 mg of milled green tea using a Vario Macro Carbon/Nitrogen Analyser.

5.3.4.3. Loss on ignition

Loss on ignition (LOI) is commonly used to measure total organic matter content in peatland palaeoecological studies, usually as a proxy for carbon content in soils (Hoogsteen *et al.,* 2015). Organic matter content in peat soils decreases with aeration and oxidation, resulting in a relative increase in inorganic compounds in decayed peat, therefore reduced LOI can be viewed as reflective of increased decay (Dean, 1974; Heiri *et al.,* 2001; Leifield *et al.,* 2011). Dried and milled samples of green tea were weighed in ceramic crucibles of known weight before ashing at 550°C for 6 hours (Heiri *et al.,* 2001). Ashed samples were re-weighed, and the percentage of mass lost calculated as % LOI.

5.3.5. Coring methods and palaeoecological analysis

Palaeoecological analyses were conducted upon material taken from a 1.5 m-long core (BO17) sampled from the site during November 2017. The core was sampled using a 5 cm diameter Russian corer, with 5 cm of overlap between core sections (Jowsey, 1966). The coring location was c. 3 m from the experimental site and was characterised by a *Sphagnum pulchrum* lawn. The uppermost 50 cm was extracted using a monolith tin. Extracted core sections were stored in guttering, wrapped in cling film, and refrigerated at 4°C prior to sub-sampling. The chronology of core BO17 used in this study is based upon a Bayesian model generated using the ‘rplum’ package in R (Aquino-López *et al.,* 2018; 2020) from a combination of radiocarbon, spheroidal carbonaceous particles, macrocharcoal horizons, tephrochronology and ^{210}Pb dates (Andrews *et al.,* submitted). The chronological data and age-depth model are included in the supplementary materials (Supplementary Table 2.3. and 2.5).

Samples throughout core BO17 were sub-sampled at 1 cm contiguous intervals and analysed using the methods described above. The sampling period covers the past c. 1500 years. This period was chosen since climatic conditions during this period are well known for many regions, and climatic variation during this time (~0.2°C) is close to simulated temperature differences imparted by our experiment (0.1°C – 0.9°C) (Bradley and Jonest, 1993; Mann *et al.,* 2009; Andrews *et al.,* submitted). To account for increased decomposition throughout the peat column, the data were detrended by calculating residual % transmission, using the linear relationship between measured % light transmission and depth (Chambers *et al.,* 2011).

5.3.6. Statistical analyses

All statistical analyses were carried out in R version 4.0.5 (R core team, 2021). Treatment effects were tested for generalised linear mixed effect models (GLMMs) using the 'lme4' (Bates *et al.,* 2015) and 'lmerTest' (Kuznetsova *et al.,* 2017) packages. Model residuals were tested for heteroscedasticity and ANOVA was used to determine the significance of fixed factors. Environmental variables, TBI parameters and paleoenvironmental proxies were tested in turn as response variables, with treatment, burial depth, and their interaction, as well as vegetation group included as fixed factors. Treatment effects were considered significant at p = <0.05. Variation between the palaeoecological and TBI parameters was summarised using redundancy analysis (RDA). Analyses were performed using the ‘rda’ function in the package ‘vegan’ (Oksanen *et al.,* 2019). Numeric values for response (palaeoecological proxies) and explanatory (TBI parameter) variables were square root transformed and standardised prior to analysis, accounting for the skewed distributions and different base units of measurement for each variable. Surface and buried tea bags were analysed separately to assess differences between above- and below-ground relationships. To account for pseudo-replication arising due to the hierarchical design of the experiment, plots (nested in blocks) were included as random factors for the GLMMs. For the RDA analyses, permutation tests using 999 iterations were used to determine test significance, with permutations restricted by plots within blocks, using the package ‘permute’ (Simpson, 2019).

5.4. Results

5.4.1. Climate manipulation effects upon environmental variables

Time series data for air and soil temperatures and water table depths averaged across all plots are shown in Figure 5.3. Ambient climatic conditions (measured within the control treatments) and water table depths (measured across all plots) throughout the incubation period (92 days from mid-September until mid-December) are detailed in Table 5.1. During this time, soil temperature in the artificially warmed plots significantly increased by 0.5 ± 0.2°C, and in the warmed and droughted plots significantly increased by 0.8 ± 0.2°C relative to controls (Figure 5.4). No significant differences in air temperatures or water table depths were identified between treatments, in contrast with earlier studies from the site (Andrews *et al*., 2021; Andrews *et al.,* submitted).

Table 5.1. Climatic conditions during the experimental incubation period on Cors Fochno. Air and soil (10cm depth) temperatures are based upon measurements taken within the control plots and represent the mean ambient temperature conditions across the experimental site. Water table depths (relative to peat surface) are based upon values across all plots since relative depth to the water table varies greatly between experimental plots.

Environmental variable	*Mean*	*Median*	*Min*	*Max*	*Range*
Air temperature (℃)	9.3	8.7	-6.5	29.1	35.6
Soil temperature (℃)	10	9.9	3.4	16.9	13.5
Water table depth (*cm*)	8.2	8.1	4.4	12.3	7.9

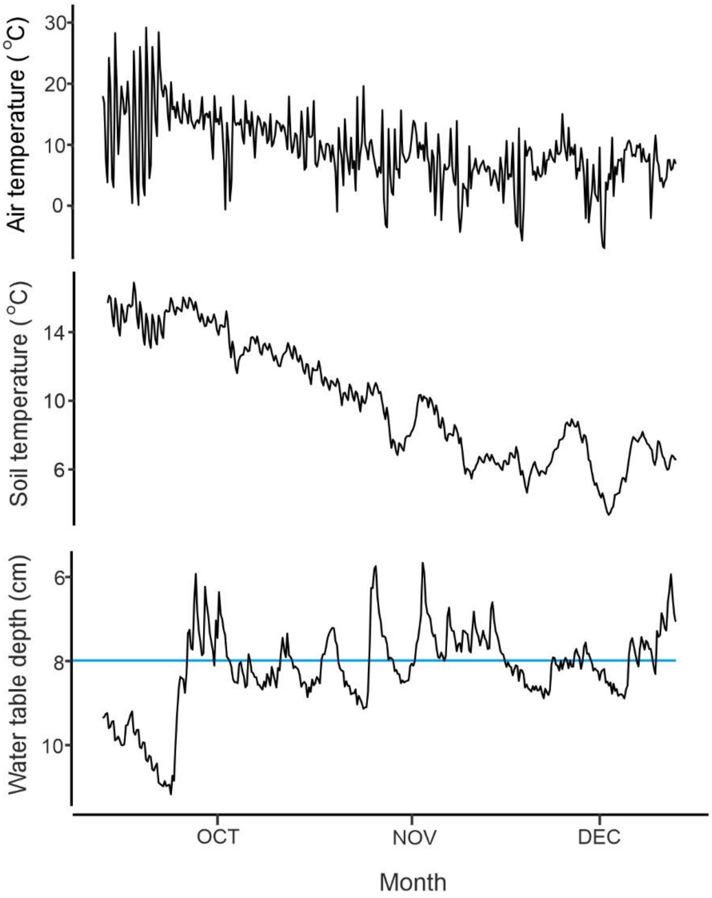

Figure 5.3. Average 6-hourly time series showing ambient air and soil temperatures (℃) (measurements taken from control plots) and water table depths (cm) averaged across all experimental plots during the experimental incubation period. The horizontal line on the water table depth plot shows the approximate depth of the buried tea bags, showing their relative position in line with the water table.

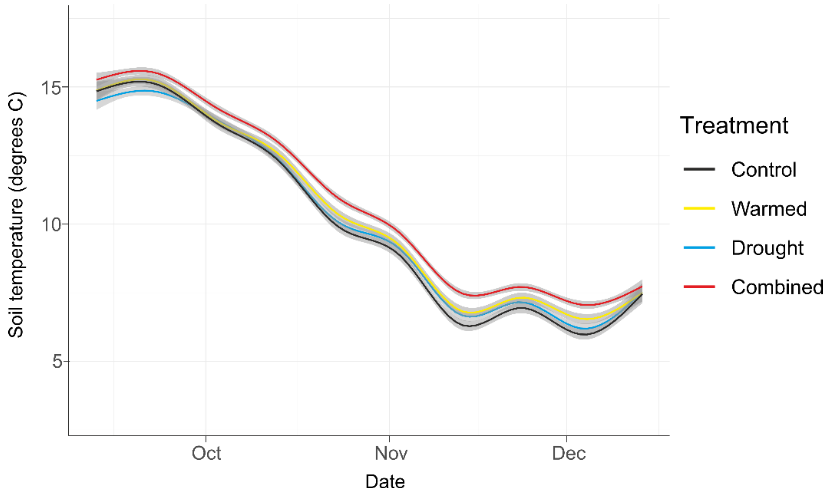

Figure 5.4. Generalised additive models fitted to the soil temperature (10 cm) time series data from the Cors Fochno experimental site, showing differences in soil temperatures between treatments. Grey shaded areas around each curve is the 95% confidence prediction interval for each model.

5.4.2. Vegetation

In 2019, the most abundant species in the experimental plots were *Rhynchospora alba*, which averaged 31.9 % of vegetation cover between all plots. *Sphagnum pulchrum* constituted a further 22.3 %. Other common species include *Erica tetralix* (10.6 %) and *Calluna vulgaris* (6.8 %). Cluster analysis separated the plots into five distinct vegetation groups (Table 5.2). The results of the average silhouette and hierarchical clustering are illustrated in Supplementary Figure 3.

Table 5.2. Cluster groups for vegetation in each plot. C: Control; W: Warmed; D: Drought; WD: Combined.

Cluster	Plots	Treatments	Most frequent species (in order of abundance)
1	4, 11	D, C	*Sphagnum pulchrum + Rhynchospora alba*
2	8, 10, 12, 2, 9	WD, W, WD, C, D	*R. alba + S. pulchrum*
3	6	D	Liverworts, *Erica tetralix + Eriophorum angustifolium*
4	1, 3	WD, W	*R. alba, Calluna vulgaris, S. pulchrum*
5	5, 7	W, C	*R. alba, E. tetralix, C. vulgaris*

5.4.3. Tea bag index; Decomposition rate (*k*) and stabilisation factor (*S*)

Differences in tea bag index parameters between treatments and depth are illustrated in Figure 5.5a-d. Both *k* and *S* were within the ranges reported from Keuskamp *et al.* (2013) for intact peatlands. No significant differences in *k* were identified due to treatment, burial, or their interactions (Figure 5.5a). The difference in *S* between surface and buried samples increased by 0.07 ± 0.02 relative to controls and decreased with drought by 0.05 ± 0.02. (Figure 5.5b). The percentage weight loss of green tea was on average 65.2 % across all samples, ranging from 47.1 to 73.2 % (Figure 5.5c). A significant interaction was identified between percentage loss of green tea between experimental treatments and burial. In warmed plots, burial reduced the amount of mass lost from the green tea by 5.7 ± 2.0 % relative to controls, whereas in droughted plots, the amount of mass loss decreased by 4.4 ± 1.8 % relative to controls. Average percentage mass loss of rooibos tea bags was less than for green tea (Figure 5.5d), at 29.0 %, ranging between 17.1 and 40.2 %. Loss of rooibos tea was significantly reduced in buried samples, decreasing by 1.8 ± 0.8 %, although this effect was not significant.

5.4.4. Peat decomposition proxies

Differences in each decomposition proxy between treatments and depth are shown in Figure 5.5e-g. Loss on ignition was on average 96.8 % across all samples, and was significantly affected by burial, which increased LOI by 1.5 ± 0.3% (Figure 5.5e). Mean C/N ratios were 9.2 ± 0.7 across all samples, ranging between 8.0 and 12.3 (Figure 5.5f). No significant effects due to treatment, burial or their interactions were found for C/N ratios. % Light transmission (Figure 5.5g) ranged between 41.5 % to 77.6 % and was significantly higher in buried samples, increasing by 13.9 ± 2.8 %.

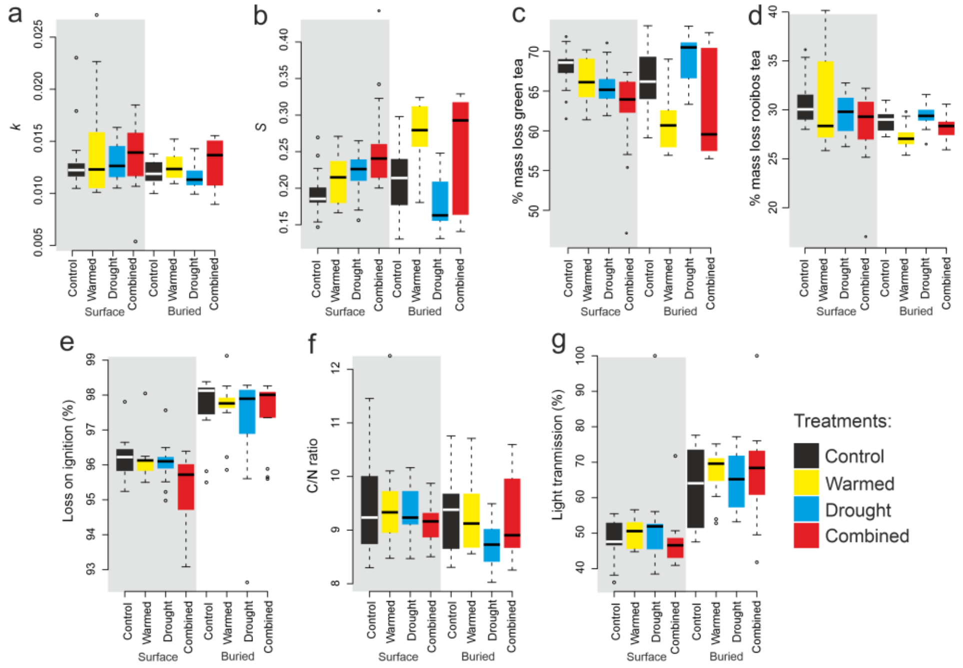

Figure 5.5. Box plots showing the variation in the data and differences between experimental treatments and surface and buried samples. The top row of plots illustrates the tea bag parameters (a: decomposition rate *k*, b: stabilisation factor *S*, c: % mass loss of green (labile) tea and d: % mass loss of (recalcitrant) rooibos tea. The lower row shows the data distribution and differences between each measured palaeoecological proxy of decomposition by treatment and burial: e: Loss on ignition (LOI), f: C/N ratio and g: humification (% light transmission). Shaded areas delineate the box plots for surface (grey) and buried (unshaded) tea bags.

5.4.5. Variance of palaeoecological proxy values explained by decomposition

For surface samples, the solution fit for the redundancy analysis comparing TBI parameters with the palaeoecological proxies was not significant, explaining only 21.5 % of all the variance (Supplementary Figure 3.2a). The solution fit was significant for buried samples, explaining 44.0 % of the variance in the palaeoecological proxies (Supplementary Figure 3.2b). A significant proportion of the variance was explained by *S* (23.7 %), which showed a close positive relationship with % light transmission.

Vegetation explained 15.1 % of the variation, but this was slightly below the level of significance.

5.4.6. Core derived proxy reconstruction

The results of the palaeoecological analyses of LOI, C/N ratios and residual % light transmission analysis are illustrated in Figure 5.6. These are contrasted with previously analysed vegetational changes assessed by plant macrofossil analysis and testate amoebae derived reconstructed water tables, described in Andrews *et al.* (2021). Percentage LOI is high throughout the core, ranging between 71.2 and 99.8 %, with a mean value of 95.5 %. Values are stable throughout most of the peat column, although two periods of change are evident. LOI was higher between c. 600 – 1250 CE, where mean values were 97.0 %. After this, average LOI declined slightly to 94.4 %, exhibiting higher variability. At the top of the profile above 4 cm (c. 2011 CE), LOI rapidly falls. Ashed residues from these surface samples were visually inspected under high power magnification (100 – 400x) revealing that the ash was composed almost completely of diatom frustules. C/N ratios fluctuate throughout the profile, ranging between 14.8 to 74.1, with a mean of 33.8. This value falls within the median range (55 ± 33) for northern peatlands (Loisel *et al.,* 2014). Residual % light transmission values fluctuate greatly; however, broad trends may be discerned. C/N ratios fall by c. 20 % between c. 600 – 900 CE, broadly corresponding to a shift in vegetation composition from *S. austinii* to *Erica tetralix*-dominated communities. Residual % light transmission also increases during this period. C/N ratios then increase until c. 1100 CE, during a period where the vegetation record is mostly represented by *S. austinii,* while residual % light transmission values fluctuate by c. 30 %, showing no discernible trend. C/N ratios fall again until c. 1460 CE, corresponding with a decline in residual % light transmission, although this ends around c. 1360 CE. This directional shift in C/N ratios is initially abrupt, reflecting a period characterised by low *Sphagnum* and abundant *E. tetralix* seeds. This trend levels off by c. 1300 CE until c. 1500 CE as *S. papillosum* becomes the dominant peat-forming vegetation. During this time, residual % light transmission fluctuates greatly, although there is a general trend towards increased light transmission. C/N ratios increase from c. 1500 to c. 1930 CE, as aquatic vegetation dominated by *S. denticulatum* give way to more terrestrial conditions characterised by *S. pulchrum,* coincident with a period of water table lowering. Residual % light transmission peaks at c. 1800 CE, before declining again. C/N ratios then decrease until c. 1991 CE during a period of increasing water table conditions, as residual % light transmission also declines, attaining its lowest value at c. 1980 before starting to increase again, showing a clear trend of increasing light transmission until the end of the profile. C/N ratios increase for the final time at the end of the profile between c. 1991 and c. 2009 CE, before falling until the end of the profile as the relative abundance of liverworts and *S. tenellum* increases.

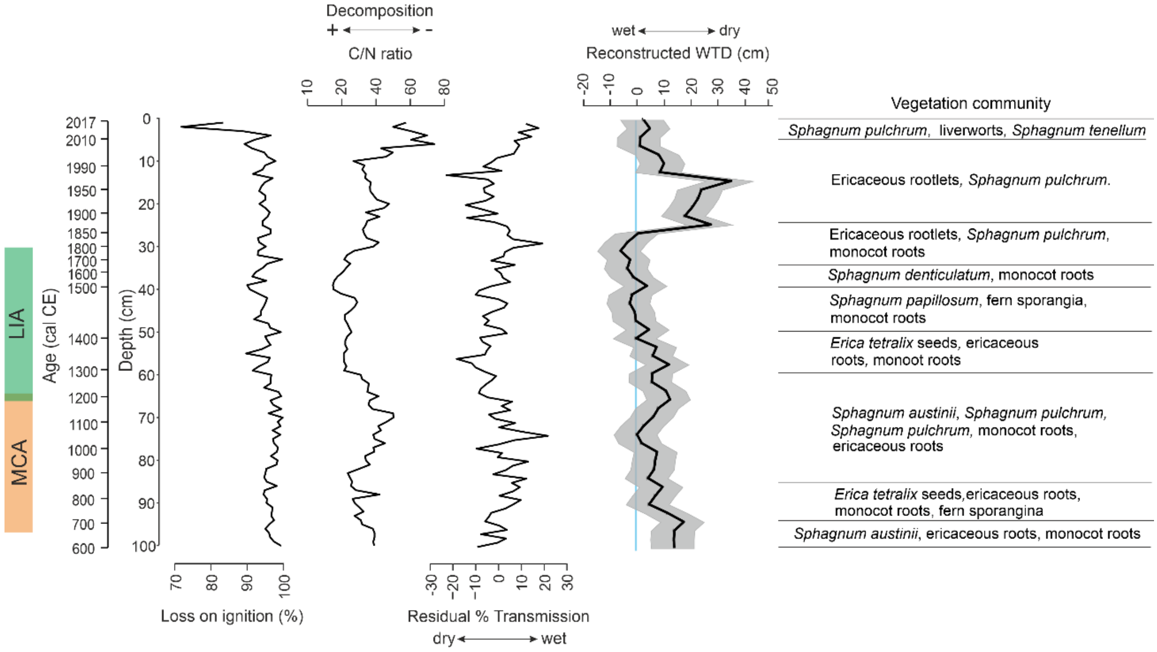

Figure 5.6. Peat physical proxies from core BO17, showing how Loss on Ignition (LOI), C/N ratios, residual % transmission, testate amoeba inferred water table depths (Andrews *et al.,* 2021) and vegetation community composition has changed throughout the stratigraphic profile of the core. The age-depth model is based on a previous study from the site (Andrews *et al.,* submitted). Median age values are given throughout the length of the core. The coloured bars on the left side of the figure denote the periods encompassing the Medieval Climate Anomaly (MCA, orange) and Little Ice Age (LIA, green).

5.5. Discussion

5.5.1. Effects of experimental treatments upon palaeoecological proxies

Burial suppressed loss of organic matter from the green tea bags. This was reflected by reduced light transmission, increased stabilisation, and reduced mass loss in the buried tea bags relative to those on the surface. This difference with burial is likely to relate to the position of the tea bags relative to the water table, which was above the burial depth (8 cm) for much of the incubation period (Figure 5.3). Reduced LOI due to burial is likely to reflect the suppression of decomposition and increased stabilisation, due to the anoxic and cooler conditions beneath the water table relative to the surface (Belyea, 1996; Laiho, 2006; Moore and Basiliko, 2006; Bragazza *et al.,* 2008). The correspondence of the tea bag index parameters and both LOI and light transmission suggests that these proxies are effective indicators of changes in organic matter decomposition resulting from burial.

The insignificance of the redundancy analysis model for the surface tea bags (Supplementary Figure 3.2a) suggests that decomposition that occurs above the peat surface is not preserved as a palaeoclimatic signal that can be detected by the palaeoecological methods tested in this study. This may relate to the increased leaching, decay, and oxidation of water-soluble organic substances (e.g., humic and fulvic acids) under aerobic conditions (Nykvist, 1959). Only humification preserved a palaeoclimatic signal of decay, with % light transmittance showing a positive relationship with *S* (Supplementary Figure 3.2b). Despite evidence that humification preserved a signal of decomposition, all proxies were insensitive to the treatment effects imparted by our experiment. The effect of warming on soil temperature (c. + 0.5°C at 10 cm depth) is slightly higher than the estimated range for temperature differences during the transition between the Medieval Climate Anomaly (MCA), a period of relatively warmer conditions throughout much of the Northern Hemisphere around the mid-9th to the mid-13th century CE (Mann, 2002; Matthews and Briffa., 2005; Neukom *et al.,* 2019), and the Little Ice Age (LIA), a cooler period lasting approximately between the 14th until the mid-19th century CE (Mann *et al.,* 1999). The average temperature difference between these two climatic events in the Northern Hemisphere is estimated to have been around 0.2℃ (Mann *et al.,* 2009).

The variation in proxies from the BO17 peat core during the MCA-LIA transition (Figure 5.6) exceeds that found in our experiment (Figure 5.5e-g). This suggests the variation in these proxies throughout the past c. 1500 years relates to edaphic changes in the peat, as opposed to being a climatic signal of decay. For LOI, a decline in organic matter content around c. 1250 CE occurs during the MCA-LIA boundary. This precedes a burning event at the coring location (Andrews *et al.,* 2021) and a change in vegetation community composition (Figure 5.6), These changes may reflect local changes in land use during the medieval and post-medieval periods, as evidenced by palynological and geochemical records from Cors Fochno, where increased agricultural and industrial disturbance during this time correspond to increased evidence for inorganic matter input, derived from soil erosion (Mighall *et al.,* 2017).

The lack of sensitivity of C/N ratios to decomposition or burial agrees with a study by Zaccone *et al.* (2018) where C/N ratios failed to correlate with other humification indices in a study testing the comparability of a suite of decomposition proxies. C/N ratios are known to differ widely between peatland plants (Hornibrook *et al.,* 2000). We see this in our paleoenvironmental reconstruction, where changes in C/N ratios occur along with changes in the vegetation composition of the peat. C/N ratios decline across the MCA-LIA boundary, corresponding to a shift in vegetation from *Sphagnum austinii*-dominated peat to peat characterised by low *Sphagnum* abundance and *Erica tetralix* seeds (Figure 5.6). Such a decline in C/N ratios is indicative of reduced decomposition, which is unlikely given the humified nature of the peat composition at this time.

Residual light transmission curves show reasonable levels of correspondence with the C/N ratios, despite no evidence that the latter proxy preserves a signal of decay (Figure 5.6). This suggests that changes in peat humification may reflect changes in the botanical composition of the peat, rather than preserving a climatic signal in our record (Zaccone *et al.,* 2014; 2018). Additionally, light transmission values fluctuate throughout the BO17 record, despite no clear changes in peat stratigraphy during many periods (Supplementary Table 3.3). The high noise-to-signal ratio in colorimetric peat humification data is frequently noted in peatland palaeoecological studies (e.g., Turner *et al.,* 2014). The noisiness and correspondence with C/N ratios and stratigraphic changes suggests that these effects obscure any palaeoclimatic signal that may be present in the humification record of core BO17. Such findings are corroborated by Payne and Blackford (2008), who tested regional correspondence in humification records across multiple sites in southeast Alaska, finding no evidence for climate forcing of humification in these sites. As with C/N, the botanical composition of the peat has long been known to influence peat humification records (Overbeck, 1947) and may obscure any palaeoclimatic signal (Yeloff and Mauquoy, 2006). Other factors, such as wildfire and anthropogenic disturbance, may further influence the humification record (Zaccone *et al.,* 2014; Payne and Blackford, 2008).

It appears that the decomposition proxies examined in this study failed to preserve a climatic signal. Our incubation period was relatively short (three months) and imparted relatively small changes in environmental conditions. We cannot dismiss the possibility that these proxies may be sensitive to decomposition over longer time-periods or higher temperatures. The length of this study was in keeping with the standard methodology detailed by Keuskamp *et al.* (2013). Too long of an incubation period may result in the full decomposition of the labile fraction of the green tea*,* as was the case for Górecki *et al.* (2021) where an incubation period of 172 days resulted in negative values for *S.* Decomposition may have also been reduced as microbial communities are usually adapted to decompose local plant litter that is characteristic of the site, while tea is an exotic material (Preston *et al*., 2012). Soil temperature increases exerted by the warming treatments were above the estimated range for temperature variation during the MCA – LIA transition, and this is likely to have influenced differences in decomposition for the buried tea bags. Furthermore, the long-term effects of the warming and drought treatments upon vegetation community composition and soil microbiota may have had a cumulative effect upon soil decomposition mechanisms. Warming increased the abundance of ericaceous shrubs in the warmed plots which can influence microbial communities, food webs and organic matter decomposition (Jassey *et al.,* 2013). Likewise, water table drawdown in peatlands can have lasting effects upon decomposition after former water levels are restored, due to drought-induced changes in soil water chemistry (Fenner and Freeman, 2011).

While it is possible that some of the changes seen in this study may result from contamination of humic substances in the peat affecting the final tea-bag weight, this effect is unlikely to have had a significant effect upon the results, as dissolved organic carbon concentrations in the pore-water were low within the experimental plots (Supplementary Table 2.4). Our findings agree with many studies that have questioned the reliability of peat decay as a proxy for palaeoclimatic reconstruction (Yeloff and Mauquoy, 2006; Payne and Blackford, 2008; Zaccone *et al.,* 2018). This study represents, to our knowledge, the only instance where the sensitivity of these commonly used palaeoecological proxies have been tested in an *in-situ* experimental setting and compared with experimental records from the same site.

While LOI is more commonly used as a proxy for %C content or as a direct measure of organic/inorganic matter content than as a proxy for palaeoclimatic change (Hoogstein *et al.,* 2015), colorimetric peat humification and C/N ratios are still commonly applied in peatland palaeoecological studies (e.g., Zhang *et al.,* 2021; Tsyganov *et al.,* 2021; Babeshko *et al.,* 2021). Colorimetric humification analysis does appear to record some measure of a signal for decomposition, but this effect is small and is obscured by noise and changes in the botanical composition of the peat. We cannot rule out that these proxy methods are not sensitive to larger or more sustained changes in temperature or drought. However, these findings also agree with a large body of existing literature that states the unreliability of these methods to reconstruct past changes in climate.

We recommend that palaeoecological studies avoid using colorimetric peat humification or C/N ratios as records of past climatic change, and instead apply only methods that have been independently validated (e.g., H/C ratios or testate amoebae; Zaccone *et al.,* 2018). This will improve the reliability of peat-based palaeoecological studies, allowing for comparison between these records and climate models.

The results reported in this study are based upon reconstructions from a single core, and do not allow us account for the spatial heterogeneity that characterises peatlands. Although reconstructed trends from cores taken from the same site are usually well replicated (e.g., Barber *et al.,* 1999; Hendon *et al.,* 2001), it Is impossible to discern whether the changes in the proxy records reconstructed from core used in this study represent autogenic (internal) feedbacks operating within the site, or are the result of climate driven, allogenic feedbacks (Bacon *et al*., 2017). Analysis of multiple cores would have allowed for comparisons between different records and the identification of allogenic, climate driven changes.

5.5.2. Treatment effects upon tea bag index parameters

We find that the relative difference in organic matter stabilisation between surface and buried samples is affected by warming and drought. The stabilisation of below-ground labile organic material occurs as labile organic matter is converted into more stable, complex molecules by environmental and chemical transformations (Keuskamp *et al.,* 2013; Górecki *et al.,* 2021). Warming reduced the difference between carbon retention in below-ground material relative to surface litter, whereas drought had the opposite effect. There was no difference with combined warming and drought relative to controls, suggesting that the opposite interactive effects of warming and drought upon above and belowground carbon retention are compounded in these plots, negating both effects.

The processes that govern organic matter stabilisation processes are complex and poorly understood in peatlands (Song *et al.,* 2019). Known drivers of organic matter stabilisation in peat soils include oxygen availability, vegetation communities, microbial activity, and pore-water biogeochemistry (Marley *et al.,* 2019; Song *et al.,* 2019; Górecki *et al.,* 2021). For this study, changes in stabilisation due to warming may relate to the significant increase in soil temperatures, or the long-term effects of the experimental treatment upon soil biota. Over the course of 2019, air temperatures were significantly higher in the warmed plots, attaining temperature differences between 0.2 – 0.7°C (Andrews *et al.,* 2021) and over the course of the experiment, temperature increases have been between 0.1 – 0.9°C (Andrews *et al.,* submitted). This degree of warming may have had a persistent effect upon soil microbiota (Jassey *et al.,* 2013). Climate change stressors may alter these drivers, leading to changes in decomposition and ecosystem functioning. For example, Jassey *et al.* (2013) found that for a fen peatland in the Jura Mountains, France, warming destabilised peatland microbial communities by modifying their interactions with vegetation and soil chemistry, reducing predatory testate amoebae, and increasing bacterial abundance. They suggested that warming may destabilise carbon cycling due to changes in above- and below-ground linkages in the soil. The effect of drought upon organic matter stabilisation at different depths likely relates to changes in enzyme activity in the peat following water table drawdown and soil oxidation, increasing phenol oxidase activity (Fenner and Freeman, 2011). Normally, low oxygen levels in waterlogged peat supress phenol oxidase activity, which breaks down phenolic compounds (Freeman *et al.,* 2001). By exposing previously waterlogged peat to oxygen, phenol oxidase can degrade phenolic compounds, greatly increasing decomposition rates as hydrolase enzymes are no longer inhibited (Freeman *et al.,* 2001). The effect of drought is relatively poorly understood in peatlands, but has important implications for climate change, since increased aeration of peat may remove an important mechanism restricting the re-release of CO_2 into the atmosphere, imparting a positive feedback mechanism upon global climate (Fenner and Freeman, 2011). Our results suggest that the strength and direction of these changes may depend upon the complex, interacting processes underlying decomposition in peatlands, and that these effects vary throughout the peat column. Understanding the chemical and microbial drivers governing peatland soil stabilisation and decomposition and their responses to climate change will improve our understanding of future peatland carbon cycle responses to climate change (Bragazza *et al.,* 2008; Song *et al.,* 2019). These drivers can be expected to differ between peatlands (Fisk *et al*., 2003), due to differences in vegetation, litter quality and nutrient status between sites (Aerts *et al*., 1999; Bragazza *et al*., 2007), meaning that the results of this study are unlikely to apply to all peatlands in the Northern Hemisphere, meaning more work is required in this area.

In the context of the direct and indirect consequences of climate change, it is crucial to understand the response of organic matter decomposition to warming and drought and how this varies between material of different depths. Below-ground litter derived from roots and rhizomes is also an important component of the peatland carbon cycle (Laiho *et al.,* 2004), however, most studies have been concerned with decay at the peat surface (Bragazza *et al.,* 2008; Laiho *et al.,* 2004). Since vascular plant cover is likely to increase in peatlands due to climate change, the role of below-ground litter and its response to climate change is an important consideration for future peatland carbon cycling (Weltzin *et al.,* 2003; Buttler *et al.,* 2015; Malhotra *et al.,* 2020). There are relatively few studies that assess above- and below-ground linkages in peatland soils and how these may be affected by climate change (Jassey *et al.,* 2013).

This study indicates that warming, drought, and burial did not influence the rate of organic matter decay in the tea bag experiment. This contradicts multiple studies where peatland organic matter decay is positively correlated with increased temperature under non-limiting water table conditions (e.g., Domisch *et al.,* 2006; Glatzel *et al.,* 2006) and is restricted under drought conditions (e.g., Laiho *et al.,* 2004; Aerts 2006; Gerdol *et al.,* 2008). The temperature sensitivity of decomposition rates derived using the TBI method was previously demonstrated by Keuskamp *et al.* (2013). The lack of a significant effect due to warming and the small range of *k* may relate to the insignificant differences in air temperatures imparted by our warming plots, as well as the decay inhibiting properties of peat. Low temperature increases by OTCs are typical of such studies in temperate regions (Johnson *et al.,* 2013), and small temperature increases frequently have little impact upon litter-bag decay rates (Bragazza *et al.,* 2008). For example, Górecki *et al.* (2021) found no significant effects with warming in an experimental climate manipulation study on a poor fen in Poland using the TBI method. Global temperatures are likely to increase by c. 1.5℃ under current mid-range climate change projections between 2030 to 2050 (IPCC, 2021). Therefore, we cannot rule out the possibility that future changes in temperature will eventually increase decomposition rates in peatlands.

Several soil decompositions studies have indicated that climate-induced changes in litter decomposition rates will be negligible without a corresponding shift in plant communities resulting in a change in litter quality (Hobbie, 1996; Cornwell *et al.,* 2008). For example, Bell *et al.* (2018) reported differential responses of various litterbag substrates to warming and water table drawdown due to differential decomposability rates between the various litter types. This study found no influence of vegetation groups upon any of the tea bag index decay parameters or proxies. Multiple studies have suggested that vegetation affects organic matter decomposition by influencing biogeochemical and microbial conditions within the peat (Song *et al.,* 2019). For example, in an experimental climate manipulation study combining warming with plant functional type removals, Ward *et al.* (2015) found that vegetation community composition regulated short-term litter decomposition and below-ground microbial communities. The use of a consistent substrate in our study means we are unable to measure how decay rates will be altered by changing plant litter quality resulting from vegetation shifts, a common criticism of litterbag studies (Bragazza *et al.,* 2008). Instead, this approach allows the strength of vegetation-mediated controls upon organic matter decay to be tested. Our results indicate that these factors were unaffected by the differences in vegetation between our experimental plots. This is an important finding since climate change is likely to alter vegetation community composition in peatlands, driving an increase in vascular plant composition, particularly in ericaceous shrubs (e.g., Weltzin *et al.,* 2003; Buttler *et al.,* 2015; Malhotra *et al.,* 2020) and potentially a decrease in *Sphagnum* (Norby *et al.,* 2019).

Based upon the results of our tea bag decomposition study, we recommend that more research is carried out to test the effects of experimental climate manipulation upon organic litter decomposition at different depths relative to the water table, and over a long time period (one year or more). We recommend that these experiments are combined with studies evaluating the effects of experimental warming and drought upon the peat chemistry and microbiota, to better understand the drivers of these responses. Such an understanding will improve our understanding of peatland above- and below-ground linkages and how these will change in response to the direct and indirect effects of climate change, potentially leading to improved modelling of peatland carbon cycle responses to climate change.

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Conflict of interest

The authors declare no conflict of interest.

5.7. References

Aaby, B., (1976). Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. Nature, 263(5575), 281-284

Aaby, B. and Tauber, H., (1975). Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Deninark. *Boreas*, *4*(1), 1-17.

Aerts, R., (2006). The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, 94(4), 713-724.

Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology,* 80(7), 2170-2181.

Allen, M. R., Fuglestvedt, J. S., Shine, K. P., Reisinger, A., Pierrehumbert, R. T., & Forster, P. M. (2016). New use of global warming potentials to compare cumulative and short-lived climate pollutants. *Nature Climate Change*, 6(8), 773-776.

Andrews, L. (2021): LA Plant community responses to experimental.xlsx. figshare. Dataset. https://doi.org/10.6084/m9.figshare.15395199.v1

Andrews, L. O., Rowson, J. G., Caporn, S. J. M., Dise, N. B., Beckwith, M., Blake, W., Garrett, E., Gehrels, W. R., Gehrels, M., Payne, R. J. (submitted). Carbon cycle responses to experimental drought and warming in a Welsh ombrotrophic peatland in the context of late Holocene carbon accumulation.

Andrews, L.O., Rowson, J.G., Caporn, S.J., Dise, N.B., Barton, E., Garrett, E., Roland. Gehrels, W., Gehrels, M., Kay, M. and Payne, R.J., (2021). Plant community responses to experimental climate manipulation in a Welsh ombrotrophic peatland and their palaeoenvironmental context. *Global Change Biology*.

Aquino-López, M.A., Blaauw, M., Christen, J.A., and Sanderson, N.K., (2018). Bayesian Analysis of ^{210}Pb Dating. *Journal of Agricultural, Biological and Environmental Statistics*, *23*(3), 317-333.

Aquino-López, M.A., Ruiz-Fernández, A.C., Blaauw, M. and Sanchez-Cabeza, J.A., 2020. Comparing classical and Bayesian 210Pb dating models in human-impacted aquatic environments. *Quaternary Geochronology*, *60*, p.101106.

Babeshko, K.V., Shkurko, A., Tsyganov, A.N., Severova, E.E., Gałka, M., Payne, R.J., Mauquoy, D., Mazei, N.G., Fatynina, Y.A., Krasnova, E.D. and Saldaev, D.A., (2021). A multi-proxy reconstruction of peatland development and regional vegetation changes in subarctic NE Fennoscandia (the Republic of Karelia, Russia) during the Holocene. *The Holocene*, *31*(3), 421-432.

Bacon, K.L., Baird, A.J., Blundell, A., Bourgault, M.A., Chapman, P.J., Dargie, G., Dooling, G.P., Gee, C., Holden, J., Kelly, T.J., and McKendrick-Smith, K.A., (2017). Questioning ten common assumptions about peatlands. *Mires and Peat,* 19, 1-23.

Barber, K.E., (1981). Peat stratigraphy and climatic change. *Balkema, Rotterdam*, *220*.

Barber, K.E., Battarbee, R.W., Brooks, S.J., Eglinton, G., Haworth, E.Y., Oldfield, F., Stevenson, A.C., Thompson, R., Appleby, P.G., Austin, W.E.N. and Cameron, N.G., 1999. Proxy records of climate change in the UK over the last two millennia: documented change and sedimentary records from lakes and bogs. *Journal of the Geological Society*, 156(2), 369-380.

Barber, K.E., Chambers, F.M. and Maddy, D., (2003). Holocene palaeoclimates from peat stratigraphy: macrofossil proxy climate records from three oceanic raised bogs in England and Ireland. *Quaternary Science Reviews*, *22*(5-7), 521-539.

Bartsch, I., & Moore, T. R. (1985). A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. *Canadian Journal of Botany*, 63(7), 1241-1248.

Bates, D., Mächler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1–48.

Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J., Freeman, C., and Clark, J.M., (2018). Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma*, *331*, 29-37.

Belyea, L.R., (1996). Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, 529-539.

Blackford, J.J. and Chambers, F.M., (1991). Proxy records of climate from blanket mires: evidence for a Dark Age (1400 BP) climatic deterioration in the British Isles. *The Holocene*, *1*(1), 63-67.

Blackford, J.J. and Chambers, F.M., (1993). Determining the degree of peat decomposition for peat-based paleoclimatic studies. *International Peat Journal;(Finland)*, *8*(5).

Blackford, J.J. and Chambers, F.M., (1995). Proxy climate record for the last 1000 years from Irish blanket peat and a possible link to solar variability. *Earth and Planetary Science Letters*, *133*(1-2), 145-150.

Blume-Werry, G., Di Maurizio, V., Beil, I., Lett, S., Schwieger, S. and Kreyling, J., (2021). Don’t drink it, bury it: comparing decomposition rates with the tea bag index is possible without prior leaching. *Plant and Soil*, 1-9.

Blundell, A. and Barber, K., (2005). A 2800-year palaeoclimatic record from Tore Hill Moss, Strathspey, Scotland: the need for a multi-proxy approach to peat-based climate reconstructions. *Quaternary Science Reviews*, *24*(10-11), 1261-1277.

Bonnett, S. A., Ostle, N., & Freeman, C. (2006). Seasonal variations in decomposition processes in a valley-bottom riparian peatland. *Science of the Total Environment*, 370(2-3), 561-573.

Borgmark, A. and Schoning, K., (2006). A comparative study of peat proxies from two eastern central Swedish bogs and their relation to meteorological data. *Journal of Quaternary Science*, *21*(2), 109-114.

Bouyoucos, G.J., (1934). A method for determining the degree of decomposition that unknown decayed vegetable organic materials have already undergone in nature. *Soil Science*, *38*(6), 477-482.

Bradley, R.S. and Jonest, P.D., (1993). 'Little Ice Age'summer temperature variations: their nature and relevance to recent global warming trends. *The Holocene*, *3*(4), 367-376.

Bragazza, L., Buttler, A., Robroek, B.J., Albrecht, R., Zaccone, C., Jassey, V.E. and Signarbieux, C., (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, *22*(12), 4114-4123.

Bragazza, L., Siffi, C., Iacumin, P., & Gerdol, R. (2007). Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. *Soil Biology and Biochemistry,* 39(1), 257-267.

Bragazza, L., Buttler, A., Siegenthaler, A., and Mitchell, E.A., (2008). Plant litter decomposition and nutrient release in peatlands. In *Carbon Cycling in Northern*

Peatlands (*Geophysical Monograph Series)* (Vol. 184, 99-110). American Geophysical Union (AGU).

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A. and Bragazza, L., (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science*, *26*(5), 964-974.

Chambers, F.M., Beilman, D.W. and Yu, Z., (2011). Methods for determining peat humification and for quantifying peat bulk density, organic matter, and carbon content for palaeostudies of climate and peatland carbon dynamics. *Mires and Peat*, *7*(7), 1-10.

Chambers, F.M. and Charman, D.J., (2004). Holocene environmental change: contributions from the peatland archive. *The Holocene*, *14*(1), 1-6.

Charman, D.J., (2001). Biostratigraphic and palaeoenvironmental applications of testate amoebae. *Quaternary Science Reviews*, *20*(16-17), 1753-1764.

Charman, D.J., Barber, K.E., Blaauw, M., Langdon, P.G., Mauquoy, D., Daley, T.J., Hughes, P.D. and Karofeld, E., (2009). Climate drivers for peatland palaeoclimate records. *Quaternary Science Reviews*, *28*(19-20), 1811-1819.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D. and Jackson, S.T., (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, *10*(2), 929-944.

Clymo, R.S., (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *303*(1117), 605-654

Clymo, R.S., Turunen, J. and Tolonen, K., (1998). Carbon accumulation in peatland. *Oikos*, 368-388.

Cornwell, W.K., Cornelissen, J.H., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E..Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N. and Quested, H.M., (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*(10), 1065-1071.

de Jong, R., Blaauw, M., Chambers, F.M., Christensen, T.R., De Vleeschouwer, F., Finsinger, W., Fronzek, S., Johansson, M., Kokfelt, U., Lamentowicz, M. and Le Roux, G., (2010). Climate and peatlands. In *Changing Climates, Earth Systems and Society* (85-121). Springer, Dordrecht.

Dean, W.E., (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research*, *44*(1), 242-248.

Didion, M., Repo, A., Liski, J., Forsius, M., Bierbaumer, M., & Djukic, I. (2016). Towards harmonizing leaf litter decomposition studies using standard tea bags—a field study and model application. *Forests*, 7(8), 167.

Domisch, T., Finér, L., Laine, J. and Laiho, R., (2006). Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. *European Journal of Soil Biology*, *42*(2), 74-81.

Duddigan, S., Shaw, L. J., Alexander, P. D., & Collins, C. D. (2020). Chemical underpinning of the tea bag index: an examination of the decomposition of tea leaves. *Applied and Environmental Soil Science*, 2020.

Fenner, N. and Freeman, C., (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, *4*(12), 895-900.

Fisk, M. C., Ruether, K. F., & Yavitt, J. B. (2003). Microbial activity and functional composition among northern peatland ecosystems. *Soil Biology and Biochemistry,* 35(4), 591-602.

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B. and Fenner, N., (2001). Export of organic carbon from peat soils. *Nature*, *412*(6849), 785-785.

Freeman, C., Liska, G., Ostle, N.J., Lock, M.A., Reynolds, B. and Hudson, J., (1996). Microbial activity and enzymic decomposition processes following peatland water table drawdown. *Plant and Soil*, 180(1), 121-127.

Freeman, C., Ostle, N.J., Fenner, N. and Kang, H., (2004). A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biology and Biochemistry*, *36*(10), 1663-1667.

Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S. and Blyakharchuk, T., (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature climate change*, *8*(10), 907-913.

Gerdol, R., Bragazza, L. and Brancaleoni, L., (2008). Heatwave 2003: high summer temperature, rather than experimental fertilization, affects vegetation and CO2 exchange in an alpine bog. *New Phytologist*, *179*(1), 142-154.

Glatzel, S., Lemke, S. and Gerold, G., (2006). Short-term effects of an exceptionally hot and dry summer on decomposition of surface peat in a restored temperate bog. *European Journal of Soil Biology*, *42*(4), 219-229.

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łuców, D., Kayzer, D. and Juszczak, R., (2021). Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate Sphagnum-peatland. *Science of The Total Environment*, *771*, p.145452.

Gorham, E., (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological applications*, *1*(2), 182-195.

Heimann, M. and Reichstein, M., (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, *451*(7176), 289-292.

Heiri, O., Lotter, A.F. and Lemcke, G., (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of paleolimnology*, *25*(1), 101-110.

Hendon, D., and Charman, D.J., (1997). The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene*, *7*(2), 199-205.

Hendon, D., Charman, D. J., & Kent, M. (2001). Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications. *The Holocene*, 11(2), 127-148.

Hobbie, S.E., (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological monographs*, *66*(4), 503-522.

Holden, J., (2005). Peatland hydrology and carbon release: why small-scale process matters. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *363*(1837), 2891-2913.

Hoogsteen, M.J., Lantinga, E.A., Bakker, E.J., Groot, J.C. and Tittonell, P.A., (2015). Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss. *European Journal of Soil Science*, *66*(2), 320-328.

Hornibrook, E.R., Longstaffe, F.J., Fyfe, W.S. and Bloom, Y., (2000). Carbon-isotope ratios and carbon, nitrogen and sulfur abundances in flora and soil organic matter from a temperate-zone bog and marsh. *Geochemical Journal*, *34*(3), 237-245.

Imbrie, J. and Kipp, N.G., (1971). A new micropaleontological method for quantitative paleoclimatology: application to a Late Pleistocene Caribbean core. Turekian, K.K., in: *The Late Cenozoic Glacial Ages* Yale University Press New Haven, 71–181

IPCC, (2021): *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University. In Press.

Jassey, V.E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E.A., Toussaint, M.L., Francez, A.J. and Gilbert, D., (2013). Above-and belowground linkages in Sphagnum peatland: Climate warming affects plant-microbial interactions. *Global Change Biology*, *19*(3), 811-823.

Johnson, C.P., Pypker, T.G., Hribljan, J.A. and Chimner, R.A., (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO 2/CH 4 dynamics in a northern Michigan peatland. *Ecosystems*, *16*(5), 736-748.

Jovani-Sancho, A. J., Cummins, T., & Byrne, K. A. (2021). Soil carbon balance of afforested peatlands in the maritime temperate climatic zone*. Global Change Biology,* 27(15), 3681-3698.

Jowsey, P.C., (1966). An improved peat sampler. *New phytologist*, *65*(2), 245-248.

Keuskamp, J.A., Dingemans, B.J., Lehtinen, T., Sarneel, J.M. and Hefting, M.M., (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution*, *4*(11), 1070-1075.

Kuhry, P. and Vitt, D.H., (1996). Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology*, *77*(1), 271-275.

Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H., (2017). lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, *82*(1), 1-26.

Lecerf, A. (2017). Methods for estimating the effect of litterbag mesh size on decomposition. *Ecological Modelling*, 362, 65-68.

Laiho, R., (2006). Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry*, *38*(8), 2011-2024.

Laiho, R., Laine, J., Trettin, C.C. and Finér, L., (2004). Scots pine litter decomposition along drainage succession and soil nutrient gradients in peatland forests, and the effects of inter-annual weather variation. *Soil Biology and Biochemistry*, *36*(7), 1095-1109.

Lamb, H.H., (1965). The early medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *1*, 13-37.

Lee, J. Y., J. Marotzke, G. Bala, L. Cao, S. Corti, J. P. Dunne, F. Engelbrecht, E. Fischer, J. C. Fyfe, C. Jones, A. Maycock, J. Mutemi, O. Ndiaye, S. Panickal, T. Zhou, (2021). Future Global Climate: Scenario Based Projections and Near-Term Information. In: *Climate Change 2021: The Physical Science Basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan,

S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Leifeld, J., Klein, K. and Wüst-Galley, C., (2020). Soil organic matter stoichiometry as indicator for peatland degradation. *Scientific reports*, *10*(1), 1-9.

Leifeld, J., Müller, M. and Fuhrer, J., (2011). Peatland subsidence and carbon loss from drained temperate fens. *Soil Use and Management*, *27*(2), 170-176.

Loisel, J., Yu, Z., Beilman, D.W., Camill, P., Alm, J., Amesbury, M.J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K. and Belyea, L.R., (2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *the Holocene*, *24*(9), 1028-1042.

Lowe, J.A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G. and Fung, F., (2018). UKCP18 science overview report. *Met Office Hadley Centre: Exeter, UK*.

Luo, Y., & Zhou, X. (2010). *Soil respiration and the environment.* Elsevier.

MacDonald, E., Brummell, M.E., Bieniada, A., Elliott, J., Engering, A., Gauthier, T.L., Saraswati, S., Touchette, S., Turmel-Courchesne, L. and Strack, M., (2018). Using the Tea Bag Index to characterize decomposition rates in restored peatlands. *Boreal Environment Research*, 23, 221-235.Maechler M, Rousseeuw P, Struyf A, Hubert M and Hornik K, (2021). *cluster: Cluster Analysis Basics and Extensions*. R package version 2.1.2 https://CRAN.R-project.org/package=cluster.

Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Vander Stel, H., Feron, S.C., Hanson, P.J. and Iversen, C.M., (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences*, *117*(30), 17627-17634.

Malmer, N. and Holm, E., (1984). Variation in the C/N-quotient of peat in relation to decomposition rate and age determination with 210 Pb. *Oikos*, 171-182.

Mann, M.E., (2002). Medieval climatic optimum. *Encyclopedia of global environmental change*, *1*, 514-516. Munn, R. E. (Ed.), Chichester: Wiley.

Mann, M.E., Bradley, R.S. and Hughes, M.K., (1999). Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters*, *26*(6), 759-762.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. and Ni, F., (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, *326*(5957), 1256-1260.

Marley, A.R., Smeaton, C., and Austin, W.E., (2019). An assessment of the tea bag index method as a proxy for organic matter decomposition in intertidal environments. *Journal of Geophysical Research: Biogeosciences*, *124*(10), 2991-3004.

Matthews, J.A., and Briffa, K.R., (2005). The ‘Little Ice Age’: re-evaluation of an evolving concept. *Geografiska Annaler: Series A, Physical Geography*, *87*(1), 17-36.

Mauquoy, D., Engelkes, T., Groot, M.H.M., Markesteijn, F., Oudejans, M.G., van Der Plicht, J., and van Geel, B., (2002). High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *186*(3-4), 275-310.

Mighall, T., Timberlake, S., Martínez-Cortizas, A., Silva-Sánchez, N., and Foster, I.D.L., (2017). Did prehistoric and Roman mining and metallurgy have a significant impact on vegetation? *Journal of Archaeological Science: Reports*, *11*, 613-625.

Mitchell, E.A., Charman, D.J. and Warner, B.G., (2008). Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present, and future. *Biodiversity and Conservation*, *17*(9), 2115-2137.

Moore, T. and Basiliko, N., (2006). Decomposition in boreal peatlands. In *Boreal peatland ecosystems* (125-143). Springer, Berlin, Heidelberg.

Munsell Color (2010). *Munsell Soil Color Charts: with Genuine Munsell Color Chips*. Grand Rapids,

Neukom, R., Steiger, N., Gómez-Navarro, J.J., Wang, J. and Werner, J.P., (2019). No evidence for globally coherent warm and cold periods over the preindustrial Common Era. *Nature*, *571*(7766), 550-554.

Norby *et al.,* 2019 Norby, R.J., Childs, J., Hanson, P.J. and Warren, J.M., (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, *9*(22), 12571-12585.

Nykvist, N., (1959). Leaching and decomposition of litter I. Experiments on leaf litter of Fraxinus excelsior. *Oikos*, *10*(2), 190-211.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P R., O'Hara, R. B., Simpson, G., Solymos, P., Stevens, M. H. M., Szoecs, E. and Wagner, H. (2019). vegan: Community Ecology Package. R package version 2.5-6 https://CRAN.Rproject.org/package=vegan

Overbeck, F., (1947). Studien zur Hochmoorentwicklung in Niedersachsen und die Bestimmung der Humifizierung bei stratigraphisch-pollenanalytischen Mooruntersuchungen. *Planta*, *35*(1./2. H), 1-56.

Payne, R., (2007). Laboratory experiments on testate amoebae preservation in peats: implications for palaeoecology and future studies. *Acta Protozoologica*, *46*(4), 325-332.

Payne, R.J., and Blackford, J.J., (2008). Peat humification and climate change: a multi-site comparison from mires in south-east Alaska. *Mires and peat*, 1-11.

Payne, R.J., Lamentowicz, M. and Mitchell, E.A., (2011). The perils of taxonomic inconsistency in quantitative palaeoecology: experiments with testate amoeba data. *Boreas*, *40*(1), 15-27.

Poucher P. (2009). *Wetland Margins Survey: Cors Fochno.* Dyfed Archaeological Trust

Prescott, C.E., (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry*, *101*(1), 133-149.

Preston, M. D., Smemo, K. A., McLaughlin, J. W., & Basiliko, N. (2012). Peatland microbial communities and decomposition processes in the James Bay Lowlands, Canada. *Frontiers in microbiology,* 3, 70.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ritson, J.P., Bell, M., Brazier, R.E., Grand-Clement, E., Graham, N.J., Freeman, C., Smith, D., Templeton, M.R. and Clark, J.M., (2016). Managing peatland vegetation for drinking water treatment. *Scientific reports*, 6(1), 1-9.

Roos-Barraclough, F., van der Knaap, W.O., van Leeuwen, J.F.N. and Shotyk, W., (2004). A Late-glacial and Holocene record of climatic change from a Swiss peat humification profile. *The Holocene*, *14*(1), 7-19.

Seelen, L.M., Flaim, G., Keuskamp, J., Teurlincx, S., Font, R.A., Tolunay, D., Fránková, M., Šumberová, K., Temponeras, M., Lenhardt, M. and Jennings, E., 2019. An affordable and reliable assessment of aquatic decomposition: Tailoring the Tea Bag Index to surface waters. *Water Research*, 151, 31-43.

Sillasoo, U., Mauquoy, D., Blundell, A., Charman, D., Blaauw, M., Daniell, J.R., Toms, P., Newberry, J., Chambers, F.M. and Karofeld, E., (2007). Peat multi-proxy data from Männikjärve bog as indicators of late Holocene climate changes in Estonia. *Boreas*, *36*(1), 20-37.

Simpson, G.L., Team, R.C., Bates, D.M., Oksanen, J. and Simpson, M.G.L., (2019). Package 'permute'. CRAN-r project.

Song, Y., Song, C., Ren, J., Ma, X., Tan, W., Wang, X., Gao, J. and Hou, A., (2019). Short-term response of the soil microbial abundances and enzyme activities to experimental warming in a boreal peatland in Northeast China. *Sustainability*, *11*(3), p.590.

Swindles, G.T., Holden, J., Raby, C.L., Turner, T.E., Blundell, A., Charman, D.J., Menberu, M.W. and Kløve, B., (2015). Testing peatland water table depth transfer functions using high-resolution hydrological monitoring data. *Quaternary Science Reviews*, *120*, 107-117.

Swindles, G.T., Morris, P.J., Baird, A.J., Blaauw, M. and Plunkett, G., (2012). Ecohydrological feedbacks confound peat-based climate reconstructions. *Geophysical Research Letters*, *39*(11).

Swindles, G.T., Roland, T.P., Amesbury, M.J., Lamentowicz, M., McKeown, M.M., Sim, T.G., Fewster, R.E. and Mitchell, E.A., (2020). Quantifying the effect of testate amoeba decomposition on peat-based water table reconstructions. *European Journal of Protistology*, *74*, p.125693.

Teatime4Science (2021) Availability of Tea, [online], available at: <http://www.teatime4science.org/method/availability-of-tea/> [accessed 05/12/2021].

Tfaily, M.M., Cooper, W.T., Kostka, J.E., Chanton, P.R., Schadt, C.W., Hanson, P.J., Iversen, C.M. and Chanton, J.P., (2014). Organic matter transformation in the peat column at Marcell Experimental Forest: humification and vertical stratification. *Journal of Geophysical Research: Biogeosciences*, *119*(4), 661-675.

Tsyganov, A.N., Zarov, E.A., Mazei, Y.A., Kulkov, M.G., Babeshko, K.V., Yushkovets, S.Y., Payne, R.J., Ratcliffe, J.L., Fatyunina, Y.A., Zazovskaya, E.P. and Lapshina, E.D., (2021). Key periods of peatland development and environmental changes in the middle taiga zone of Western Siberia during the Holocene. *Ambio*, 1-14.

Turner, T.E., Swindles, G.T. and Roucoux, K.H., (2014). Late Holocene ecohydrological and carbon dynamics of a UK raised bog: impact of human activity and climate change. *Quaternary Science Reviews*, *84*, 65-85.

Turner, T.E., Swindles, G.T. and Roucoux, K.H., (2014). Late Holocene ecohydrological and carbon dynamics of a UK raised bog: impact of human activity and climate change. *Quaternary Science Reviews*, *84*, 65-85.

Waddington, J. M., & Roulet, N. T. (1997). Groundwater flow and dissolved carbon movement in a boreal peatland. *Journal of Hydrology*, 191(1-4), 122-138.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K. and Moore, P.A., (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, *8*(1), 113-127.

Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H. and Bardgett, R.D., (2015). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, *96*(1), 113-123.

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J. and Harth, C., (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, *9*(2), 141-151.

Woodland, W.A., Charman, D.J. and Sims, P.C., (1998). Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae. *The Holocene*, *8*(3), 261-273.

Xu, J., Morris, P.J., Liu, J. and Holden, J., (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena*, *160*, 134-140.

Yeloff, D. and Mauquoy, D., (2006). The influence of vegetation composition on peat humification: implications for palaeoclimatic studies. *Boreas*, *35*(4), 662-673.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W. and Hunt, S.J., (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters*, *37*(13).

Yu, Z.C., (2012). Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, *9*(10), 4071-4085.

Zaccone, C., Plaza, C., Ciavatta, C., Miano, T.M. and Shotyk, W., (2018). Advances in the determination of humification degree in peat since Achard (1786): applications in geochemical and paleoenvironmental studies. *Earth-Science Reviews*, *185*, 163-178.

Zaccone, C., Rein, G., D'Orazio, V., Hadden, R.M., Belcher, C.M. and Miano, T.M., (2014). Smouldering fire signatures in peat and their implications for palaeoenvironmental reconstructions. *Geochimica et Cosmochimica Acta*, *137*, 134-146.

Zhang, D., Chen, L., Feng, Z., Ran, M., Yang, Y., Zhang, Y. and Liu, Q., (2021). Four peat humification-recorded Holocene hydroclimate changes in the southern Altai Mountains of China. *The Holocene*, p.09596836211011674.

Chapter 6: Discussion

6.1. Core findings of this study and their implications

This thesis compared two contrasting approaches to test the hypothesis that peatlands will impart a net positive climate feedback under future climate change conditions. This section will detail how this research allows us to accept or reject this hypothesis, and the consequences of these findings for future global atmospheric greenhouse gas concentrations and climate feedbacks under climate change.

6.1.1. Effects of experimental warming upon carbon cycling

Peatland carbon cycling responses are of great concern for predicting future atmospheric greenhouse gas concentrations, due to the large amounts of carbon stored within these ecosystems and their potential to exert both strong positive *and* strong negative climate feedbacks in response to changes in environmental and climatic conditions (Limpens *et al.,* 2008). In this study, ten years of passive experimental warming increased air temperatures by between 0.1 – 0.9°C relative to controls, causing the warmed plots to accumulate c. 40 g C m^{-2} y^{-1} less carbon than the control plots. This effect was exacerbated by combining warming with drought, which resulted in these plots accumulating c. 67 g C m^{-2} y^{-1} less carbon, causing these plots to become net sources of atmospheric carbon. The changes were driven by differences in annual net ecosystem respiration, which increased by an estimated 56 % in warmed plots and 106 % in the combined warmed and drought plots.

The mechanisms driving these changes are difficult to unpick from this study. In the experimental plots, net ecosystem respiration (NER) was mostly governed by air temperature whereas gross primary productivity was driven by changes in air temperature and photosynthetically active radiation. Increased shrub cover, evident in the warmed plots, may also increase greenhouse gas emissions (Weltzin *et al.,* 2000; Dieleman *et al.,* 2015; Ward *et al.,* 2013; 2015; Norby *et al.,* 2019; Bell *et al.,* 2018). These effects may be intensified in the combined treatment plots due to the experimental water table drawdown promoting the activity of phenol oxidase, an enzyme that degrades phenolic compounds that ordinarily inhibit decay in peatlands (Freeman *et al.,* 2004; Fenner and Freeman, 2011). However, no significant differences in greenhouse gas emissions were identified between the drought only treatments and the control plots, suggesting that the mechanism driving this effect were more pronounced with additional warming.

The experimental site used in this study was designed to simulate changes in climate relevant to the region by c. 2070 (Lowe *et al.,* 2018). However, future UK temperature projections exceed the warming (0.1 – 0.9 °C) simulated by the open top chambers in this study. For example, the UKCP18 projections present a range of probabilistic projections for warming based upon different emission scenarios. For all emission scenarios, warming levels of 1.5 °C are predicted to occur before 2070, with RCP8.5 predicting that mean UK temperatures will increase by 4 °C by 2065 (Lowe *et al*., 2018). The climate warming effects simulated by this study are therefore optimistic when compared with current projected changes, and the effects upon carbon cycling and greenhouse gas production may be greater or differ from those reported by this study.

Climate change is projected to be even more pronounced in the higher latitudes, increasing by 0.6 °C per decade in this region (Schuur *et al.,* 2015; Hoegh-Guldberg *et al*., 2018; Lee *et al*., 2021). Changes in future climate more pronounced than the modest temperature increases exerted by this experiment may cause increased emissions and further enhance the future warming effect of peatlands.

The results of this study suggest that moderate warming increased CO_2 emissions from the experimental plots, causing the site to contribute to climate warming. It is accepted that warming will increase decomposition rates in many peatlands (Bu *et al.,* 2011; Loisel *et al*., 2021). However, other studies have reported productivity rates increasing with warming, in some cases offsetting increases in decomposition, driving an increase in carbon accumulation rates (e.g., Bridgham *et al*., 2008; Chivers *et al*., 2009; Johnson *et al*., 2013; Hanson *et al.,* 2020), due to warming and longer growing seasons (Lund *et al*., 2010). Peatlands across the Northern Hemisphere are likely to differ in terms of their response to climate change, depending upon regional and local differences in the rate and magnitude of climate warming and changes in their soil-water balance. Qiu *et al*. (2020) simulated how carbon cycling in peatland ecosystems may respond to different climate change scenarios until the end of the 21st century, finding that mean carbon accumulation rates doubled under RCP2.6 and RCP6.0 scenarios, whereas under the RCP8.5 scenario, peatlands became either neutral or net CO_2 emitters.

6.1.2. Effect of warming on methane production

Warming reduced estimated annual CH_4 emissions in the experimental plots by c. 1.7 g CH_4 m^{-2} y^{-1}. This result was unexpected, contradicting the findings of most other studies that typically report increasing CH_4 emissions with warming (e.g., Turetsky *et al.,* 2008; Frolking *et al.,* 2011; Munir and Strack, 2014) and is difficult to explain based upon a kinetic response of soil microbial activity (Moore and Roulet, 1993; Bubier *et al.,* 1995). Field measurements such as those used in this study to correlate changes in CH_4 emissions with environmental variables such as temperature and water table depth do not allow the underlying mechanisms underlying these correlations to be discerned (Arah and Stephen, 1998). This response may be driven by changes in soil microbiota, geochemistry and/or vegetation within the treatment plots. The changes seen in this study may be due to the effects of sustained warming over ten years upon microbial communities, with warming potentially favouring bacterial communities over methanogens (Kim *et al.,* 2012), resulting in changes in CO_2 and CH_4 emissions. Alternatively, this response could be an artefact of the experimental warming, as the open-top chambers used to warm the plots may increase evapotranspiration rates, drying the soil and increasing oxidation (Dabros and Fyles, 2010; Huguet *et al.,* 2013). This may limit the area in which anaerobic decay leading to CH_4 production can occur (Moore and Knowles, 1989; Granberg *et al.,* 1997). Eriksson *et al.* (2010a; 2010b) also report a similar reduction in CH_4 with warming, coincident with increased CO_2 emissions. They suggest that this response reflects enhanced decomposition of labile carbon at the peat surface due to warming, reducing the remaining substrate available for CH_4 production.

These findings suggest that some sites may release less CH_4 into the atmosphere with warming under non-limiting hydrological conditions. However, even if this result is not an artefact of the experimental warming, it is still highly unusual and is unlikely to be reflective of the future response of most northern peatlands under warmer climatic conditions. In general, CH_4 emissions from northern peatlands are expected to increase with warming (e.g., Ballentyne *et al.,* 2014; Deng *et al*., 2015; Hanson *et al*., 2020) however, other studies have found no effect of warming upon CH_4 emissions (Li *et al*., 2021). CH_4 emissions from peatlands vary due to differences in water-balance, climate, and vegetation both between and within sites, and are also affected by anthropogenic disturbances that can show great regional and local variation (Bubier *et* al., 1995; Nilsson *et al.,* 2001; Lai, 2009). Projected changes in climatic and anthropogenic influence affecting water-table depths in northern peatlands are projected to reduce CH_4 emissions by the end of this century (Huang *et al*., 2021). However, Huang *et al*. (2021) do not consider the effects of permafrost thaw upon CH_4 dynamics in their calculations (Schuur *et al.,* 2015; Huang *et al*., 2021). The production of thermokarst lakes and small thaw ponds following permafrost thaw may continue to contribute increasing CH_4 emissions with future warming in the higher latitudes (Wickland *et al*., 2006; Negandhi *et al*., 2013; Mateev *et al*., 2016).

The effects of changes in water table depth on CH_4 emissions tend to override the effects of temperature changes in experimental studies (Olefeldt *et al.,* 2017), owing to fluctuations in water table depth and soil drying rapidly decreasing methane production, resulting in lags in methane fluxes (Goodrich *et al*., 2015; Keane *et al*., 2021). These suggest that climate change-driven increases in water table depth are likely to be a more important determinant of future atmospheric CH_4 concentrations than warming. Huang *et al.* (2021) synthesised the literature for experimental studies measuring the direct impacts of water table drawdown on peatland greenhouse gas emissions and modelled these effects against future water table depth projections. They found that increased water table depths drove reductions in CH_4 emissions and increased CO_2 efflux from peatlands, and that under future high emission climate scenarios, these changes result in a net-positive climate effect (Huang *et al.,* 2021).

In this study, reductions in CO_2 equivalent emissions of CH_4 over a 100-year period do not compensate for increased CO_2 emissions from the experimentally manipulated plots. However, the GWP100 method used to come to this conclusion does not consider the warming effect of cumulative releases of CH_4 and CO_2 over time. In reality, the long-term effect of a reduction in CH_4 emissions is likely to have a greater effect upon CH_4 atmospheric concentrations and therefore climate warming (Allen *et al*., 2016; Lynch *et al*., 2020). Peatlands are important sources of atmospheric CH_4, emitting an estimated 30 million tonnes each year (Frolking *et al*., 2011). Changes in the net contribution of CH_4 to the atmosphere from peatlands are likely to have a profound effect upon future climate change and atmospheric concentration of greenhouse gases (Lynch et al., 2020).

6.1.3. Effect of increased drought frequency upon carbon fluxes and vegetation

Simulated droughts (an additional month of water table drawdown every 2.5 years) did not influence greenhouse gas emissions, vegetation community composition or net ecosystem carbon budgets in the experimental plots. This finding disagrees with the results of other experimental studies that manipulate water table height (e.g., Strack *et* *al.,* 2006; Murphy *et al.,* 2009; Bragazza *et al.,* 2013). However, most other studies induce a permanent step-change in the water table, whereas this study simulates episodic drought by temporarily drawing down water tables. While this result suggests that increased drought severity will not have an effect upon ecosystem functioning in temperate ombrotrophic peatlands, this result may relate to the short duration, timing, and design of the simulated water table drawdowns. Changes in vegetation typically occur in response to extended periods of water table drawdown (e.g., Breeuwer *et al*., 2009; Churchill *et al*., 2015). Therefore, more intense, frequent droughts than those simulated by this experiment may induce changes in peatland vegetation, resulting in increased vascular plant cover. The long-term effects of drought upon vegetation or carbon cycling could not be corroborated by comparison with the long-term record, since only prolonged periods of water table drawdown were recorded in the long-term record from Cors Fochno (e.g., the period of drainage between c. 1800 to 1970 CE). However, sustained changes in water table depth frequently drove shifts in vegetation communities, agreeing with experimental studies that replicate prolonged changes in water table depth (Strack *et al.,* 2006; Murphy *et al.,* 2009; Bragazza *et al.,* 2013). There is evidence that sedges were more abundant during wetter periods throughout the past c. 1500 years at the coring location in Cors Fochno. This suggests that prolonged drying may result in a decline in sedge cover, potentially reducing CH_4 emissions from the site (Strack *et al.,* 2006).

Future climate projections, based upon the UKCP18 Science Overview Report (Lowe et al., 2018) suggest that the UK will experience significant changes in temperature and precipitation rates during the 21st century, resulting in wetter, warmer winters, and drier summers than present. The probability that an extreme summer drought comparable to the 1976 heatwave (16 months of dry conditions and an average summer temperature of 17.8°C) will occur is projected to increase from 5 % (based upon a 1981 – 2000 baseline) to between 54 - 66 % by 2050, increasing further to c. 90 % towards the end of the century (Lowe et al., 2018). This experiment did not simulate increases in drought intensity at these magnitudes, therefore the results of this study may not apply should droughts of this magnitude become more frequent.

A number of studies indicate that future warming and drying may disrupt the hydroclimatic balance maintaining carbon accumulation in peatlands (Ise *et al.,* 2008; Dorrepaal *et al.,* 2009; Fenner and Freeman; 2011). A key area of uncertainty relates to how drought frequency will change regionally in the future under climate change (Lee *et al.,* 2021). Drought events, while likely to increase in frequency and severity in some regions, will be unevenly distributed around the world. For example, recent modelling work by Balting *et al.* (2021) showed that drought risk by 2100 under high emission scenarios were greatest for tropical and temperate regions, with areas such as Europe and much of south and central America experiencing significant increases in drought relative to areas in the boreal zone, which will either become wetter or will undergo minor change. Likewise, IPCC projections suggest (albeit with limited confidence) that the majority of areas where peatlands are abundant will receive increased precipitation as a result of climate change, but that drought frequency will increase (Lee *et al.,* 2021). This suggests that peatlands in temperate regions, such as the UK, will be most at risk from carbon losses due to combined warming and drought, although peatlands in the northernmost latitudes will experience the largest changes in temperature.

As well as drought, increased precipitation extremes are expected to increase in frequency in some regions of the Northern Hemisphere due to climate change (Kirchmeier-Young and Zhang, 2020; Kahraman *et al*., 2021). For the UK, the frequency and severity of winter storms is projected to increase (Senior *et al.,* 2016). The majority of carbon budgeting studies do not monitor hydrological fluxes at a resolution sufficient to capture these short-lived events, despite most of the DOC (~ 50 %) and POC exported from peatland catchments annually being lost following periods of high discharge (Clark *et al*., 2007; Rosset *et al*., 2019). To develop more accurate carbon budgets for peatlands and to better understand how future changes in extreme weather events will affect peatland carbon cycling, more studies that measure hydrological fluxes at high-resolution sampling frequencies are necessary. Presently, hydrological fluxes of POC and DIC are rarely measured for ombrotrophic peatlands (Lindsay, 2010), despite both fluxes showing seasonal and interannual variability related to climatic and hydrological conditions (Dinsmore *et al*., 2013; Leach *et al*., 2016).

6.1.4. Effects of warming upon peatland vegetation

Temperature increases of 0.1 – 0.9°C between 2010 to 2020 in the warmed and combined warming and drought treatment plots resulted in an increase in ericaceous shrub abundance by 200 % and 90 %, respectively. This result was corroborated by changes in the long-term record of vegetation change at Cors Fochno during warmer periods, where the peat was composed of more ericaceous shrub remains and *Calluna vulgaris* seeds. The results presented in this thesis indicate that enhanced shrub cover is a re-occurring response to periods of increased temperature and suggest that plant communities may respond similarly in other sites in the Northern Hemisphere. That ericaceous shrubs will increase with warming is supported by the number of studies in which vascular plant abundance increases in response to warming (e.g., Weltzin *et al.,* 2005; Buttler *et al.,* 2015), and by observations seen in arctic regions in response to recent climate warming (Myers-Smith *et al.,* 2011; Loranty and Goetz, 2012; Gałka *et al.,* 2017). This response has been attributed to warming of the sub-soil, extending the below-ground growing season and leading to increased fine-root growth (Malhotra *et al.,* 2021). This finding has important consequences for peatland carbon cycling processes, since Ward *et al.* (2015) found that vegetation community composition exerts more of a control upon decomposition than environmental conditions, with increased ericaceous shrub cover often resulting in increasing decomposition rates and a decline in carbon accumulation (Bragazza *et al.,* 2012; 2013).

While peatland vegetation succession with warming and drought is often characterised by increased vascular plant cover, most frequently by ericaceous shrubs, responses to warming are often species specific and the dominant species driving these changes may differ from site to site (e.g., Buttler *et al.,* 2015). The results of this study are therefore unlikely to apply to all northern peatlands, which encompass a wide variety of different peat-forming ecosystems, which differ in terms of their vegetation characteristics across temperate, boreal, and subarctic climatic zones, as well as minerotrophic gradients (Rydin and Jeglum, 2006; Page and Baird, 2016). Vegetation responses to climate warming will largely depend upon changes in growing season length (Antala *et al.,* 2022). These changes will be more pronounced in the highest latitudes, where the largest changes in temperature and precipitation rates are already taking place (Ruosteenoja *et* *al.,* 2016). This warming may extend the growing season length in higher hemisphere regions, potentially increasing annual net carbon accumulation in these areas (Gallego-Sala *et al.*, 2018).

6.1.5. Treatment effects upon Sphagnum abundance

Despite increases in ericaceous shrubs, there was no effect of any treatment upon *Sphagnum* abundance throughout the 10-year experimental record. This is of significance since *Sphagnum* is an important indicator of peatland functioning, facilitating carbon accumulation in most northern peatlands (van Breemen, 1995). The response of *Sphagnum* to climate change may determine the future role of peatlands in the global climate system (Norby *et al.,* 2019). The results of this study suggest that *Sphagnum* will not decline in response to moderate increases in temperatures (0.1 – 0.9°C over ten years), or drought frequency at the severity imparted by this experiment. In the literature, *Sphagnum* responds differently to experimental climate manipulations*,* either showing no change (e.g., Weltzin *et al.,* 2000; 2003; Walker *et al.,* 2006); increasing (Dorrepaal *et al.,* 2004; Robroek *et al.,* 2007) or declining (Dieleman *et al.,* 2015; Bragazza *et al.,* 2016; Norby *et al.,* 2019). *Sphagnum* productivity usually declines when studies impart temperature increases above 5°C (e.g., Dieleman *et al.,* 2015; Bragazza *et al.,* 2016; Norby *et al.,* 2019). This supports findings by Gallego-Sala *et al.* (2018) that peatlands may become sources of carbon once a critical temperature threshold is crossed. While these temperature increases are relatively high, they are within the range of average projected temperature increases for the Northern Hemisphere by the year 2100 (Lee *et al.,* 2021). Understanding how *Sphagnum* responds to temperature increases of this magnitude is important for understanding how peatlands will respond to future projected climate changes in the Northern Hemisphere, where the greatest changes in temperatures and precipitation rates are projected to occur (Lee *et al.,* 2021).

While *Sphagnum* may have a critical threshold above which they cannot survive, individual *Sphagnum* species have different temperature preferences (Balagurova *et al.,* 1996; Breeuwer *et al.,* 2008; Jassey *et al.,* 2019). Oke and Hager (2017) modelled *Sphagnum* responses to climate warming for North America, finding that projected changes in temperature and precipitation under climate change would expand the current climatic range of peatlands, allowing for peatland development to increase and increasing *Sphagnum* productivity. Some studies suggest that *Sphagnum* can even be resilient to rapid increases in temperature. Dorrepaal *et al*. (2004) reported enhanced shoot length and productivity of *Sphagnum fuscum* in a Swedish peat bog with warming. Furthermore, despite much greater increases in temperatures occurring in higher latitudes over the past century, Sim *et al*. (2021) report that *Sphagnum* and other bryophytes growing on sub-arctic permafrost peatlands have remained stable and resilient to change. Robroek *et al.* (2017) demonstrated that taxonomic and functional turnover are decoupled in peatlands, meaning that despite species turnover due to climate change, species tended to be replaced by others with different climatic tolerances but similar functional traits. The replacing vegetation fulfil the same role in the ecosystem and therefore maintain ecosystem functioning. Understanding the global response of *Sphagnum* to future changes in climate is further complicated by the uncertainty and complexity in the changing trends of global precipitation (Antala *et al*., 2022). *Sphagnum* benefit from wetter conditions (Sonesson *et al*., 2002). Therefore, in areas where water availability increases due to enhanced rainfall, *Sphagnum* abundance will also be likely to increase (Jassey *et al.,* 2018).

Taken together, this suggests that relatively intact peatlands in temperate zones such as Cors Fochno may be resilient to future warming, as long as temperature increases remain below a threshold of approximately 5°C. Declines in one species of *Sphagnum* may allow another to replace it and perform its ecological role. However, once this temperature threshold is exceeded, the carbon sink function of peatlands may be compromised. While some *Sphagnum* species and other peatland vegetation may migrate northwards in response to climate changes, this may not be possible in some regions. For example, in some temperate regions, the fragmented nature of most peatlands limits the ability of *Sphagnum* to expand beyond the confines of relatively small areas (Antala *et al*., 2022). Some boreal peatlands already span the edge of the terrestrial surface, meaning they have nowhere to expand into (Antala *et al*., 2022). Topographical and geographical limits on the expansion of peatlands may allow increases in decomposition to overcome increases in productivity over time, causing peatlands to become net sources of atmospheric carbon as their climatic range decreases.

6.1.6. Comparing aCAR with net ecosystem carbon budgets

In Cors Fochno, the response of the apparent carbon accumulation rate (aCAR) to warmer/drier conditions during the Late Holocene differs from that seen in the experimental plots with warming. As documented in the core, warmer, drier conditions promoted increases in aCAR, suggesting that carbon accumulation rates are accelerated during warmer periods. This is a common result of peatland palaeoecological carbon accumulation studies (Charman *et al.,* 2013; Gallego-Sala *et al.,* 2018) and contradicts the findings of most experimental studies (e.g., Dorrepaal *et al.,* 2009; Bragazza *et al.,* 2016; Hanson *et al.,* 2020). This study investigated the disparity between these two approaches to find which result was closest to reality. By comparing aCAR with contemporary carbon fluxes from the experimental plots, it was demonstrated how aCAR in the acrotelm was close to the values for annual gross primary productivity (GPP). As each additional carbon flux was deducted from GPP, carbon accumulation rates in the experimental plots fall closer to the value of the long-term rate of carbon accumulation for the site since peat initiation began (LORCA). This was also comparable to aCAR rates beneath the catotelm, indicating that for Cors Fochno, core-derived and contemporary carbon accumulation rates were comparable. When estimates for particulate organic carbon and dissolved inorganic carbon fluxes were deducted from the annual net ecosystem carbon budgets however, the average net ecosystem carbon budget fell below the range of aCAR and LORCA. However, these fluxes, along with DOC, were likely to have been overestimated in this study.

This study finds that contemporary and core-derived carbon accumulation rates are more likely to converge if a site has lost little carbon during its history, as appears to be the case for Cors Fochno. This agrees with the findings of Frolking *et al.* (2014) and Ratcliffe *et al.* (2018) where substantial carbon losses from core-derived accumulation rates resulted in large discrepancies with net ecosystem carbon balances.

6.1.7. Drivers of long-term carbon accumulation rates

Changes in aCAR throughout the Late Holocene record for Cors Fochno correspond with changes in the palaeo-vegetation throughout the core. In turn, shifts in the palaeo-vegetation are driven by long-term changes in hydrological conditions, but also following anthropogenic disturbances such as drainage or fire. Notable shifts in plant community composition appear in the long-term record, including a shift from bog-pool conditions dominated by *Sphagnum denticulatum* towards dominance by *Sphagnum pulchrum,* following a period of drainage lasting from c. 1800 – 1970 CE. aCAR shows a large increase in response to this change.

The response of carbon accumulation and vegetation changes in response to warming and water table drawdown in the long-term record differs from that seen in the experimental study in response to warming. Whereas relatively short-term (ten-year) increases in temperature drove only slight increases in ericaceous shrub abundance and had no effect upon *Sphagnum* abundance, in the long-term record the dominant *Sphagnum* species changed a number of times, usually abruptly. Following wildfire, *Sphagnum* disappeared temporarily from the record, with *Sphagnum austinii*, the primary peat-forming species prior to its decline, disappearing from the record altogether following a fire event c. 1400 CE. These changes corresponded throughout the record to changes in aCAR.

aCAR was generally higher during warmer, drier periods, contrasting with the responses of NEE and NER to the climate manipulations. This suggests that while short-term effects of changes in plant community composition may reduce carbon accumulation rates, long-term changes in plant communities and their functional diversity may produce vegetation that ultimately retains more carbon. This indicates that the main drivers of vegetation change and carbon accumulation rates differ between sub-decadal and multidecadal timescales, and that these differences result in positive and negative climate feedback mechanisms, respectively, that operate over different timescales (Belyea, 2009). Over long time-periods, plant succession under drier/warmer conditions have led to the development of plant communities that produce more decay-resistant litter than those that occur during wetter, cooler periods. As a result of this difference, the peat formed between periods of climate change differs in its botanical composition, with the peat composed of more resistant material promoting greater carbon accumulation rates.

In summary, the results of this study indicate that while peatland functioning is largely resilient to short-term changes in climatic conditions (Dise, 2009), vegetation may relatively rapidly shift in response to long-term changes in hydrology or following disturbance, resulting in changes in carbon accumulation rates, ecosystem functioning and resilience to future climate perturbations (Malmer and Wallén, 2004; Gałka *et al.,* 2017; van Bellen *et al.,* 2020). These changes usually result in increased carbon accumulation during warmer periods and may thus impart a negative climate feedback over longer periods.

6.1.8. Effects of the experimental manipulations upon organic matter stabilisation

Despite the air temperatures not being significantly different between plots with and without open top chambers during the tea bag incubation period, the results of the decomposition experiment indicate that increased stabilisation of below-ground organic matter under warmer conditions will increase carbon retention in below-ground peat relative to that at the surface. These effects may be driven by the compounded effects of the experimental treatments upon soil chemistry, vegetation, and microbial activity over ten years (Jassey *et al*., 2013; Fenner and Freeman, 2011), or they could be the result of increases in soil temperature of c. 0.5°C seen in the warmed plots during the experimental incubations. This may indicate that older, previously accumulated peat may become more stable under warmer climatic conditions in the future, while surface peat will decompose more quickly. Alternatively, this difference may be related to changes in the supply of labile material to the sub-soil following enhanced surface decay with warming (Eriksson *et al.,* 2010a; 2010b). Although the tea bag decomposition study found no significant differences in net decomposition rates or stabilisation between treatments, this 'stratification' of stabilisation may have important consequences for future peatland organic matter decomposition. Increased supply of below-ground carbon via root exudates or below-ground plant litter (Basiliko *et al.,* 2012; Fenner and Freeman, 2020; Zhang *et al.,* 2021) may occur as vascular plant cover increases. Increased stabilisation of organic matter may enhance the proportion of this carbon that enters the long-term carbon store (Keuskamp *et al.,* 2013), potentially compensating for future increases in decomposition at the surface due to warming.

The opposite is true for increased drought severity. Stabilisation decreased in the sub-soil relative to the surface. This may reflect the effect of enhanced phenol oxidase activity increasing decomposition in the sub-soil peat relative to the still living organic material on the surface (Fenner and Freeman, 2011; Freeman *et al.,* 2004). In terms of long-term carbon accumulation, this may result in the decay of older, previously accumulated peat, resulting in an apparent reduction in carbon accumulation rates in peat deposited prior to drought (Young *et al.,* 2019). In the combined treatment plots, there were no difference in stabilisation rates with burial. This may reflect the opposite effects of warming and drought, effectively cancelling each other out, suggesting that these effects are driven by different mechanisms. These findings may not be broadly applicable to all peatlands across the Northern Hemisphere due to differences in microbial communities and peat biogeochemistry between sites (Aerts *et al.,* 1999; Fisk *et al.,* 2003; Jaatinen *et al*., 2007; Peltoniemi *et al*., 2009; Jassey *et al*., 2013).

6.1.9. Issues with inferring future peatland responses from palaeoecological records

Approximately 15 % of the world's peatlands are in a state of degradation (Turetsky and St. Louis, 2006; Joosten, 2016) and many of Europe's peatlands have undergone substantial drying throughout the past c. 300 years due to human activity (Swindles *et al.,* 2019). Even in cases where peatlands are relatively pristine or have been restored to their previous functioning, they may still be affected by present climate change, past disturbances, or atmospheric pollution (e.g., Berendse *et al.,* 2001; Talbot *et al.,* 2014; Swindles *et al.,* 2016). These disturbances can drive changes in plant community composition (Turetsky and St. Louis, 2006), affecting peatland ecosystem services (Ward *et al.,* 2009; Dieleman *et al.,* 2015). This was also the case for Cors Fochno, as demonstrated by comparing the vegetation communities between the experimental plots and those that occurred in the past. Human induced drainage resulted in persistent drier conditions that prompted the development of the *Sphagnum pulchrum*-dominated vegetation community seen today. Similar disturbances in other sites may also result in the development of novel vegetation communities not before seen throughout a sites' history (Alexander *et al.,* 2015; Ordonez *et al.,* 2016). Modern day vegetation communities such as the *Sphagnum pulchrum*- dominated community on Cors Fochno may not be accurately represented throughout the palaeo record, and such, are likely to respond differently to future warming and drought compared to how they have responded in the past. Likewise, past peatland responses are likely to differ from those that will occur the future, especially in cases where the past vegetation communities have no close modern analogue, e.g., for Cors Fochno and several other sites in Wales and Europe, periods dominated by *Sphagnum austinii* (Hughes *et al.,* 2007). The lack of a modern analogue for pre-disturbance conditions in most areas means that vegetation responses inferred from field-based experimental studies and past changes are likely to differ (Barber and Charman, 2003). Taking all the evidence into account, we conclude that inferring peatland responses to future climate change from past changes documented in the palaeoecological record may be problematic. Palaeoenvironmental records of vegetation and environmental changes from peatlands can still provide important context for peatland responses to climate change under pre-disturbance conditions, providing insights that cannot be obtained by experimental studies (Graumlich, 2002). However, this effect may be less pronounced for some sites in the northernmost latitudes, which may have experienced limited atmospheric deposition of anthropogenic pollutants and minimal disturbance as a result of human activity, and as a result may be considered 'pristine' and can still trace a reliable record of climatic change within their stratigraphy.

6.1.10. Sensitivity of palaeoecological proxies to climate change

An important uncertainty affecting the interpretation of peat-based palaeoenvironmental records is what aspect of the climate is being recorded, and how to interpret this (Payne, 2014). Understanding whether peatland palaeoecological proxies actually measure changes in palaeo-climate is important for their continued use in palaeoecological studies, so that peatland-based reconstructions can be used to compare and test climate models more accurately. This study represents the first time that the sensitivity and effectiveness of loss on ignition, C/N ratios and colorimetric peat humification, three commonly used palaeoecological proxies to measure changes in palaeoclimate as a decay signal, were experimentally tested with an *in-situ* experimental climate manipulation study.

The results of this study showed that the palaeoecological proxies of decomposition were insensitive to changes in climate imparted by the field manipulation experiment, which for changes in soil temperature (0.5°C) and long-term changes in air temperature over the ten years of the experiment (0.1 – 0.9°C) were close to those experienced during the transition between the MCA to the LIA of c. 0.2°C (Mann *et al.,* 2009). Comparison with the long-term palaeoecological record of Cors Fochno showed that variability in each proxy throughout the past c. 1500 years was greater than the change seen in the experimental study, with shifts in C/N and light transmission both showing good correspondence with changes in the long-term plant macrofossil record.

These findings agree with a number of studies that have found these methods to be unreliable for reconstructing past changes in climate, instead reflecting changes in the botanical composition of peat (Yeloff and Mauquoy, 2006; Payne and Blackford, 2008; Zaccone *et al.,* 2018). While LOI is typically used as a measure of organic content, which can be affected by decomposition, as opposed to being a proxy for decomposition (Hoogstein *et al.,* 2015), colorimetric peat humification and C/N analysis are frequently applied in peatland palaeoenvironmental studies as a measure of palaeoclimatic change (e.g., Zhang *et al.,* 2021; Tsyganov et al, 2021; Babeshko *et al.,* 2021). While colorimetric decomposition appears to record a slight signal of decomposition, this effect was likely obscured in the long-term record as a result of both the noisiness of this proxy and by changes in the botanical composition of the peat.

6.2. Limitations of this study and recommendations for future research

There are a number of potential sources of uncertainty in this thesis. These weaknesses and remaining uncertainties are addressed below. In addition, recommendations for similar studies and avenues for future research are made.

6.2.1. Limitations of the palaeoecological analyses

A limitation of the palaeoecological aspect of this study is that the high-resolution palaeoecological reconstructions of carbon accumulation and environmental change for the past millennium are based on a single core (Korhola *et al.,* 1996; Roulet *et al.,* 2007; van Bellen *et al.,* 2011). This was due to the time intensive nature of high-resolution multi-proxy studies and the financial cost of developing a well-defined chronology. The climate sensitivity of the locations from which cores are taken within the same site can show high spatial variation owing to differences in the climate sensitivity of the microsite from which the core was taken (e.g., *Sphagnum* lawn, hummock), as well as spatial differences in autogenic ecohydrological feedbacks (Ohlson and Økland, 1998; Loisel and Garneau, 2010; Swindles *et al.,* 2012). Analyses based upon a single core mean that autogenic feedbacks cannot be separated from allogenic responses to climate (Bacon *et al.,* 2017). Studies that compare multiple cores from the same site show that major palaeoclimatic changes are usually well replicated (e.g., Barber *et al.,* 1999; Hendon *et al.,* 2001). However, autogenic effects become more important in high-resolution studies, with records with less than a 100 year chronological resolution between sampling intervals often exhibiting a greater degree of variation (Blaauw and Mauquoy, 2012). These effects can result in large variations in core-derived estimates of carbon accumulation between cores taken from the same site. For example, when average carbon accumulation rates were analysed for multiple cores from a peatland in Norway, they varied from 26 to 454 g C m^{-2} y^{-1} (Ohlson and Økland, 1998).

While this limitation does not invalidate the findings of this study, additional well-dated, high-resolution analyses of multiple cores from Cors Fochno would have allowed for regional signals to be differentiated from local noise. It is recommended that future studies incorporating climate manipulation experiments with palaeoecology consider analysing multiple cores, in order to improve interpretations of past climatic changes.

6.2.2. Limitations of the experimental site

Most *in-situ* climate manipulation field studies are small-scale and relatively short-term. While field based climate manipulation studies are important tools for understanding how peatlands will respond to global change, their statistical power is often limited by a low number of replicates (Yang *et al.,* 2021). Low replication in these studies increases the chance that the effects of the experimental treatments are either under or over-estimated, potentially resulting in increased type I and type II errors (Lemoine *et al.,* 2016). The experiment at Cors Fochno is no exception, having only three replicate plots per treatment. Greater replication of the plots would allow for stronger analyses and would allow for the identification and the exclusion of outliers. In the case of this site, increased replication was not possible due to practical and logistical limitations common in such studies. Future field manipulation experiment designs should maximise their scale and replicate number, to increase their statistical power. By doing so, these studies would allow for improved quantification of peatland ecosystem responses to climate change (Lemoine *et al.,* 2016).

This study was based on the analysis of a record from a single experimental site, located in the relatively undisturbed central dome of a lowland raised bog. The vegetation within these plots was representative for this area, with similar vegetation types and abundances having been reported in site surveys and other studies (Comas *et al*., 2013; Schulz, 2005). An approximate c. 4 km^2 of the site is surrounded by degraded peatland that has experienced extensive drainage, burning and peat cutting over the past c. 200 years (Poucher, 2009). In these extensive areas, the vegetation is markedly different to that in the middle portion of the bog. Although there have been several ditch-blocking efforts in recent years to restore the hydrology of some of the degraded areas of the bog, the remaining ditches also provide relatively large areas of open water filled with aquatic vegetation. Hydrological and greenhouse gas fluxes from these areas are likely to be markedly different to those within the experimental stand at Cors Fochno, owing to differences in the vegetation and their effects upon physical and biotic conditions that moderate carbon fluxes and ecosystem functioning in peatlands (Armstrong *et al.*, 2012). Given that c. 15 % of all peatlands globally are considered to be in a degraded state due to anthropogenic disturbance (Turetsky and St. Louis, 2006; Meyer *et al.,* 2015; Joosten, 2016) degraded areas should be considered in peatland ecosystem carbon budgets. It is also important that results from experimental sites are considered in the context of their local vegetation and environmental conditions, as opposed to being considered representative of the response of the site as a whole (Bu *et al.*, 2011).

It is also important that the effects of future climate changes upon carbon cycling is understood for degraded areas. These areas are more likely to release large quantities of particulate organic carbon due to erosion and subsidence (Lindsay, 2010) and are also likely to receive a large supply of inorganic carbon and nutrient runoff from nearby farmland, particularly in the peripheral areas that are already relatively enriched, which may further influence emissions of CH_4 (Juutinen *et al.*, 2018) but also for N_2O. This may be further enhanced when warming coincides with combined with the expansion of shrub-type vegetation (Luan *et al.*, 2019; Anthony and Silver, 2021). While areas such as the central portion of Cors Fochno are likely to be more resilient to gradual changes in climate (Gallego-Sala and Prentice, 2013) those that are in poor condition may be more susceptible to increased decay and erosion with future warming and increased drought frequency (Turetsky *et al.*, 2015). Understanding how degraded peatlands may respond to future climate change is important due to their potential for emitting substantial amounts of greenhouse gases into the atmosphere.

6.2.3. Representation of different peatland types

A key uncertainty in this study relates to the fact that Cors Fochno as a site is not representative of all northern peatlands. In order to improve our understanding of how peatlands will respond to future climate change impacts, experimental and palaeoecological studies should be carried out across a wider range of peatland types. Peatlands differ in terms of their continental setting, trophic status, latitude, and vegetation (Charman, 2002). Peatlands can also show large variations in their carbon cycling functions, both geographically (Moore *et al.,* 1998; Loisel *et al.,* 2012; Griffiths *et al.,* 2017; Sim *et al.,* 2021) and between sites of different trophic status (Moore *et al.,* 1990), owing to differences in the functional characteristics of their overlying vegetation (Weltzin *et al.,* 2000). For example, fens can show enhanced sensitivity to changes in climate, compared with ombrotrophic bogs such as Cors Fochno (Wu and Roulet, 2014). Permafrost peatlands are also functionally very different from non-permafrost peatlands, being subject to mechanisms that are unique to cold regions, such as permafrost thaw (Sim *et al.,* 2021). These account for approximately half of the estimated carbon stock stored in peatlands (Tarnocai *et al.,* 2009). These differences between sites are likely to influence peatland responses to climate warming and increased drought occurrence (Gignac and Vitt, 1994; Ward *et al.,* 2013; 2015; Wu and Roulet, 2014). Quantifying this variability in peatland carbon cycling is important for understanding past, future, and present carbon dynamics and to better understand how peatlands will respond to future projected changes in climate. As is the case in this study, most previous work examining the effects of climate changes upon peatland ecosystem functioning and carbon cycling has been based upon small-scale experimental manipulation experiments (Griffiths *et al.,* 2017). This uncertainty can be reduced by conducting more experiments over a larger number of sites, allowing for the variability and mechanisms of change across all peatland types to be considered.

6.2.4. Inability to fully explain the underlying mechanisms driving changes seen in the experimental treatments

Most peatland research has mainly focussed on the kinetic response of peatland carbon cycling to climate change (e.g., Worrall *et al.,* 2009), relying on empirical relationships between environmental variables such as water table and air temperature and ecosystem functions such as greenhouse gas emissions. In recent years, there has been increasing interest in how climate change will influence the microbial and chemical processes that govern peatlands carbon cycling and resilience to climate change (Ritson *et al.,* 2021). Microbial processes govern carbon cycling in peatlands (Andersen *et al.,* 2013), but how these processes operate and interact with greenhouse gas emissions is currently poorly understood (Ritson *et al.,* 2021).

In this study, the climate manipulations significantly influenced greenhouse gas fluxes, plant community composition and decomposition rates. However, the mechanisms of change could not be discerned from the data collected. Jassey *et al.* (2013) demonstrated that experimental warming in peatlands can destabilise carbon cycling by causing significant changes in the structure of microbial communities, changes in vegetation composition, and their interactions with the peat chemistry. Kim *et al.* (2012)

found that experimental warming increased bacterial communities and caused a decline in methanogen abundance, although this change did not significantly affect CH_4 emissions between the plots. In the case of this study, non-linearity in the relationship between CH_4 emissions and warming could not be adequately explained by changes in environmental variables. A better understanding of how the peat microbial communities responded to the warming treatments might explain this response.

Understanding the microbial processes that drive carbon cycling in peatlands, as well as their interactions with soil chemistry and vegetation (Jassey *et al.,* 2013), and how these will respond to future changes in climate may be beneficial for improving our understanding of the mechanisms behind peatland responses to future warming and drought (Bardgett *et al.,* 2008; Ritson *et al.,* 2021). Such an understanding can be achieved using experimental climate manipulation experiments such as the Cors Fochno Experiment, by comparing soil microbial responses between the experimental treatments and relating these to greenhouse gas fluxes and other ecosystem functions (e.g., Basinska *et al.,* 2020).

6.2.5. Limitations of the tea bag decomposition experiment and testing of climate proxies

The tea bag decomposition experiment had several limitations that may affect the results of this study. The experiment could have benefitted from examining decomposition rates at a number of different depths throughout the peat profile, as opposed to just the surface and 8 cm depth. The buried samples were under the average depth of the water table for most of the incubation period; however, their position meant that these samples were more likely to reflect differences in decomposition that occur at the interface between the acrotelm and the catotelm (the ’mesotelm’). By comparing changes in Tea Bag Index (TBI) parameters between these depths with the catotelm as well, more inferences could be made about the effects of each experimental treatment upon decomposition of old, stable organic matter relative to the recently accumulated material at the surface. Furthermore, litter from different vegetation decomposes at different rates (Bell *et al.,* 2018). Non-native vegetation is also likely to decompose more slowly in peatlands, as the microbial communities are not adapted to break down exotic organic matter (Prescott, 2010) such as the green and rooibos tea used in the tea bag experiment. By incorporating different types of plant litter into the experiment and comparing their responses to experimental incubation with the TBI parameters, a better understanding of peatland organic matter decomposition may be developed.

While the methodology was in keeping with Keuskamp *et al.* (2013), it is possible that the TBI parameters and palaeoecological proxies may have been more sensitive to changes in climate had the incubation times been longer. The incubation time used in this project was relatively short, at three months, and spanned the period from mid-September to mid-December, during which time air temperatures fell in keeping with the seasons. As a result of these incubations being late in the year, there was no significant treatment effect on air temperature, although soil temperature significantly increased, possibly due to the open top chambers shielding the plots from wind (Samson *et al.,* 2018). Greater decomposition effects could be expected with a wider temperature span and longer incubation times, and it is possible that the palaeoecological proxies tested may have also been sensitive to greater differences in temperature. Understanding how the decomposition rate of organic matter changes throughout the year at multiple depths would provide greater insights into peatland decay processes and how they may be affected by warming and drought throughout the peat column and during different seasons, and this work provides an impetus for further research in this area.

6.3. References

Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology,* 80(7), 2170-2181.

Alexander, J. M., Diez, J. M., and Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature,* 525(7570), 515–518.

Andersen, R., Chapman, S. J., and Artz, R. R. E. (2013). Microbial communities in natural and disturbed peatlands: a review. *Soil Biology and Biochemistry*, *57*, 979-994.

Antala, M., Juszczak, R., van der Tol, C., & Rastogi, A. (2022). Impact of climate change-induced alterations in peatland vegetation phenology and composition on carbon balance. *Science of the total environment*, 154294.

Anthony, T. L., & Silver, W. L. (2021). Hot moments drive extreme nitrous oxide and methane emissions from agricultural peatlands. *Global Change Biology,* 27(20), 5141-5153.

Arah, J. R. M., and Stephen, K. D. (1998). A model of the processes leading to methane emission from peatland. *Atmospheric Environment*, *32*(19), 3257-3264.

Armstrong, A., Holden, J., Luxton, K., & Quinton, J. N. (2012). Multi-scale relationship between peatland vegetation type and dissolved organic carbon concentration. *Ecological Engineering*, 47, 182-188.

Babeshko, K.V., Shkurko, A., Tsyganov, A.N., Severova, E.E., Gałka, M., Payne, R.J., Mauquoy, D., Mazei, N.G., Fatynina, Y.A., Krasnova, E.D. and Saldaev, D.A., (2021). A multi-proxy reconstruction of peatland development and regional vegetation changes in subarctic NE Fennoscandia (the Republic of Karelia, Russia) during the Holocene. *The Holocene*, *31*(3), 421-432.

Bacon, K.L., Baird, A.J., Blundell, A., Bourgault, M.A., Chapman, P.J., Dargie, G., Dooling, G.P., Gee, C., Holden, J., Kelly, T.J., and McKendrick-Smith, K.A., (2017). Questioning ten common assumptions about peatlands. *Mires and Peat*, *19*, 1-23.

Balagurova, N., Drozdov, S. and Grabovik, S., (1996), Cold and heat resistance of five species of Sphagnum. In *Annales Botanici Fennici* (33-37). Finnish Zoological and Botanical Publishing Board.

Ballantyne, D. M., Hribljan, J. A., Pypker, T. G., & Chimner, R. A. (2014). Long-term water table manipulations alter peatland gaseous carbon fluxes in Northern Michigan. *Wetlands ecology and management*, 22(1), 35-47.

Balting, D. F., AghaKouchak, A., Lohmann, G., and Ionita, M. (2021). Northern Hemisphere drought risk in a warming climate. *npj Climate and Atmospheric Science*, *4*(1), 1-13.

Barber, K.E. and Charman, D.J., (2003). Holocene palaeoclimate records from peatlands. In: *Global change in the Holocene*, 210-226.

Barber, K.E., Battarbee, R.W., Brooks, S.J., Eglinton, G., Haworth, E.Y., Oldfield, F., Stevenson, A.C., Thompson, R., Appleby, P.G., Austin, W.E.N. and Cameron, N.G., (1999). Proxy records of climate change in the UK over the last two millennia: documented change and sedimentary records from lakes and bogs. *Journal of the Geological Society*, *156*(2), 369-380.

Bardgett, R. D., Freeman, C., and Ostle, N. J. (2008). Microbial contributions to climate change through carbon cycle feedbacks. *The ISME journal*, *2*(8), 805-814.

Basiliko, N., Stewart, H., Roulet, N.T. and Moore, T.R., (2012). Do root exudates enhance peat decomposition?. *Geomicrobiology Journal*, *29*(4), 374-378.

Basińska, A.M., Reczuga, M.K., Gąbka, M., Stróżecki, M., Łuców, D., Samson, M., Urbaniak, M., Leśny, J., Chojnicki, B.H., Gilbert, D. and Sobczyński, T., (2020). Experimental warming and precipitation reduction affect the biomass of microbial communities in a Sphagnum peatland. *Ecological Indicators*, *112*, p.106059.

Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J., Freeman, C., and Clark, J.M., (2018). Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma*, 331, 29-37.

Belyea, L.R., (2009). Nonlinear dynamics of peatlands and potential feedbacks on the climate system. *Carbon cycling in northern peatlands*, *184*, 5-18.

Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., Lee, J. A., Mitchell, E., Saarinen, T., Vasander, H., and Wallén, B. (2001). Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Global Change Biology*, 7(5), 591– 598.

Blaauw, M. and Mauquoy, D., (2012). Signal and variability within a Holocene peat bog—chronological uncertainties of pollen, macrofossil, and fungal proxies. *Review of Palaeobotany and Palynology*, 186, 5-15.

Bragazza, L., Buttler, A., Habermacher, J., Brancaleoni, L., Gerdol, R., Fritze, H., Hanajík, P., Laiho, R. and Johnson, D., (2012). High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon accumulation. *Global Change Biology*, *18*(3), 1163-1172.

Bragazza, L., Buttler, A., Robroek, B.J., Albrecht, R., Zaccone, C., Jassey, V.E. and Signarbieux, C., (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, *22*(12), 4114-4123.

Bragazza, L., Parisod, J., Buttler, A., and Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, *3*(3), 273-277.

Breeuwer, A., Heijmans, M. M., Robroek, B. J., and Berendse, F. (2008). The effect of temperature on growth and competition between Sphagnum species. *Oecologia*, *156*(1), 155-167.

Breeuwer, A., Robroek, B. J., Limpens, J., Heijmans, M. M., Schouten, M. G., & Berendse, F. (2009). Decreased summer water table depth affects peatland vegetation. *Basic and Applied Ecology, 10*(4), 330-339.

Bridgham, S.D., Pastor, J., Dewey, B., Weltzin, J.F. and Updegraff, K., (2008). Rapid carbon response of peatlands to climate change. *Ecology*, *89*(11), 3041-3048.

Bu, Z., Hans, J., Li, H., Zhao, G., Zheng, X., Ma, J. and Zeng, J., (2011). The response of peatlands to climate warming: A review. *Acta Ecologica Sinica*, *31*(3), 157-162.

Bubier, J. L., Moore, T. R., Bellisario, L., Comer, N. T., and Crill, P. M. (1995). Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles*, *9*(4), 455-470.

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A. and Bragazza, L., (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of vegetation Science*, *26*(5), 964-974.

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A. and Bragazza, L., (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of vegetation Science*, *26*(5), 964-974.

Charman, D. (2002). *Peatlands and environmental change*. John Wiley and Sons Ltd.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D. and Jackson, S.T., (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, *10*(2), 929-944.

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W. and McGuire, A.D., (2009). Effects of experimental water table and temperature manipulations on ecosystem CO 2 fluxes in an Alaskan rich fen. *Ecosystems*, *12*(8), 1329-1342.

Churchill, A.C., Turetsky, M.R., McGuire, A.D., and Hollingsworth, T.N., (2015). Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen. *Canadian Journal of Forest Research*, *45*(2), 185-193.

Clark, J. M., Lane, S. N., Chapman, P. J., & Adamson, J. K. (2007). Export of dissolved organic carbon from an upland peatland during storm events: Implications for flux estimates. *Journal of Hydrology*, 347(3-4), 438-447.

Comas, X., Kettridge, N., Binley, A., Slater, L., Parsekian, A., Baird, A.J., Strack, M. and Waddington, J.M., 2014. The effect of peat structure on the spatial distribution of biogenic gases within bogs. *Hydrological processes*, 28(22), 5483-5494.

Dabros, A., and Fyles, J. W. (2010). Effects of open-top chambers and substrate type on biogeochemical processes at disturbed boreal forest sites in northwestern Quebec. *Plant and Soil*, *327*(1), 465-479.

Deng, J., Li, C., & Frolking, S. (2015). Modeling impacts of changes in temperature and water table on C gas fluxes in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*, 120(7), 1279-1295.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability. *Global change biology*, *21*(1), 388-395.

Dinsmore, K.J., Billett, M.F. and Dyson, K.E., (2013). Temperature and precipitation drive temporal variability in aquatic carbon and GHG concentrations and fluxes in a peatland catchment. *Global Change Biology*, *19*(7), 2133-2148.

Dise, N.B., (2009). Peatland response to global change. *Science*, *326*(5954), 810-811.

Dorrepaal, E., Aerts, R., Cornelissen, J. H., Callaghan, T. V., and van Logtestijn, R. S. (2004). Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure, and production in a sub-arctic bog. *Global Change Biology*, *10*(1), 93-104.

Dorrepaal, E., Toet, S., van Logtestijn, R. S., Swart, E., van De Weg, M. J., Callaghan, T. V., and Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, *460*(7255), 616-619

Eriksson, T., Öquist, M.G. and Nilsson, M.B., (2010a). Effects of decadal deposition of nitrogen and sulphur, and increased temperature, on methane emissions from a boreal peatland. *Journal of Geophysical Research: Biogeosciences*, *115*(G4).

Eriksson, T., Öquist, M.G. and Nilsson, M.B., (2010b). Production and oxidation of methane in a boreal mire after a decade of increased temperature and nitrogen and sulfur deposition. *Global Change Biology*, *16*(7), 2130-2144.

Fenner, N. and Freeman, C., (2020). Woody litter protects peat carbon stocks during drought. *Nature Climate Change*, *10*(4), 363-369.

Fenner, N., and Freeman, C. (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, *4*(12), 895-900.

Fisk, M. C., Ruether, K. F., & Yavitt, J. B. (2003). Microbial activity and functional composition among northern peatland ecosystems. *Soil Biology and Biochemistry,* 35(4), 591-602.

Freeman, C., Ostle, N.J., Fenner, N. and Kang, H., (2004). A regulatory role for phenol oxidase during decomposition in peatlands. *Soil Biology and Biochemistry*, *36*(10), 1663-1667.

Frolking, S., Roulet, N. T., Tuittila, E., Bubier, J. L., Quillet, A., Talbot, J., & Richard, P. J. H. (2010). A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth System Dynamics*, 1(1), 1-21.

Frolking, S., Talbot, J., and Subin, Z.M., (2014). Exploring the relationship between peatland net carbon balance and apparent carbon accumulation rate at century to millennial time scales. *The Holocene*, *24*(9), 1167-1173.

Frolking, S., Talbot, J., Jones, M. C., Treat, C. C., Kauffman, J. B., Tuittila, E. S., and Roulet, N. (2011). Peatlands in the Earth's 21st century climate system. *Environmental Reviews*, *19*(NA), 371-396.

Gałka, M., Szal, M., Watson, E. J., Gallego-Sala, A., Amesbury, M. J., Charman, D. J., Roland. T. P., Edward Turner, T and Swindles, G. T. (2017). Vegetation succession, carbon accumulation and hydrological change in subarctic peatlands, Abisko, Northern Sweden. *Permafrost and Periglacial Processes*, *28*(4), 589-604.

Gallego-Sala, A.V. and Prentice, I.C., (2013). Blanket peat biome endangered by climate change. *Nature Climate Change*, *3*(2), 152-155.

Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S. and Blyakharchuk, T., (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature Climate Change*, *8*(10), 907-913.

Gignac, L.D. and Vitt, D.H., (1994). Responses of northern peatlands to climate change: effects on bryophytes. *The Journal of the Hattori Botanical Laboratory*, *75*, 119-132.

Goodrich, J. P., Campbell, D. I., Roulet, N. T., Clearwater, M. J., & Schipper, L. A. (2015). Overriding control of methane flux temporal variability by water table dynamics in a Southern Hemisphere, raised bog. *Journal of Geophysical Research: Biogeosciences, 120*(5), 819-831.

Granberg, G., Mikkelä, C., Sundh, I., Svensson, B. H., and Nilsson, M. (1997). Sources of spatial variation in methane emission from mires in northern Sweden: A mechanistic approach in statistical modeling. *Global Biogeochemical Cycles*, *11*(2), 135-150.

Graumlich, L. J. (2002). Long-term vegetation change in mountain environments: Palaeoecological insights into modern vegetation dynamics. In M. Beniston (Ed.), *Mountain environments in changing climates* (158–168). Routledge.

Griffiths, N.A., Hanson, P.J., Ricciuto, D.M., Iversen, C.M., Jensen, A.M., Malhotra, A., McFarlane, K.J., Norby, R.J., Sargsyan, K., Sebestyen, S.D. and Shi, X., (2017). Temporal and spatial variation in peatland carbon cycling and implications for interpreting responses of an ecosystem-scale warming experiment. *Soil Science Society of America Journal*, *81*(6), 1668-1688.

Hanson, P.J., Griffiths, N.A., Iversen, C.M., Norby, R.J., Sebestyen, S.D., Phillips, J.R., Chanton, J.P., Kolka, R.K., Malhotra, A., Oleheiser, K.C. and Warren, J.M., (2020). Rapid net carbon loss from a whole-ecosystem warmed Peatland. *AGU Advances*, *1*(3), p.e2020AV000163.

Hendon, D., Charman, D. J., and Kent, M. (2001). Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications. *The Holocene*, *11*(2), 127-148.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F. and Guiot, J., (2018). Impacts of 1.5° C Global Warming on Natural and Human Systems. In: *Global warming of 1.5° C. An IPCC Special Report on the impacts of global warming of 1.5° C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change*. World Meteorological Organization Technical Document.

Hoogsteen, M.J., Lantinga, E.A., Bakker, E.J., Groot, J.C. and Tittonell, P.A., (2015). Estimating soil organic carbon through loss on ignition: effects of ignition conditions and structural water loss. *European Journal of Soil Science*, *66*(2), 320-328.

Huang, Y., Ciais, P., Luo, Y., Zhu, D., Wang, Y., Qiu, C., Goll, D.S., Guenet, B., Makowski, D., De Graaf, I. and Leifeld, J., (2021). Tradeoff of CO2 and CH4 emissions from global peatlands under water table drawdown. *Nature Climate Change*, 1-5.

Hughes, P.D.M., Lomas-Clarke, S.H., Schulz, J. and Jones, P., 2007. The declining quality of late-Holocene ombrotrophic communities and the loss of Sphagnum austinii (Sull. ex Aust.) on raised bogs in Wales. *The Holocene*, *17*(5), 613-625.

Huguet, A., Fosse, C., Laggoun-Défarge, F., Delarue, F., and Derenne, S. (2013). Effects of a short-term experimental microclimate warming on the abundance and distribution of branched GDGTs in a French peatland. *Geochimica et Cosmochimica Acta*, *105*, 294-315.

Ise, T., Dunn, A. L., Wofsy, S. C., and Moorcroft, P. R. (2008). High sensitivity of peat decomposition to climate change through water table feedback. *Nature Geoscience*, *1*(11), 763-766.

Jaatinen, K., Fritze, H., Laine, J., & Laiho, R. (2007). Effects of short-and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global Change Biology, 13*(2), 491-510.

Jassey, V.E., Reczuga, M.K., Zielińska, M., Słowińska, S., Robroek, B.J., Mariotte, P., Seppey, C.V., Lara, E., Barabach, J., Słowiński, M. and Bragazza, L. (2018). Tipping point in plant–fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. *Global Change Biology, 24*(3), 972-986.

Jassey, V. E., and Signarbieux, C. (2019). Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. *Global Change Biology*, *25*(11), 3859-3870.

Jassey, V.E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E.A., Toussaint, M.L., Francez, A.J. and Gilbert, D., (2013). Above-and belowground linkages in Sphagnum peatland: Climate warming affects plant-microbial interactions. *Global Change Biology*, *19*(3), 811-823.

Johnson, C.P., Pypker, T.G., Hribljan, J.A. and Chimner, R.A., (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO 2/CH 4 dynamics in a northern Michigan peatland. *Ecosystems*, *16*(5), 736-748.

Joosten, H., (2016). Peatlands across the globe. In *Peatland restoration and ecosystem services: Science, policy, and practice* (Vol. 2016, 19-43). Cambridge: Cambridge University Press.

Juutinen, S., Moore, T.R., Bubier, J.L., Arnkil, S., Humphreys, E., Marincak, B., Roy, C. and Larmola, T. (2018). Long-term nutrient addition increased CH4 emission from a bog through direct and indirect effects. *Scientific Reports,* 8(1), 1-11.

Keane, J. B., Toet, S., Ineson, P., Weslien, P., Stockdale, J. E., & Klemedtsson, L. (2021). Carbon Dioxide and Methane Flux Response and Recovery From Drought in a Hemiboreal Ombrotrophic Fen. *Frontiers in Earth Science,* 706.

Keuskamp, J. A., Dingemans, B. J., Lehtinen, T., Sarneel, J. M., and Hefting, M. M. (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution*, *4*(11), 1070-1075

Kim, S. Y., Freeman, C., Fenner, N., and Kang, H. (2012). Functional and structural responses of bacterial and methanogen communities to 3-year warming incubation in different depths of peat mire. *Applied Soil Ecology*, *57*, 23-30.

Kirchmeier-Young, M. C., & Zhang, X. (2020). Human influence has intensified extreme precipitation in North America. *Proceedings of the National Academy of Sciences*, 117(24), 13308-13313.

Korhola, A., Alm, J., Tolonen, K., Turunen, J., and Jungner, H. (1996). Three-dimensional reconstruction of carbon accumulation and CH4 emission during nine millennia in a raised mire. *Journal of Quaternary Science: Published for the Quaternary Research Association*, *11*(2), 161-165.

Lai, D.Y.F., (2009). Methane dynamics in northern peatlands: a review. *Pedosphere*, *19*(4), 409-421.

Leach, J. A., Larsson, A., Wallin, M. B., Nilsson, M. B., & Laudon, H. (2016). Twelve-year interannual and seasonal variability of stream carbon export from a boreal peatland catchment. *Journal of Geophysical Research: Biogeosciences,* 121(7), 1851-1866.

Lee, J. Y., J. Marotzke, G. Bala, L. Cao, S. Corti, J. P. Dunne, F. Engelbrecht, E. Fischer, J. C. Fyfe, C. Jones, A. Maycock, J. Mutemi, O. Ndiaye, S. Panickal, T. Zhou, (2021). Future Global Climate: Scenario Based Projections and Near-Term Information. In: *Climate Change 2021: The Physical Science Basis. In:* Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E.

Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Lemoine, N.P., Hoffman, A., Felton, A.J., Baur, L., Chaves, F., Gray, J., Yu, Q. and Smith, M.D., (2016). Underappreciated problems of low replication in ecological field studies. *Ecology*, *97*(10), 2554-2561.

Li, Q., Leroy, F., Zocatelli, R., Gogo, S., Jacotot, A., Guimbaud, C. and Laggoun-Défarge, F., (2021). Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change. *Soil Biology and Biochemistry*, *153*, p.108077.

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H. and Schaepman-Strub, G., (2008). Peatlands and the carbon cycle: from local processes to global implications–a synthesis. *Biogeosciences*, *5*(5), 1475-1491.

Lindsay, R. (2010). *Peatbogs and carbon: a critical synthesis to inform policy development in oceanic peat bog conservation and restoration in the context of climate change*. University of East London, Environmental Research Group.

Loisel, J., and Garneau, M. (2010). Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*(3-4), 493-533.

Loisel, J., Gallego-Sala, A.V. and Yu, Z., (2012). Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. *Biogeosciences*, *9*(7), 2737-2746.

Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W., Benavides, J.C., Blewett, J., Camill, P., Charman, D.J. and Chawchai, S., (2021).

Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*(1), 70-77.

Loranty, M. M., and Goetz, S. J. (2012). Shrub expansion and climate feedbacks in Arctic tundra. *Environmental Research Letters*, *7*(1), 011005.

Lowe, J.A., Bernie, D., Bett, P., Bricheno, L., Brown, S., Calvert, D., Clark, R., Eagle, K., Edwards, T., Fosser, G. and Fung, F., (2018). UKCP18 science overview report. *Met Office Hadley Centre: Exeter, UK*.

Luan, J., Wu, J., Liu, S., Roulet, N., & Wang, M. (2019). Soil nitrogen determines greenhouse gas emissions from northern peatlands under concurrent warming and vegetation shifting. *Communications biology,* 2(1), 1-10.

Lund, M., Lafleur, P.M., Roulet, N.T., Lindroth, A., Christensen, T.R., Aurela, M., Chojnicki, B.H., Flanagan, L.B., Humphreys, E.R., Laurila, T. and Oechel, W.C., (2010). Variability in exchange of CO2 across 12 northern peatland and tundra sites. *Global Change Biology*, *16*(9), 2436-2448.

Lynch, J., Cain, M., Pierrehumbert, R., and Allen, M. (2020). Demonstrating GWP*: a means of reporting warming-equivalent emissions that captures the contrasting impacts of short-and long-lived climate pollutants. *Environmental Research Letters*, *15*(4), 044023.

Malhotra, A., Brice, D.J., Childs, J., Graham, J.D., Hobbie, E.A., Vander Stel, H., Feron, S.C., Hanson, P.J. and Iversen, C.M., (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences*, *117*(30), 17627-17634.

Malmer, N. and Wallén, B., (2004). Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. *The Holocene*, *14*(1), 111-117.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G. and Ni, F., (2009). Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, *326*(5957), 1256-1260.

Masson-Delmotte, V., Zhai, P., Pörtner, H.O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R. and Connors, S., (2018). *An IPCC Special Report on the impacts of global warming of Global warming of 1.5 C,* 1(5).

Matveev, A., Laurion, I., Deshpande, B. N., Bhiry, N., & Vincent, W. F. (2016). High methane emissions from thermokarst lakes in subarctic peatlands. *Limnology and Oceanography, 61*(S1), S150-S164.

Meyer, C., Diaz-de-Quijano, M., Monna, F., Franchi, M., Toussaint, M. L., Gilbert, D., and Bernard, N. (2015). Characterisation and distribution of deposited trace elements transported over long and intermediate distances in north-eastern France using Sphagnum peatlands as a sentinel ecosystem. *Atmospheric Environment*, *101*, 286-293.

Moore, T. R., and Knowles, R. (1989). The influence of water table levels on methane and carbon dioxide emissions from peatland soils. *Canadian Journal of Soil Science*, *69*(1), 33-38.

Moore, T. R., and Knowles, R. (1990). Methane emissions from fen, bog, and swamp peatlands in Quebec. *Biogeochemistry*, *11*(1), 45-61.

Moore, T. R., and Roulet, N. T. (1993). Methane flux: water table relations in northern wetlands. *Geophysical Research Letters*, *20*(7), 587-590.

Moore, T.R., Roulet, N.T. and Waddington, J.M., (1998). Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change*, *40*(2), 229-245.

Munir, T. M., and Strack, M. (2014). Methane flux influenced by experimental water table drawdown and soil warming in a dry boreal continental bog. *Ecosystems*, *17*(7), 1271-1285.

Murphy, M., Laiho, R., and Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems*, *12*(8), 1268-1282.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E. and Boudreau, S., (2011). Shrub expansion in tundra ecosystems: dynamics, impacts, and research priorities. *Environmental Research Letters*, *6*(4), p.045509

Negandhi, K., Laurion, I., Whiticar, M. J., Galand, P. E., Xu, X., & Lovejoy, C. (2013). Small thaw ponds: an unaccounted source of methane in the Canadian High Arctic. *PLoS One, 8*(11), e78204.

Nilsson, M., Mikkelä, C., Sundh, I., Granberg, G., Svensson, B. H., & Ranneby, B. (2001). Methane emission from Swedish mires: National and regional budgets and dependence on mire vegetation. *Journal of Geophysical Research: Atmospheres, 106*(D18), 20847-20860.

Norby, R. J., Childs, J., Hanson, P. J., and Warren, J. M. (2019). Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. *Ecology and Evolution*, *9*(22), 12571-12585.

Ohlson, M., and Halvorsen Økland, R. (1998). Spatial variation in rates of carbon and nitrogen accumulation in a boreal bog. *Ecology*, *79*(8), 2745-2758.

Oke, T. A., and Hager, H. A. (2017). Assessing environmental attributes and effects of climate change on Sphagnum peatland distributions in North America using single-and multi-species models. *PloS one*, *12*(4), e0175978.

Olefeldt, D., Euskirchen, E. S., Harden, J., Kane, E., McGuire, A. D., Waldrop, M. P., and Turetsky, M. R. (2017). A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability. *Global Change Biology*, *23*(6), 2428-2440.

Ordonez, A., Williams, J. W., and Svenning, J. C. (2016). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change,* 6(12), 1104–1109

Page, S.E., and Baird, A.J., (2016). Peatlands and global change: response and resilience. *Annual Review of Environment and Resources*, 41, 35-57.

Payne, R.J., and Blackford, J.J., (2008). Peat humification and climate change: a multi-site comparison from mires in south-east Alaska. *Mires and peat*, 1-11.

Payne, R.J., (2014). A natural experiment suggests little direct temperature forcing of the peatland palaeoclimate record. *Journal of Quaternary Science*, *29*(6), 509-514.

Peltoniemi, K., Fritze, H., & Laiho, R. (2009). Response of fungal and actinobacterial communities to water-level drawdown in boreal peatland sites. *Soil Biology and Biochemistry,* 41(9), 1902-1914.

Poucher P. (2009). *Wetland Margins Survey: Cors Fochno*. Dyfed Archaeological Trust

Prescott, C.E., (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils?. *Biogeochemistry*, 101(1), 133-149.

Qiu, C., Zhu, D., Ciais, P., Guenet, B., & Peng, S. (2020). The role of northern peatlands in the global carbon cycle for the 21st century. *Global ecology and biogeography, 29(*5), 956-973.

Ratcliffe, J., Andersen, R., Anderson, R., Newton, A., Campbell, D., Mauquoy, D. and Payne, R., (2018). Contemporary carbon fluxes do not reflect the long-term carbon balance for an Atlantic blanket bog. *The Holocene*, *28*(1), 140-149.

Ritson, J.P., Alderson, D.M., Robinson, C.H., Burkitt, A.E., Heinemeyer, A., Stimson, A.G., Gallego-Sala, A., Harris, A., Quillet, A., Malik, A.A. and Cole, B., (2021). Towards a microbial process-based understanding of the resilience of peatland ecosystem service provisioning–a research agenda. *Science of the Total Environment*, *759*, p.143467.

Robroek, B. J. M., Limpens, J., Breeuwer, A., Crushell, P. H., and Schouten, M. G. C. (2007). Interspecific competition between Sphagnum mosses at different water tables. *Functional Ecology*, *21*(4), 805-812.

Robroek, B.J., Jassey, V.E., Payne, R.J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S.J., Dise, N.B., Kattge, J. and Zając, K., (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications*, *8*(1), 1-9.

Rosset, T., Gandois, L., Le Roux, G., Teisserenc, R., Durantez Jimenez, P., Camboulive, T., & Binet, S. (2019). Peatland contribution to stream organic carbon exports from a montane watershed. *Journal of Geophysical Research: Biogeosciences,* 124(11), 3448-3464.

Roulet, N. T., Lafleur, P. M., Richard, P. J., Moore, T. R., Humphreys, E. R., and Bubier, J. I. L. L. (2007). Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, *13*(2), 397-411.

Ruosteenoja, K., Jylhä, K., & Kämäräinen, M. (2016). Climate projections for Finland under the RCP forcing scenarios. *Geophysica*, 51.

Rydin, H., and Jeglum, J.K., (2006). Peatlands around the world. In: In *The biology of peatlands*. Oxford University Press.

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., Zielińska, M., Robroek, B.J., Jassey, V.E., Buttler, A. and Chojnicki, B.H., (2018). The impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in Northern Poland. *Wetlands*, 38(3), 551-563.

Schulz, J. (2005). *Late Holocene mire development of the lowland raised bogs Cors Caron and Cors Fochno: A palaeoecological approach using high resolution macrofossil analysis.* Unpublished PhD Thesis. University of Southampton.

Schuur, E.A., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M. and Natali, S.M., (2015). Climate change and the permafrost carbon feedback. *Nature*, 520(7546), 171-179.

Senior, C.A., Andrews, T., Burton, C., Chadwick, R., Copsey, D., Graham, T., Hyder, P., Jackson, L., McDonald, R., Ridley, J. and Ringer, M., 2016. Idealized climate change simulations with a high-resolution physical model: HadGEM3-GC2. *Journal of Advances in Modeling Earth Systems,* 8(2), 813-830.

Sim, T.G., Swindles, G.T., Morris, P.J., Baird, A.J., Cooper, C.L., Gallego-Sala, A.V., Charman, D.J., Roland, T.P., Borken, W., Mullan, D.J. and Aquino-López, M.A., (2021). Divergent responses of permafrost peatlands to recent climate change. *Environmental Research Letters*, *16*(3), p.034001.

Sonesson, M., Carlsson, B. Å., Callaghan, T. V., Halling, S., Björn, L. O., Bertgren, M., & Johanson, U. (2002). Growth of two peat-forming mosses in subarctic mires: species interactions and effects of simulated climate change. *Oikos,* 99(1), 151-160.

Strack, M., Waddington, J. M., Rochefort, L., and Tuittila, E. S. (2006). Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research: Biogeosciences*, *111*(G2).

Swindles, G. T., Morris, P. J., Baird, A. J., Blaauw, M., and Plunkett, G. (2012). Ecohydrological feedbacks confound peat-based climate reconstructions. *Geophysical Research Letters*, *39*(11).

Swindles, G. T., Morris, P. J., Wheeler, J., Smith, M. W., Bacon, K. L., Edward Turner, T., Headley, A., and Galloway, J. M. (2016). Resilience of peatland ecosystem services over millennial timescales: Evidence from a degraded British bog. *Journal of Ecology,* 104(3), 621–636.

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J., Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T. and Barr, I.D., (2019). Widespread drying of European peatlands in recent centuries. *Nature Geoscience*, *12*(11), 922-928.

Talbot, J., Roulet, N. T., Sonnentag, O., and Moore, T. R. (2014). Increases in aboveground biomass and leaf area 85 years after drainage in a bog. *Botany-Botanique*, **92**(10), 713– 721.

Tarnocai, C., Canadell, J. G., Schuur, E. A., Kuhry, P., Mazhitova, G., and Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, *23*(2).

Tsyganov, A.N., Zarov, E.A., Mazei, Y.A., Kulkov, M.G., Babeshko, K.V., Yushkovets, S.Y., Payne, R.J., Ratcliffe, J.L., Fatyunina, Y.A., Zazovskaya, E.P. and Lapshina, E.D., (2021). Key periods of peatland development and environmental changes in the middle taiga zone of Western Siberia during the Holocene. *Ambio*, 1-14.

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*, *113*(G3).

Turetsky, M.R. and St. Louis, V.L., (2006). Disturbance in boreal peatlands. In *Boreal peatland ecosystems* (359-379). Springer, Berlin, Heidelberg.

Turetsky, M. R., Benscoter, B., Page, S., Rein, G., Van Der Werf, G. R., & Watts, A. (2015). Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience,* 8(1), 11-14.

van Bellen, S., Dallaire, P. L., Garneau, M., and Bergeron, Y. (2011). Quantifying spatial and temporal Holocene carbon accumulation in ombrotrophic peatlands of the Eastmain region, Quebec, Canada. *Global Biogeochemical Cycles*, *25*(2).

van Bellen, S., Shotyk, W., Magnan, G., Davies, L., Nason, T., Mullan-Boudreau, G., Garneau, M., Noernberg, T., Bragazza, L. and Zaccone, C., (2020). Carbon and nitrogen accumulation rates in ombrotrophic peatlands of central and northern Alberta, Canada, during the last millennium. *Biogeochemistry*, *151*(2), 251-272.

van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends in ecology and evolution*, *10*(7), 270-275.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B. and Epstein, H.E., (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342-1346.

Ward, S. E., Orwin, K. H., Ostle, N. J., Briones, M. J., Thomson, B. C., Griffiths, R. I., ... and Bardgett, R. D. (2015). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, *96*(1), 113-123.

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., and Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, *16*(10), 1285-1293.

Ward, S.E., Bardgett, R.D., McNamara, N.P. and Ostle, N.J., (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. *Functional Ecology*, *23*(2), 454-462.

Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H. and Bardgett, R.D., (2015). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, *96*(1), 113-123.

Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J., and Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, *9*(2), 141-151.

Weltzin, J. F., Keller, J. K., Bridgham, S. D., Pastor, J., Allen, P. B., and Chen, J. (2005). Litter controls plant community composition in a northern fen. *Oikos*, *110*(3), 537-546.

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K. and Chapin, C.T., (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, *81*(12), 3464-3478.

Wickland, K. P., Striegl, R. G., Neff, J. C., & Sachs, T. (2006). Effects of permafrost melting on CO2 and CH4 exchange of a poorly drained black spruce lowland. *Journal of Geophysical Research: Biogeosciences, 111*(G2).

Worrall, F., Burt, T.P., Rowson, J.G., Warburton, J., and Adamson, J.K., (2009). The multi-annual carbon budget of a peat-covered catchment. *Science of the Total Environment*, *407*(13), 4084-4094.

Wu, J., and Roulet, N. T. (2014). Climate change reduces the capacity of northern peatlands to absorb the atmospheric carbon dioxide: The different responses of bogs and fens. *Global Biogeochemical Cycles*, *28*(10), 1005-1024.

Yang, Y., Hillebrand, H., Lagisz, M., Cleasby, I., and Nakagawa, S. (2021). Low statistical power and overestimated anthropogenic impacts, exacerbated by publication bias, dominate field studies in global change biology. *Global Change Biology*.

Yeloff, D. and Mauquoy, D., (2006). The influence of vegetation composition on peat humification: implications for palaeoclimatic studies. *Boreas*, *35*(4), 662-673.

Young, D.M., Baird, A.J., Charman, D.J., Evans, C.D., Gallego-Sala, A.V., Gill, P.J., Hughes, P.D., Morris, P.J. and Swindles, G.T., (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific Reports*, *9*(1), 1-8.

Zaccone, C., Plaza, C., Ciavatta, C., Miano, T.M. and Shotyk, W., (2018). Advances in the determination of humification degree in peat since: Applications in geochemical and paleoenvironmental studies. *Earth Science Reviews*, *185*, 163-178.

Zhang, D., Chen, L., Feng, Z., Ran, M., Yang, Y., Zhang, Y. and Liu, Q., (2021). Four peat humification-recorded Holocene hydroclimate changes in the southern Altai Mountains of China. *The Holocene*, p.09596836211011674.

Chapter 7: Conclusions

7.1. Response to project objectives

The future role of peatlands in the global climate system is uncertain under future climate change scenarios. A large source of this uncertainty derives from the lack of agreement between palaeoecological and experimental studies examining climate change impacts on peatland function, processes, and carbon cycling. The aim of this thesis was to combine palaeoecological and experimental climate manipulation studies to better understand how peatland carbon cycling will respond to future warming and drought.

Four general objectives were set in the introduction. How these objectives were met by this thesis is laid out in the following sections.

7.1.1. Calculate modern carbon budgets for the experimental treatments

The first objective was to calculate modern multi-annual carbon budgets for the experimental treatment plots, to quantify the effects of ten years of warming and increased drought frequency upon peatland greenhouse gas fluxes and carbon cycling. The evidence base for this is first explored in the literature review of chapter one. This showed that although most experimental studies indicate that future climate change will increases CO_2 emissions from peatlands, how this will impact carbon accumulation rates is less clear, due to the variable responses of plant productivity to warming and drought. The evidence base for the effects of episodic drought was limited to a few studies directly measuring the greenhouse gas responses to real drought events, suggesting that droughts can drive large reductions in carbon emissions, although this is dependent upon their severity and the timing of the drought event. In chapter three, multi-year carbon budgets from measured gas fluxes were calculated, and differences were tested for between the experimental treatments.

7.1.2. Relate the long-term context of carbon accumulation to the modern carbon budgets

The second objective sought to compare net ecosystem carbon budgets with the long term (c. 1500 year) carbon accumulation history of the site, in order to explain the disparity between experimental and palaeoecological approaches. It was found in the literature review of chapter one that these two approaches resulted in contrasting results. Experimental studies generally indicate that warmer and drier conditions can result in both increased CO_2 emissions and reduced net carbon emissions. On the other hand, palaeoclimatic studies generally showed that carbon accumulation rate increased under warmer and drier climatic conditions. In chapter four, the estimated contemporary multi-year carbon budgets for each of the experimental treatments were directly compared with core-derived records of carbon accumulation from the site.

7.1.3. Test the sensitivity and effectiveness of palaeoenvironmental proxies to simulated warming and drought

The sensitivity and effectiveness of three commonly used palaeoecological proxies of climate-mediated decomposition (loss on ignition, colorimetric peat humification and C/N ratios) were tested by comparing changes in these proxies with the results of a tea bag decomposition experiment. In chapter five, the sensitivity of the Tea Bag Index (TBI) and three paleoenvironmental proxies for decay: loss on ignition (LOI); C/N ratios and peat humification to simulated warming and drought close to temperature variations experienced during the transition between the Medieval Climate Anomaly and the Little Ice Age.

7.1.4. Compare responses in the experiment with responses to real climatic change in the past

The results of the experimental study were directly compared with those from the palaeoecological analyses, to find out how the results of these two approaches differed and why, to see which method gave results that were closest to reality. In chapter three, changes in plant community composition through time in the experimental plots were compared with the Late Holocene record of palaeo-vegetation change for the site. In chapter four, differences between net annual carbon accumulation rates were compared with mean aCAR rates for the MCA and the LIA. In chapter five, the responses of three decomposition proxies to the experimental treatments were compared with c. 1500 years of change for each proxy reconstructed from the long-term record of the site.

7.2. General summary

This thesis set to test the hypothesis that climate change would cause positive feedback mechanisms from peatlands to dominate over negative mechanisms. In general, the findings of this study appear to support accepting this hypothesis, with increased temperatures driving a reduction in carbon accumulation over short time-scales due to increased shrub abundance and increased carbon emissions. When combined with increased drought frequency and storm events peatlands can become net sources of atmospheric carbon, with these emissions potentially reflecting the decay of formerly stable carbon stocks. While negative feedbacks due to reductions in CH_4 emissions and changes in below-ground organic matter stability (provided warming is not coincident with increased drought) may reduce the positive effects of increased greenhouse gas emissions upon climate warming, they are unlikely to offset these emissions, which may be amplified in the future in areas where rainstorms or intense drought become more frequent due to climate change, as is projected for the UK.

In terms of long-term change, negative feedbacks are more likely to dominate due to changes in plant community composition during warmer, drier periods tending to favour vegetation that produces more decay-resistant litter. However, it is not possible for this study to quantify whether long-term feedbacks will dominate over short-term feedbacks in the long-term.

Anthropogenic impacts have significantly altered the functional diversity of peatland vegetation, affecting their responses to future climate change, and making peatland palaeoenvironmental records unreliable for inferring future climate change responses. Peatland palaeoecological studies may be useful when combined with experimental studies to provide the context of past environmental conditions and land use history and can be used to test climate models. For this purpose, only palaeoecological proxies that have been independently validated should be used, improving the reliability of these types of study.

It is important to note that these results are based upon the outcomes of a single experimental study conducted upon a temperate, ombrotrophic lowland bog and the results of this study are unlikely to be applicable to all sites in the northern hemisphere, particularly those in higher latitudes where changes in temperature and precipitation rates will be more pronounced than for the UK.

Appendices

Appendix I: Chapter 3 appendices. Plant community responses to experimental climate manipulation in a Welsh ombrotrophic peatland and their palaeoenvironmental context

The data from this chapter have been published online and is available via: Andrews, (2021): LA Plant community responses to experimental.xlsx. figshare. Dataset. https://doi.org/10.6084/m9.figshare.15395199.v1. Supplementary data relevant to this chapter is included in the following section.

Supplementary Text 1.1. Testing for changes in vegetation over time in the experimental study, statistical method details

Three fixed 25 x 25 cm quadrats, each enclosing a 5 x 5 grid, were used to quantify the plant community composition and abundance in each plot. The quadrats were surveyed annually using the pin-quadrat method (Levy and Madden, 1933). A pin was pushed through the top-right corner of the 25 grid squares. Total touches for each species of vascular plant were tallied for each plot. *Sphagnum* (recorded to species), liverworts, and bare peat were recorded on a presence/absence basis for each segment.

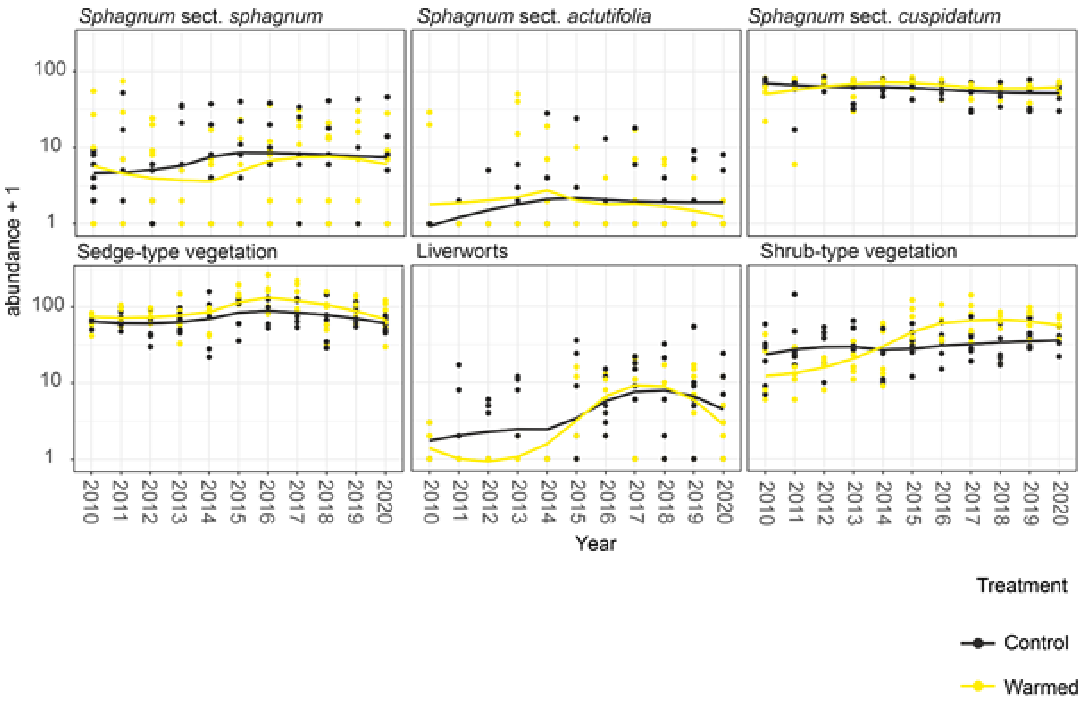
Changes in vegetation (by species and functional type) (Supplementary Table 1.1) over time across all combinations of treatments were tested by generalised linear models (GLMs) using the 'mvabund' package (Wang *et al.,* 2012; Wang *et al.,* 2021). The changes in the raw data are illustrated in Supplementary Figures 1.4 – 1.7. Changes in functional type data (Supplementary Figures 1.1 – 1.3) were compared by removing vegetation from the modern data with no analogy in the palaeoecological record. The remaining counts were summed into taxonomic groups of *Sphagnum* (sub-genera), shrubs, sedges, and liverworts. All analyses were carried out using the statistical package 'R' (R core team, 2021).

Data were fitted to negative binomial models, accounting for overdispersion. Each species/group were fitted with a separate GLM and a common set of explanatory variables (treatment, time, and their interaction) (Warton, 2011). This method provides greater statistical power than traditional distance-based methods often used for this purpose (e.g., Principal Response Curves) (van den Brink *et al.,* 2009, Warton, 2011, Warton *et al.,* 2012). The significance of fixed effects and their interactions were calculated using Wald tests (Bolker *et al.,* 2009; Guillera-Arroita and Lahoz-Monfort, 2012), with PIT-trap resampling of 999 permutations, assuming an uncorrelated response between variables (Warton *et al*., 2017). Samples were restricted to plots within blocks. When testing between sub-divisions of factors, the maximum number of permutations possible (719) were used to calculate the p-value, and there was no need to restrict sampling to blocks. Repeated measurements were accounted for by retaining sample order when permuting the entire time series. Treatment effect at the community level is the summed deviance of all species in the treatment plots (Wang *et al.,* 2012).

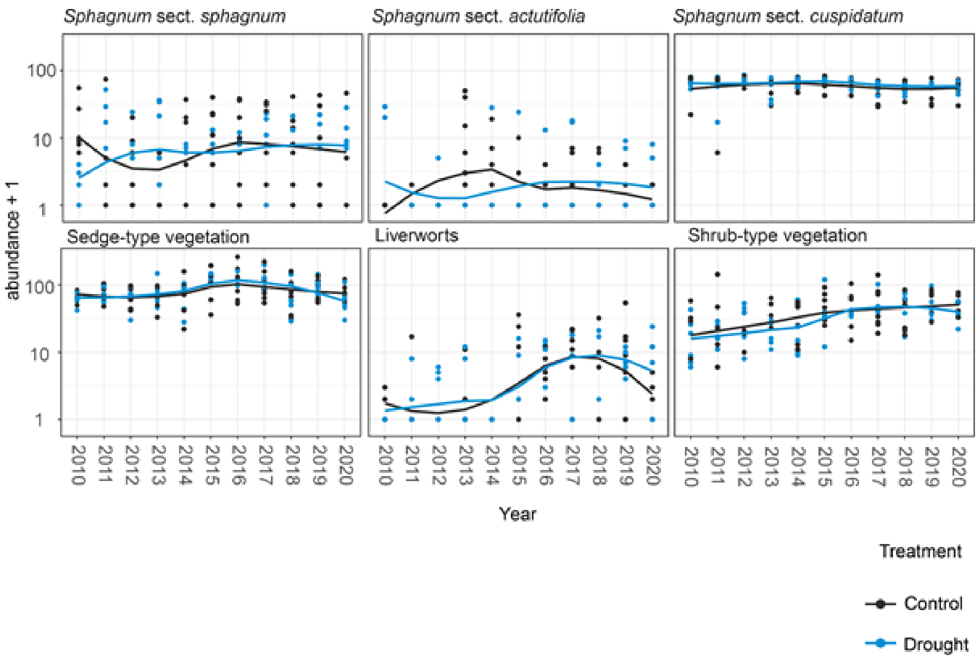
Supplementary Text 1.2. **Species codes used in the experimental vegetation surveying**

During the vegetation surveys, species were designated codes which were then retained in the analyses to identify each taxa. These codes are necessary for understanding Supplementary Figures 1.5 – 1.7. The code for each corresponding taxa is listed below:

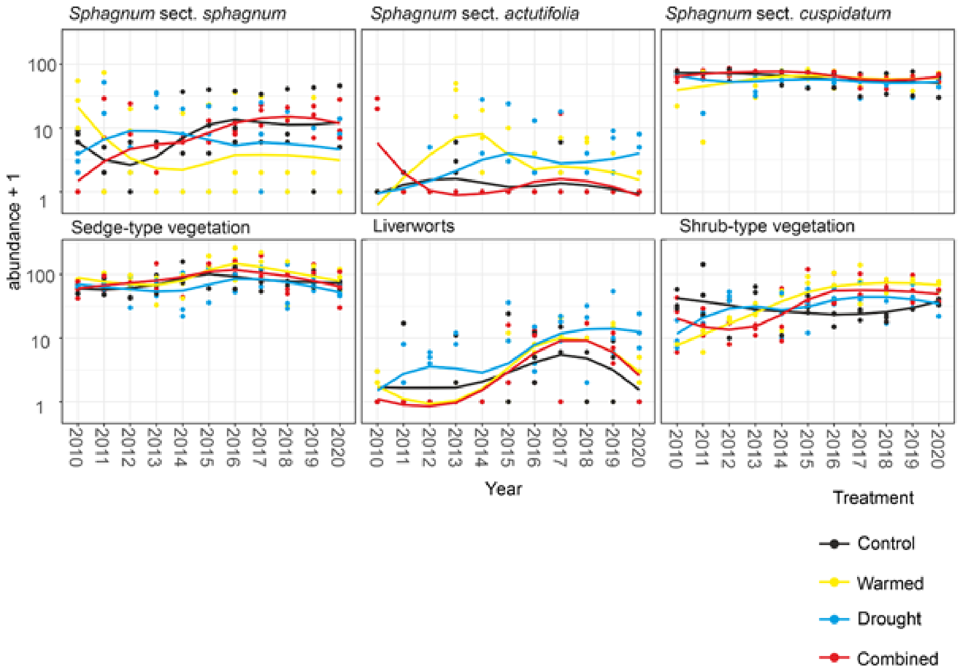
Sphpul: *Sphagnum pulchrum;* **Sphpap**: *Sphagnum papillosum***;** **Sphmag**: *Sphagnum medium;* **Sphcusp**: *Sphagnum cuspidatum;* **Sphten**: *Sphagnum tenellum*; **Sphcap**: *Sphagnum capillifolium;* **Eriovag**: *Eriophorum vaginatum*; **Rhynalba**: *Rhynchospora alba*; **Erictetr**: *Erica tetralix*; **Erioang**: *Eriophorum angustifolium*; **Calluvulg:** *Calluna vulgaris*; **Myrgale**: *Myrica gale;* **Andrpolif**: *Andromeda polifolia*; **Drosrot**: *Drosera rotundifolia*; **Nartossif**: *Narthecium ossifragum*; **Vaccoxy**: *Vaccinium oxycoccus*; **fungi**: fungi (all); **drosangl**: *Drosera anglica*; **liver**: Liverworts (all); **Molincaer**: *Molinia caerulea;* **Cladospp**: *Cladonia* spp; **Bare**: Bare peat.



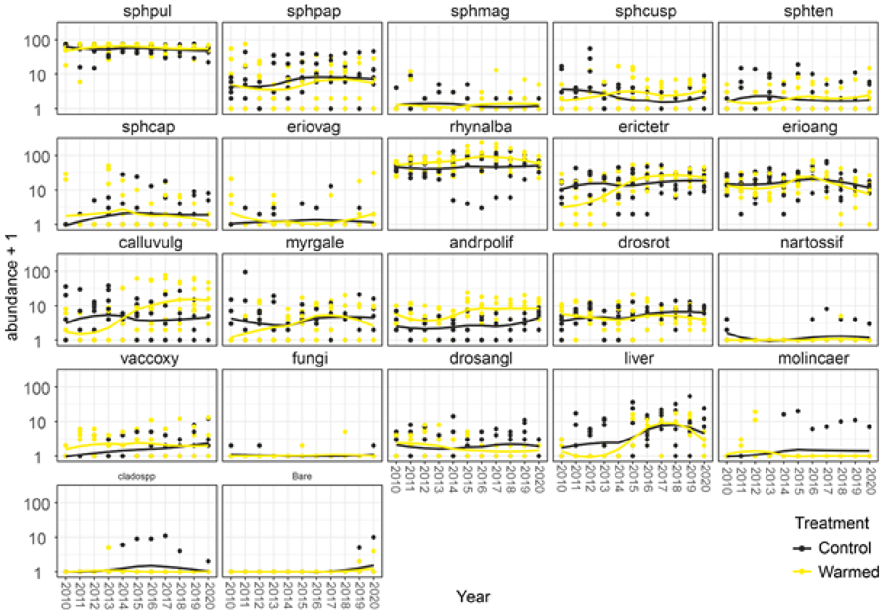
Supplementary Figure 1.1. Differences in plant functional types between plots with OTCs and control plots with time.



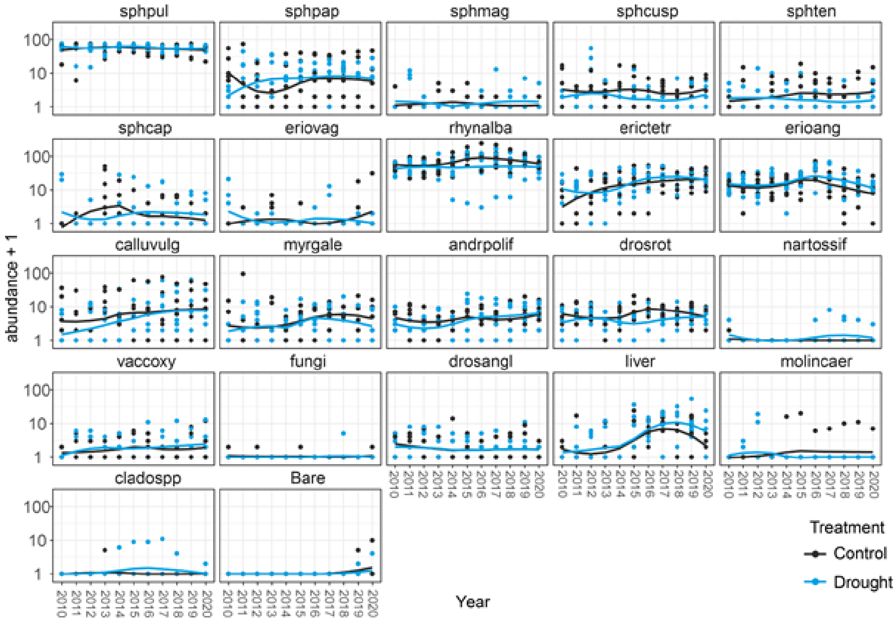
Supplementary Figure 1.2. Differences in plant functional types between pumped and control plots with time.



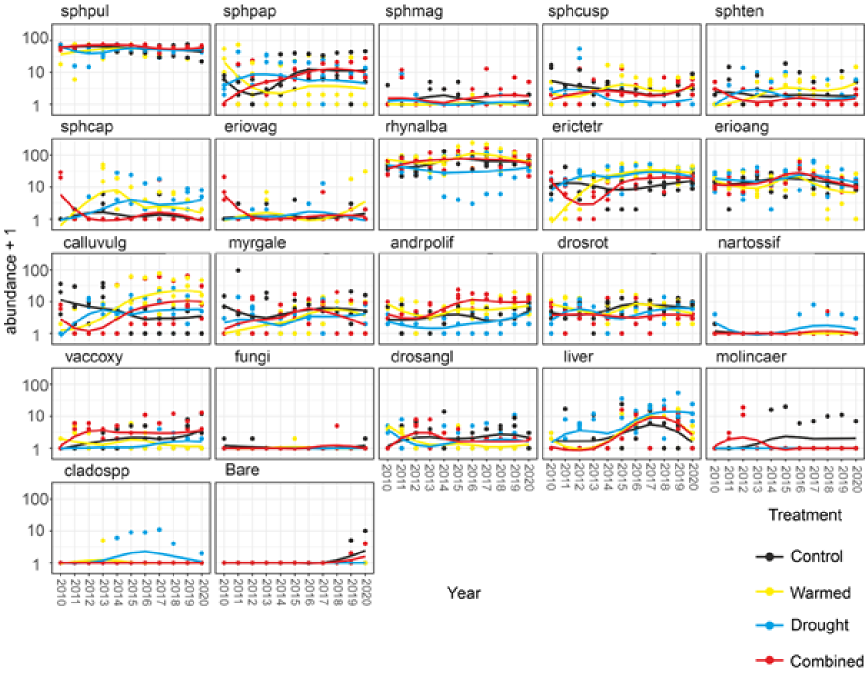
Supplementary Figure 1.3. Differences in plant functional types between all treatments with time.



Supplementary Figure 1.4. Differences in species responses between plots with OTCs and control plots with time.



Supplementary Figure 1.5. Differences in species responses between pumped plots and controls with time.



Supplementary Figure 1.6. Differences in species responses between all treatments with time

Supplementary Table 1.1. Summed vegetation/taxa counts from the experimental plots from 2010 - 2021. Species codes correspond to Supplementary Text 1.2.

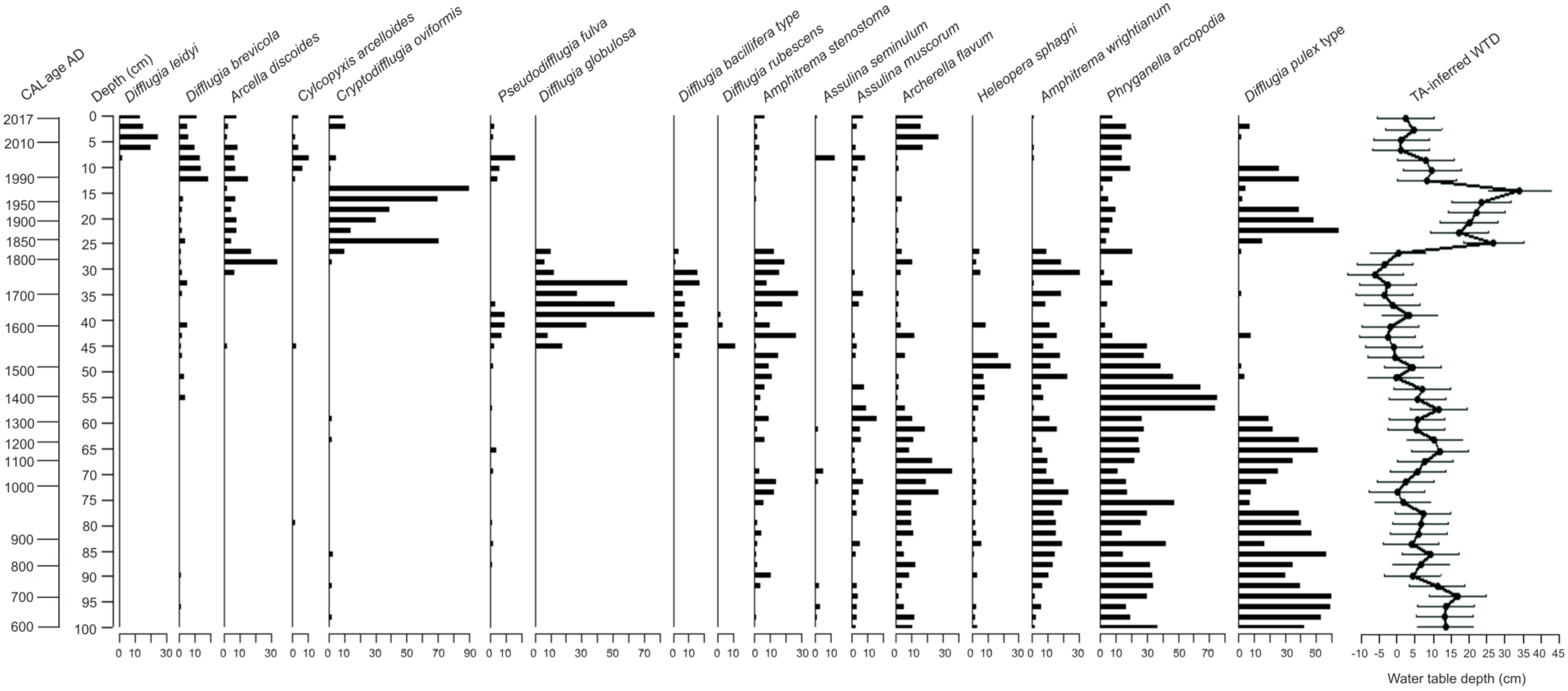
Date	plot	treatment	Sphpul	sphpap	sphmag	sphcusp	sphten	sphcap	Eriovag	rhynalba	erictetr	erioang	calluvulg	myrgale	andrpolif	drosrot	nartossif	vaccoxy	fungi	drosangl	liver	molincaer	cladospp	Bare
2010	1	combined	75	0	0	0	4	0	6	25	3	10	0	0	2	0	0	0	0	0	0	0	0	0
2010	2	control	63	5	3	0	2	0	0	52	15	15	35	6	1	4	1	0	1	0	2	0	0	0
2010	3	warmed	72	9	0	0	0	0	0	57	0	7	0	0	5	3	0	1	0	4	1	0	0	0
2010	4	drought	73	1	0	2	0	0	0	34	17	28	0	0	1	0	0	0	0	3	0	0	0	0
2010	5	warmed	48	26	0	4	0	0	0	67	0	15	0	0	6	10	0	1	0	4	2	0	0	0
2010	6	drought	72	3	0	1	0	0	0	38	5	23	0	0	3	3	3	0	0	4	0	0	0	0
2010	7	control	62	7	0	16	0	0	0	45	9	14	19	2	1	2	0	0	0	0	0	0	0	0
2010	8	combined	49	0	0	1	2	28	20	23	16	14	7	0	2	8	0	0	0	0	0	0	0	0
2010	9	drought	71	2	0	1	0	0	0	58	3	6	0	2	1	1	3	0	0	2	0	0	0	0
2010	10	warmed	17	54	0	4	0	0	0	59	0	18	1	0	6	4	0	0	0	3	0	0	0	0
2010	11	control	61	5	0	13	1	0	0	36	5	13	3	14	6	4	0	0	0	0	0	0	0	0
2010	12	combined	58	0	0	1	2	19	3	65	28	8	5	0	9	6	0	0	0	0	0	0	0	0
2011	1	combined	75	0	0	1	3	0	0	35	10	20	0	0	0	0	0	0	0	0	0	0	0	0
2011	2	control	68	4	0	1	5	0	0	21	12	26	29	94	7	2	0	0	0	0	16	0	0	0
2011	3	warmed	5	73	0	0	0	0	0	84	1	10	5	0	11	5	0	4	0	2	0	0	0	0
2011	4	drought	70	6	0	0	0	0	0	28	11	29	0	13	0	4	0	0	0	7	1	0	0	0
2011	5	warmed	74	0	0	0	0	0	0	73	0	31	0	0	10	12	0	2	0	3	0	0	0	0
2011	6	drought	15	43	8	1	0	0	0	72	17	26	0	3	1	7	0	0	0	0	7	0	0	0
2011	7	control	72	0	0	3	0	0	2	54	16	8	6	0	0	2	0	0	0	4	0	0	0	0
2011	8	combined	75	0	6	0	0	0	0	63	16	5	0	4	3	6	0	5	0	1	0	2	0	0
2011	9	drought	52	16	0	2	3	0	0	57	14	15	0	1	1	6	0	0	0	0	7	0	0	0

2011	10	warmed	75	0	0	0	0	0	0	95	0	8	0	0	5	13	0	0	0	3	0	0	0	0
2011	11	control	53	1	0	2	14	1	0	85	42	1	1	3	0	5	0	0	0	1	0	0	0	0
2011	12	combined	58	17	11	0	0	0	0	80	5	13	0	4	3	4	0	3	0	1	0	1	0	0
2012	1	combined	62	23	0	3	0	0	0	76	0	18	0	11	2	6	0	5	0	5	0	10	0	0
2012	2	control	48	0	1	3	2	0	0	55	33	5	1	2	2	4	0	0	1	0	0	0	0	0
2012	3	warmed	71	8	0	2	0	0	0	79	1	7	0	3	1	12	0	2	0	0	0	0	0	0
2012	4	drought	45	1	0	27	0	0	0	91	26	3	6	3	2	10	0	0	0	0	4	0	0	0
2012	5	warmed	67	19	0	2	0	0	0	90	5	6	0	6	9	8	0	0	0	2	0	0	0	0
2012	6	drought	14	3	1	54	2	0	0	24	33	5	12	6	1	11	0	0	0	0	3	0	0	0
2012	7	control	69	5	0	3	0	0	0	22	6	19	8	0	3	8	0	0	0	2	0	0	0	0
2012	8	combined	73	0	0	12	0	0	0	60	0	10	0	13	0	5	0	3	0	4	0	18	0	0
2012	9	drought	59	0	0	0	13	4	1	33	29	33	10	5	0	7	0	0	0	0	5	0	0	0
2012	10	warmed	74	1	0	0	0	0	0	31	18	28	0	0	0	4	0	0	0	0	0	0	0	0
2012	11	control	71	0	0	11	0	0	0	29	3	14	0	0	3	3	0	3	0	6	0	0	0	0
2012	12	combined	70	7	0	0	2	0	0	67	0	6	0	0	4	2	0	3	0	7	0	0	0	0
2013	1	combined	74	4	0	0	0	0	1	63	4	7	3	1	3	2	0	2	0	2	0	0	0	0
2013	2	control	69	0	0	4	0	2	2	73	16	21	28	1	4	2	0	2	0	3	1	0	0	0
2013	3	warmed	25	0	0	0	4	49	6	75	16	7	8	0	4	2	0	0	0	0	0	0	0	0
2013	4	drought	52	20	0	0	9	1	0	38	21	41	5	1	2	6	0	0	0	0	0	0	0	0
2013	5	warmed	40	0	0	1	4	39	3	60	28	5	6	0	0	2	0	0	0	0	1	0	0	0
2013	6	drought	35	35	0	0	1	0	1	36	22	31	7	0	0	3	0	0	0	0	7	0	0	0
2013	7	control	69	2	2	1	2	5	0	40	9	24	37	12	4	0	0	1	0	0	10	0	0	0
2013	8	combined	75	4	0	2	0	0	0	42	6	15	0	0	8	1	0	1	0	7	0	0	0	0
2013	9	drought	30	33	0	0	1	0	0	19	23	26	3	0	0	2	0	0	0	0	11	0	0	0
2013	10	warmed	69	1	0	2	0	14	0	28	20	4	0	0	2	3	0	0	0	0	0	0	4	0
2013	11	control	70	1	4	0	7	1	0	33	20	16	13	18	0	2	0	0	0	0	1	0	0	0
2013	12	combined	72	1	0	5	0	0	0	118	0	29	0	0	7	3	0	3	0	0	0	0	0	0
2014	1	combined	72	3	2	1	2	0	0	33	13	10	32	7	3	3	0	4	0	0	0	0	0	0

2014	2	control	70	1	2	2	0	0	0	55	18	25	4	0	2	6	0	0	0	0	0	0	0	0
2014	3	warmed	70	0	0	4	5	6	0	23	14	18	31	4	4	0	0	1	0	2	0	0	0	0
2014	4	drought	75	7	0	2	0	0	0	94	5	11	0	2	2	0	0	0	0	4	0	0	0	0
2014	5	warmed	43	16	0	16	0	1	0	89	34	7	3	3	6	7	0	0	0	0	0	0	0	0
2014	6	drought	54	19	0	0	0	3	0	4	44	17	5	0	0	2	0	1	0	0	0	0	0	0
2014	7	control	43	36	0	3	0	0	0	130	1	27	2	1	3	8	0	3	0	13	0	0	0	0
2014	8	combined	73	6	0	0	0	0	0	70	7	12	0	0	0	12	0	1	0	0	0	0	0	0
2014	9	drought	52	0	0	0	4	27	0	26	20	1	3	0	0	4	0	0	0	0	0	0	5	0
2014	10	warmed	68	0	0	0	0	18	0	50	6	21	2	0	4	1	0	0	0	0	0	0	0	0
2014	11	control	72	3	0	4	0	0	0	67	6	6	0	3	1	9	0	0	0	0	0	15	0	0
2014	12	combined	73	5	0	1	0	0	0	73	3	15	0	3	4	2	0	4	0	2	0	0	0	0
2015	1	combined	66	11	1	12	0	0	0	106	31	23	60	16	12	0	0	0	0	0	1	0	0	0
2015	2	control	55	2	1	1	18	0	0	105	29	30	10	2	4	3	0	0	0	1	1	0	0	0
2015	3	warmed	74	0	0	7	1	2	0	80	16	27	61	6	4	4	0	4	1	4	11	0	0	0
2015	4	drought	71	7	0	0	0	0	0	93	5	18	0	5	1	0	0	0	0	2	1	0	0	0
2015	5	warmed	40	22	0	15	3	0	0	186	52	7	8	3	4	20	0	5	0	0	8	0	0	0
2015	6	drought	42	21	0	0	0	2	3	3	39	29	15	3	1	4	0	0	0	0	35	0	0	0
2015	7	control	40	39	0	1	0	0	0	94	1	15	4	10	7	6	0	2	0	1	23	0	0	0
2015	8	combined	72	12	0	1	1	0	0	114	13	22	0	2	15	12	0	2	0	0	1	0	0	0
2015	9	drought	51	0	0	3	9	23	0	90	30	33	5	0	0	5	0	0	0	0	8	0	8	0
2015	10	warmed	68	0	0	0	7	9	0	122	21	14	1	0	7	6	0	0	0	0	0	0	0	0
2015	11	control	72	6	4	2	0	0	3	52	14	4	0	5	6	12	0	4	0	1	0	19	0	0
2015	12	combined	72	5	0	1	0	0	0	134	8	12	1	4	23	0	0	2	0	3	15	0	0	0
2016	1	combined	58	6	2	3	4	0	0	31	30	70	52	10	10	1	0	1	0	1	12	0	0	0
2016	2	control	61	5	0	1	9	1	0	111	19	20	7	8	0	8	0	0	0	0	4	0	0	0
2016	3	warmed	65	1	0	1	1	3	0	38	30	42	56	8	8	8	0	2	0	0	3	0	0	0
2016	4	drought	72	9	0	0	0	0	0	117	24	7	0	7	2	1	3	0	0	4	2	0	0	0
2016	5	warmed	31	34	1	6	4	0	0	101	53	71	8	3	2	15	0	0	0	0	7	0	0	0

2016	6	drought	57	19	0	0	0	1	2	2	46	48	12	2	0	4	0	0	0	0	3	0	0	0
2016	7	control	40	37	0	2	0	0	0	90	1	36	5	3	4	6	0	1	0	2	11	0	0	0
2016	8	combined	66	11	0	1	0	0	0	37	11	60	1	1	17	12	0	4	0	1	1	0	0	0
2016	9	drought	48	0	0	0	2	12	0	77	27	21	7	3	4	5	0	0	0	0	14	0	8	0
2016	10	warmed	72	0	0	0	5	0	0	240	20	19	7	0	10	4	0	0	0	0	5	0	0	0
2016	11	control	70	9	0	1	0	0	0	35	9	23	0	7	3	8	0	4	0	1	1	5	0	0
2016	12	combined	74	7	0	1	0	0	0	121	8	38	2	11	5	1	0	10	0	1	10	0	0	0
2017	1	combined	53	10	12	0	1	1	0	75	28	8	60	7	5	0	0	1	0	0	14	0	0	0
2017	2	control	52	6	1	2	4	5	0	99	19	20	2	4	0	9	0	0	0	0	5	0	0	0
2017	3	warmed	64	0	0	5	0	6	0	78	46	8	76	13	3	4	0	1	0	1	21	0	0	0
2017	4	drought	68	7	0	1	0	0	12	46	23	67	0	11	5	3	7	3	0	5	8	0	0	0
2017	5	warmed	33	30	0	4	6	1	0	125	43	32	25	8	3	8	0	0	0	0	20	0	0	0
2017	6	drought	28	24	0	0	0	1	0	5	51	58	20	1	0	9	0	0	0	0	21	0	0	0
2017	7	control	29	33	0	1	0	0	0	55	7	19	3	5	2	5	0	1	0	3	14	0	0	0
2017	8	combined	39	18	0	0	2	16	6	166	20	25	10	0	16	7	0	0	0	1	17	0	0	0
2017	9	drought	51	0	0	0	1	17	0	117	28	11	9	0	2	2	0	0	0	0	17	0	10	0
2017	10	warmed	65	1	0	3	1	1	0	215	23	5	3	1	6	9	0	0	0	0	10	0	0	0
2017	11	control	69	5	0	1	0	0	0	45	13	8	0	4	5	10	0	5	0	3	0	6	0	0
2017	12	combined	65	10	0	1	0	0	0	70	21	23	1	9	11	2	0	5	0	1	0	0	0	0
2018	1	combined	55	10	2	6	0	0	0	45	24	4	43	3	3	3	0	1	0	0	9	0	0	0
2018	2	control	67	5	0	1	1	0	0	72	13	5	5	4	0	7	0	0	0	0	5	0	0	0
2018	3	warmed	61	1	0	0	0	5	0	30	30	1	48	4	1	2	0	0	0	0	16	0	0	0
2018	4	drought	70	12	0	0	0	1	0	24	10	4	0	3	1	1	3	2	0	2	1	0	0	0
2018	5	warmed	52	13	0	0	3	0	0	65	29	41	14	4	3	5	0	0	0	0	0	0	0	0
2018	6	drought	50	16	1	1	0	0	0	5	31	29	26	0	0	8	0	1	0	0	31	0	0	0
2018	7	control	32	40	0	1	0	0	0	47	5	19	5	9	1	6	0	0	0	4	20	0	0	0
2018	8	combined	40	20	0	0	0	0	0	86	6	13	2	0	9	3	4	0	4	0	9	0	0	0
2018	9	drought	41	0	0	0	5	3	0	131	28	12	3	5	1	13	0	0	0	0	20	0	3	0

2018	10	warmed	63	0	0	2	1	6	0	158	32	0	7	9	14	8	0	0	0	0	9	0	0	0
2018	11	control	70	7	0	0	1	0	0	48	9	9	0	4	3	4	0	1	0	3	0	9	0	0
2018	12	combined	60	12	0	0	0	0	0	41	20	16	1	19	11	6	0	11	0	1	16	0	0	0
2019	1	combined	57	9	6	5	0	0	0	70	28	6	63	0	5	8	0	0	0	1	11	0	0	0
2019	2	control	53	8	1	1	10	0	2	105	29	8	6	1	2	12	0	0	0	0	8	0	0	1
2019	3	warmed	55	1	0	3	6	3	0	50	11	8	55	8	7	3	0	3	0	1	14	0	0	0
2019	4	drought	62	9	0	0	0	8	0	57	18	12	1	0	9	6	3	1	0	10	5	0	0	0
2019	5	warmed	25	29	0	6	6	0	0	76	38	21	30	0	5	10	0	0	0	0	16	0	0	0
2019	6	drought	28	8	1	0	1	1	0	19	41	35	14	10	3	7	0	1	0	0	53	0	0	0
2019	7	control	28	42	0	3	0	0	1	83	7	18	4	20	5	2	0	7	0	8	4	0	0	4
2019	8	combined	51	20	1	4	0	0	1	125	16	16	7	0	9	2	0	3	0	1	3	0	0	1
2019	9	drought	54	0	0	0	0	6	0	80	33	9	6	3	1	4	0	0	0	2	9	0	0	0
2019	10	warmed	65	0	0	0	0	0	17	115	40	2	10	10	19	1	0	0	0	0	0	0	0	0
2019	11	control	75	0	0	1	0	0	0	50	18	12	0	3	2	9	0	4	0	4	0	10	0	0
2019	12	combined	64	6	0	0	0	0	0	87	21	18	6	10	12	2	0	6	0	1	6	0	0	0
2020	1	combined	58	4	4	5	2	0	0	21	19	8	30	0	6	2	0	0	0	1	11	0	0	0
2020	2	control	58	12	1	1	4	0	0	69	26	7	4	1	1	9	0	0	1	1	2	0	0	0
2020	3	warmed	52	0	0	6	14	1	0	41	16	12	46	4	3	7	0	0	0	1	4	0	0	0
2020	4	drought	57	13	0	0	0	4	0	31	11	14	4	1	4	8	2	1	0	1	6	0	0	0
2020	5	warmed	43	27	0	2	5	1	0	95	35	25	15	0	3	6	0	0	0	0	2	0	0	0
2020	6	drought	42	7	0	1	0	0	0	32	17	17	7	7	1	3	0	0	0	0	23	0	0	0
2020	7	control	21	45	0	8	0	0	1	58	8	11	7	15	8	2	0	2	0	2	0	0	0	0
2020	8	combined	48	27	0	3	1	0	1	94	15	14	7	0	11	3	0	3	0	0	0	0	0	0
2020	9	drought	56	0	0	1	5	7	0	51	40	13	4	4	6	5	0	1	0	0	11	0	1	0
2020	10	warmed	66	0	0	1	0	0	30	60	44	0	8	9	15	1	0	0	0	0	1	0	0	0
2020	11	control	61	4	0	2	0	0	0	48	12	10	0	4	5	7	0	11	0	0	0	6	0	9
2020	12	combined	68	6	0	1	0	0	0	53	21	9	2	8	13	2	0	12	0	1	0	0	0	3



Supplementary Figure 1.7. Testate amoebae stratigraphic diagram for BO17, as well as the testate amoebae inferred water table depth (WTD) reconstruction generated using the pan-European training set developed by Amesbury *et al.* (2016). The code used to generate the reconstructed changes in WTD is in the supplementary materials of Amesbury *et al.* (2016). Only species with cumulative abundance greater than 5 % were included in the figure although these data were included in all other analyses. Age in cal CE is given as the median age probability (MAP)

Supplementary Table 1.2. Testate amoebae relative abundance data throughout core BO17 are presented as raw counts. Species/taxonomic group codes follow Amesbury *et al.* (2016): AMC WRI: *Amphitrema wrightianum* type ARC ARE: *Arcella arenaria* type ARC DIS: *Arcella discoides* type ARC FLA: *Archerella flavum* ASS MUS: *Assulina muscorum* type ASS SEM: *Assulina seminulum* type BUL IND: *Bullinularia indica* CEN ACU: *Centropyxis aculeata* type COR TRI: *Corythion-Trinema* type CRY SAC: *Crypotodifflugia sacculus* type CRY OVI: *Cryptodifflugia oviformis* type CYC ARC: *Cyclopyxis arcelloides* type DIF ACU: *Difflugia acuminata* type DIF GRA: *Difflugia gramen* type DIF LEI: *Difflugia leidyi* DIF LUC: *Difflugia lucida* type DIF OBL: *Difflugia oblonga* type EUG CIL: *Euglypha ciliata* type HEL PET: *Heleopera petricola* type HEL ROS: *Heleopera rosea* HYA ELE: *Hyalosphenia elegans* HYA PAP: *Hyalosphenia papilio* HYA SUB: *Hyalosphenia subflava* NEB FLA: *Nebela flabellulum* NEB MIL: *Longinebela* (*Nebela) militaris* type NEB PEN: *Gibbocarina* (*Nebela) penardiana* type NEB TIN: *Nebela tincta* type PSY GRI: *Physochila griseola* type PLA SPI: *Placocista spinosa* type SPHENO: *Sphenoderia* type TRA DEN: *Tracheleuglypha dentata* type TRI ARC: *Trigonopyxis arcula* type

Depth	AMC WRI	ARC ARE	ARC DIS	ARC FLA	ASS MUS	ASS SEM	BUL IND	CEN ACU	COR TRI	CRY SAC	CRY OVI	CYC ARC	DIF ACU	DIF GRA	DIF LEI	DIF LUC	DIF OBL	EUG CIL	HEL PET	HEL ROS	HYA ELE	HYA PAP	HYA SUB	NEB FLA	NEB MIL	NEB PEN	NEB TIN	PSY GRI	PLA SPI	SPHENO	TRA DEN	TRI ARC
2	7.5	0.0	8.0	17.2	7.5	1.7	0.0	0.0	1.1	4.6	9.2	12.1	0.0	10.9	13.2	0.6	0.6	2.3	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.6	0.0	0.0
4	1.7	0.0	2.5	15.7	3.3	0.8	0.0	0.8	0.0	7.4	10.7	16.5	0.0	5.0	15.7	2.5	0.0	8.3	0.8	0.0	1.7	0.0	0.0	1.7	0.0	0.0	0.0	4.1	0.8	0.0	0.0	0.0
6	1.9	0.0	1.9	27.2	1.0	0.0	0.0	0.0	0.0	1.9	0.0	22.3	0.0	5.8	25.2	1.9	0.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8	0.0	0.0	0.0	0.0	0.0
8	4.0	0.0	9.0	17.0	3.0	1.0	0.0	0.0	0.0	0.0	0.0	18.0	0.0	10.0	20.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	10.0	0.0	4.0	0.0	0.0	0.0
10	3.0	0.0	6.9	1.0	8.9	12.9	0.0	0.0	1.0	0.0	5.0	24.8	0.0	12.9	2.0	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0
12	1.7	0.0	7.6	1.7	4.2	0.8	0.0	0.0	0.0	26.3	1.7	26.3	0.0	13.6	0.0	5.9	0.0	2.5	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	1.7	1.7	0.8	0.0	0.0	0.0
14	1.0	0.0	15.7	0.0	2.9	0.0	0.0	0.0	0.0	39.2	0.0	9.8	0.0	18.6	0.0	4.9	0.0	2.9	0.0	1.0	0.0	0.0	0.0	2.9	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0
16	0.0	0.0	2.0	0.0	0.3	0.0	0.0	0.0	0.0	4.8	90.4	1.7	0.0	0.6	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	1.2	0.0	7.1	3.6	2.4	1.2	0.0	0.0	0.0	3.0	69.6	5.4	0.0	2.4	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	0.0	0.0	4.9	1.0	2.0	0.0	0.0	0.0	0.0	39.2	39.2	10.8	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
22	0.0	0.0	8.3	0.0	1.9	0.0	0.0	0.0	0.0	48.1	30.6	8.3	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
24	0.0	0.0	8.1	1.8	0.9	0.0	0.0	0.0	0.0	64.9	14.4	7.2	0.0	1.8	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
26	0.0	0.0	4.6	0.8	0.0	0.0	0.0	0.0	0.0	15.4	70.8	3.8	0.0	3.8	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	22.0	0.0	17.4	3.7	0.0	0.0	0.0	0.9	0.0	1.8	10.1	32.1	0.0	0.9	0.0	0.9	3.7	1.8	4.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

30	38.3	0.0	34.6	10.3	0.0	0.0	0.0	0.9	0.0	0.0	1.9	6.5	0.0	0.9	0.0	0.0	1.9	0.0	2.8	0.9	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
32	46.3	0.9	6.5	2.8	1.9	0.0	0.0	0.0	0.0	0.0	0.0	14.8	2.8	1.9	0.0	0.0	15.7	0.0	5.6	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
34	9.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	67.0	1.0	5.0	0.0	0.0	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
36	46.3	0.0	0.0	1.9	7.4	0.0	0.0	0.9	0.0	1.9	0.0	28.7	0.0	1.9	0.0	3.7	6.5	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
38	26.5	0.0	0.0	2.0	4.9	0.0	0.0	0.0	0.0	0.0	0.0	55.9	0.0	0.0	0.0	2.9	7.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
40	2.3	0.0	0.0	0.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	76.7	0.8	0.8	0.0	9.0	8.3	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
42	21.0	1.0	0.0	3.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	36.0	0.0	5.0	0.0	9.0	13.0	0.0	9.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
44	43.0	2.0	0.0	12.0	2.0	0.0	0.0	0.0	0.0	8.0	0.0	16.0	0.0	2.0	0.0	7.0	6.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46	8.5	4.7	1.9	0.0	3.8	0.0	0.0	0.9	0.0	4.7	0.9	50.9	0.9	0.9	0.0	4.7	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
48	33.1	4.2	0.0	5.9	2.5	0.0	0.8	0.0	0.0	0.0	1.7	28.8	0.0	1.7	0.0	0.0	4.2	0.0	16.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
50	20.7	3.6	0.0	0.0	0.0	0.9	0.9	0.0	0.0	1.8	3.6	39.6	0.0	0.0	0.0	1.8	0.9	0.0	25.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0
52	34.0	0.0	0.0	1.9	0.0	0.9	0.0	0.0	0.0	3.8	0.9	48.1	0.0	2.8	0.0	0.0	0.0	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
54	12.6	0.0	0.0	1.7	8.4	0.0	0.0	0.0	0.0	0.8	0.0	64.7	0.0	0.0	0.0	0.0	0.0	0.0	8.4	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	11.1	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.9	75.0	0.0	3.7	0.0	0.0	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
58	2.9	0.0	0.0	5.8	9.7	0.0	0.0	0.0	0.0	0.0	1.0	73.8	0.0	0.0	0.0	1.0	0.0	0.0	3.9	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
60	20.7	0.7	0.0	10.7	16.4	0.7	0.0	0.0	0.0	19.3	2.1	27.1	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
62	17.6	0.0	0.0	18.3	5.3	2.3	0.0	0.0	0.0	22.1	0.0	28.2	0.0	0.0	0.0	0.8	0.0	0.0	2.3	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
64	9.1	0.0	0.0	10.9	6.4	0.9	0.0	0.0	0.0	39.1	1.8	24.5	0.0	0.0	0.0	0.0	0.0	0.0	3.6	1.8	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
66	6.4	1.8	0.0	8.2	1.8	0.0	0.0	0.0	0.0	50.9	0.0	26.4	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
68	9.8	0.8	0.0	23.0	2.5	0.8	0.0	3.3	0.0	35.2	0.8	22.1	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
70	12.8	0.0	0.0	35.8	2.7	5.4	0.0	0.0	0.0	27.0	0.7	11.5	0.0	0.0	0.0	2.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
72	28.1	0.8	0.0	19.5	7.8	2.3	0.0	3.1	0.0	18.0	0.0	16.4	0.0	0.0	0.0	0.8	0.0	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
74	35.8	1.7	0.0	27.5	5.0	0.0	0.0	0.0	0.0	8.3	0.0	17.5	0.0	0.0	0.0	0.8	0.8	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
76	25.6	0.8	0.0	9.8	3.0	0.8	0.0	0.0	0.0	7.5	0.0	48.1	0.0	0.0	0.0	0.8	0.8	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
78	14.6	0.0	0.8	9.8	3.3	0.8	0.0	0.8	0.0	39.0	0.0	30.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
80	16.7	0.0	0.0	9.5	0.0	0.8	0.0	0.0	0.0	40.5	0.0	28.6	0.0	0.0	0.0	1.6	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
82	19.8	0.0	0.0	11.5	0.8	0.8	0.0	0.0	0.0	47.3	0.8	14.5	0.0	0.0	0.0	0.8	0.0	0.0	3.1	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
84	21.5	0.0	0.0	3.7	5.6	0.9	0.0	0.0	0.0	16.8	0.0	42.1	0.0	0.0	0.0	1.9	0.9	0.0	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

86	15.3	0.0	0.0	5.4	2.7	0.0	0.0	0.0	0.0	56.8	2.7	14.4	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
88	15.2	1.0	0.0	12.4	0.0	1.0	0.0	0.0	0.0	35.2	1.0	32.4	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
90	20.7	0.0	0.0	8.6	0.9	0.0	0.0	0.0	0.0	30.2	0.9	33.6	0.0	0.9	0.0	0.0	0.9	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
92	10.1	0.0	0.0	3.7	3.7	2.8	0.0	0.0	0.0	39.4	5.5	33.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
94	2.0	0.0	0.0	2.0	3.9	0.0	0.0	0.0	0.0	59.8	1.0	30.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
96	6.2	0.0	0.0	5.3	3.5	3.5	0.0	0.0	0.0	59.3	0.9	16.8	0.0	0.9	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
98	3.7	0.0	0.9	12.1	3.7	1.9	0.0	0.0	0.0	53.3	1.9	19.6	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
100	1.8	0.0	0.0	10.8	2.7	0.0	0.0	0.0	0.0	42.3	0.0	36.9	0.0	0.0	0.0	0.9	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9

Supplementary Table 1.3. Plant macrofossil data (Main peat components relative % abundance)

Depth	UOM %	*Sphagnum* (total)	*Sphagnum pulchrum*	*Sphagnum tenellum*	*Sphagnum cuspidatum*	*Sphagnum papillosum*	*Sphagnum medium*	*Sphagnum austinii*	*Sphagnum palustre*	*Sphagnum capillifolium*	*Sphagnum denticulatum*	*Ericaceous rootlets*	Monotoctyledon smooth radicells	Ericaceous bark undiff.	*Monocot stem undiff.*	*Calluna valugaris*	*Erica tetralix*	*Andromeda polifolia*	*Myrica gale*	*Vaccinium oxycoccus*	*Eriophorum vaginatum*	*Eriophorum angustifolia*	*Rhynchospora alba*	*Menyanthes trifoliata*	Kurzia sp.	*Odontoshisma sphagnii*	*Alucomnium palustre*	*Racomitrium lanuginosum*
1	4	62	15	36	1	7	4	0	0	0	0	24	1	0	0	0	3	0	0	0	0	0	2	0	1	3	0	0
2	5	63	39	21	1	1	0	0	0	0	0	9	0	0	0	0	4	0	0	0	0	0	4	0	10	5	0	0
3	4	56	47	9	0	0	0	0	0	0	0	18	1	0	0	0	3	0	0	0	0	0	10	0	4	4	0	0
4	5	41	32	8	0	1	0	0	0	0	0	18	3	0	0	0	8	0	0	0	0	0	17	0	2	5	0	0
5	2	59	49	3	0	5	1	0	0	1	0	27	4	0	0	0	0	0	0	0	0	0	5	0	0	2	0	0
6	9	40	26	11	0	2	0	0	0	0	0	28	2	0	0	0	1	0	1	0	0	0	14	0	3	2	0	0
7	4	32	21	10	0	1	0	0	0	0	0	28	10	0	0	1	2	0	2	0	0	0	16	0	1	5	0	0
8	3	41	30	11	0	0	0	0	0	0	0	32	7	0	0	0	2	0	2	0	0	0	8	0	3	1	0	0
9	2	44	22	22	0	0	0	0	0	0	0	39	6	0	0	0	0	0	1	0	0	0	4	0	0	4	0	0
10	4	34	6	23	0	4	0	0	0	0	0	45	10	0	0	0	2	0	2	0	0	0	4	0	0	0	0	0
11	2	40	20	17	0	2	0	0	0	1	0	43	9	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0
12	6	36	24	11	0	0	1	0	0	1	0	50	6	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0

13	5	39	12	12	0	0	8	0	0	7	0	46	8	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
14	2	53	26	14	0	0	11	0	0	2	0	33	9	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0
15	1	53	10	21	0	0	16	0	0	5	0	36	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	2	49	18	20	0	0	10	0	0	0	0	35	7	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
17	1	52	27	15	0	0	9	0	0	1	0	36	9	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
18	2	53	14	11	1	0	26	0	0	1	0	35	9	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
19	1	49	17	18	0	0	9	0	0	5	0	39	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	2	51	35	12	0	0	2	0	0	2	0	40	5	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
21	4	38	29	3	4	2	1	0	0	0	0	38	14	0	0	1	0	0	2	0	0	0	3	0	0	0	0	0
22	3	40	35	1	1	4	0	0	0	0	0	38	14	1	0	1	0	0	0	0	0	0	3	0	0	0	0	0
23	2	43	37	0	0	6	0	0	0	0	0	37	16	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
24	5	45	29	0	0	15	0	0	0	0	0	28	20	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
25	20	35	27	0	0	8	0	0	0	0	0	18	25	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
26	35	35	32	0	0	3	0	0	0	0	0	6	21	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
27	5	61	53	1	2	5	0	0	0	0	0	1	31	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
28	8	63	48	1	3	11	0	0	0	0	0	2	25	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
29	6	65	47	2	2	7	0	0	0	0	8	3	20	0	2	0	0	0	1	0	0	0	2	0	0	0	0	0
30	3	69	39	3	5	5	0	0	0	0	19	2	22	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0
31	19	61	35	1	5	4	0	0	0	0	17	0	17	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0
32	27	45	30	1	0	2	0	0	0	0	12	1	17	0	0	0	0	0	0	0	0	8	0	2	0	0	0	0
33	36	31	8	1	4	1	0	0	0	0	16	2	23	0	1	0	0	0	0	0	0	4	2	2	0	0	0	0
34	25	50	20	0	0	0	0	0	0	0	29	1	21	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
35	20	56	5	0	0	0	0	0	0	0	51	1	19	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0
36	34	49	0	0	1	0	0	0	0	0	47	0	15	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
37	37	43	0	0	0	0	0	0	0	0	42	0	17	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0
38	39	33	0	0	0	0	0	0	0	0	33	2	17	0	0	1	0	0	0	0	0	0	0	8	0	0	0	0
39	49	13	1	0	0	6	0	0	0	0	6	3	22	0	0	1	1	0	0	0	0	1	0	9	0	0	0	0
40	50	12	5	0	0	6	1	0	0	0	1	2	30	0	0	0	1	0	0	0	0	3	1	1	0	0	0	0

41	41	21	6	0	0	14	0	0	0	0	0	4	31	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
42	50	24	6	0	0	18	0	0	0	0	0	4	19	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0
43	52	23	4	0	0	18	0	0	0	0	0	1	21	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0
44	43	22	5	0	0	16	0	0	0	0	0	4	28	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
45	30	33	4	1	0	24	0	0	0	0	4	4	24	0	0	0	2	0	0	0	0	0	1	6	0	0	0	0
46	37	15	2	0	0	13	0	0	0	0	1	12	35	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
47	26	38	5	0	0	30	3	0	0	0	0	6	26	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
48	33	20	4	0	0	16	1	0	0	0	0	11	31	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
49	33	15	2	0	0	12	0	0	0	0	0	16	33	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
50	35	6	1	0	0	5	0	0	0	0	0	22	32	0	0	0	1	0	0	0	0	0	0	4	0	0	0	0
51	35	1	0	0	0	1	0	0	0	0	0	26	35	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0
52	33	1	0	0	0	1	0	0	0	0	0	32	31	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
53	33	1	0	0	0	1	0	0	0	0	0	32	30	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0
54	35	4	0	0	0	1	0	0	0	0	0	27	35	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
55	33	3	0	0	0	0	0	2	0	0	1	25	36	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0
56	41	0	0	0	0	0	0	0	0	0	0	11	44	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0
57	17	0	0	0	0	0	0	1	0	0	0	27	44	0	0	0	1	1	0	0	0	0	0	0	0	0	0	9
58	35	3	0	0	0	0	0	2	0	0	0	23	37	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
59	26	27	1	0	0	0	0	26	0	0	0	24	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	30	21	6	0	0	0	0	15	0	0	0	25	23	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
61	30	15	14	0	0	1	0	0	0	0	0	28	25	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
62	30	19	12	0	0	1	0	7	0	0	0	28	21	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
63	24	20	2	0	0	0	0	18	0	0	0	22	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	29	26	15	0	0	1	0	9	0	0	0	25	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	31	24	4	0	0	1	0	19	0	0	0	28	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	29	23	3	1	0	1	0	18	0	0	0	26	20	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
67	23	31	8	0	0	14	0	8	0	0	0	21	24	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
68	25	35	7	0	0	0	0	28	0	0	0	19	19	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0

69	14	42	10	1	0	4	0	26	0	0	1	17	25	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
70	8	48	8	3	0	1	0	36	0	0	0	22	19	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
71	11	43	25	1	0	0	0	17	0	0	0	21	22	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
72	13	43	21	1	0	3	0	18	0	0	0	19	24	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
73	33	30	16	0	0	4	0	10	0	0	0	21	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
74	11	40	10	0	0	2	0	28	0	0	0	20	22	0	0	0	0	0	0	0	0	0	5	2	0	0	0	0
75	12	40	0	0	0	1	0	39	0	0	1	19	25	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0
76	26	27	0	0	0	3	0	23	0	0	0	25	21	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
77	16	32	5	0	0	6	0	21	0	0	0	32	18	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
78	29	26	6	0	0	12	0	8	0	0	0	22	22	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
79	17	30	5	0	0	4	0	22	0	0	0	21	29	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
80	28	29	3	0	0	9	0	16	0	0	0	13	29	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
81	12	35	0	0	0	1	0	33	0	0	0	18	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
82	27	28	1	0	0	18	0	9	0	0	0	18	25	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
83	11	36	5	0	0	11	0	20	0	0	0	24	28	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
84	16	34	9	0	0	14	0	11	0	0	0	19	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
85	34	14	7	0	0	2	0	5	0	0	0	19	30	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
86	30	14	3	0	0	4	0	6	0	0	0	21	33	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
87	30	10	6	0	0	4	0	0	0	0	0	21	36	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
88	16	7	3	0	0	3	0	0	0	0	0	37	37	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0
89	20	5	1	0	0	2	0	1	0	0	0	31	36	0	0	0	0	0	0	0	0	2	2	3	0	0	0	0
90	27	6	1	0	0	5	0	0	0	0	0	25	39	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
91	30	3	1	0	0	0	0	2	0	0	0	25	41	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
92	26	3	1	0	0	2	0	0	0	0	0	20	50	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
93	32	4	2	0	0	2	0	0	0	0	0	13	48	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
94	26	23	1	0	0	1	0	8	12	0	1	23	24	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0
95	34	20	1	0	0	6	0	14	0	0	0	23	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	28	33	1	0	0	2	0	30	0	0	0	20	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

97	18	39	1	0	0	1	0	37	0	0	0	24	17	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0
98	16	38	3	0	0	2	0	31	0	0	1	26	19	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
99	10	36	11	0	0	1	0	25	0	0	0	36	17	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
100	13	37	17	0	0	0	0	20	0	0	0	37	12	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary Table 1.4. Plant macrofossil data (Macrocharcoal, seeds and other ecofacts). Samples are presented as count data (number counted per sample).

Depth (cm)	***Sphagnum* operculum (n)**	***Sphagnum* sporangia (n)**	***Erica tetralix* seeds (n)**	***Calluna vulgaris* seeds (n)**	***Andromeda polifolia* seeds (n)**	***Eriophorum angustifolium* seeds (n)**	***Rhynchospora alba* seed (n)**	***Myrica gale* bud scale (n)**	***Menyanthes trifoliata* seed (n)**	***Betula* sp. Seed (n)**	***Narthecium ossifragum* seeds (n)**	**Fern sporangia (n)**	***Drosera intermedia* seeds (n)**	***Drosera rotundifolia/anglica* seeds (n)**	**Macrocharcoal (n/1 cm^3)**
1	0	0	9	7	0	0	3	0	0	0	0	0	0	2	24
2	0	0	3	0	0	0	2	0	0	0	0	0	0	1	0
3	0	0	7	1	0	0	3	0	0	0	0	0	0	2	2
4	0	0	4	3	0	0	1	0	0	1	0	0	0	2	2
5	0	0	8	3	0	0	3	0	0	0	0	0	0	1	4
6	0	0	2	0	0	0	2	0	0	0	0	0	0	1	6
7	2	0	0	3	0	0	1	0	0	0	0	0	0	3	12
8	0	0	3	0	0	0	0	0	0	0	0	0	0	0	10
9	1	1	1	9	0	0	2	0	0	0	0	0	0	2	7

10	0	0	6	6	0	0	1	0	0	0	0	0	0	1	5
11	0	1	8	6	0	0	5	0	0	0	0	0	0	5	42
12	2	0	24	14	0	0	9	0	0	0	0	0	0	8	390
13	1	2	20	2	0	0	16	0	0	0	0	0	0	3	158
14	3	3	16	2	0	0	5	0	0	0	0	0	0	4	52
15	0	1	27	6	0	0	1	0	0	0	0	0	0	2	33
16	4	1	31	6	0	0	0	0	0	0	0	0	0	4	5
17	0	2	21	18	0	0	1	0	0	0	0	0	0	2	15
18	0	0	5	2	0	0	0	0	0	0	0	0	0	0	3
19	0	0	9	5	0	0	1	0	0	0	0	0	0	1	23
20	0	0	16	7	0	0	0	0	0	0	0	0	0	1	9
21	0	0	5	26	0	0	3	0	0	0	0	1	0	1	165
22	0	1	6	6	0	0	4	0	0	0	0	0	0	9	50
23	2	0	2	5	0	0	4	0	0	0	0	0	0	4	10
24	7	4	6	0	0	0	3	0	0	0	0	0	0	2	9
25	10	18	7	1	0	0	2	0	0	0	0	0	0	1	101
26	27	48	5	3	0	0	2	0	0	0	0	1	0	1	18
27	9	8	1	0	0	0	0	0	0	0	0	1	0	0	5
28	11	6	1	0	0	0	0	1	0	0	0	0	0	0	1
29	2	0	0	3	0	0	1	0	0	0	0	3	0	0	6
30	0	0	2	0	0	0	1	1	0	0	0	0	0	0	2
31	0	1	1	2	0	0	0	1	0	0	0	4	1	0	0
32	1	0	6	3	0	0	3	1	0	0	0	1	0	1	23
33	0	0	13	6	0	0	4	0	0	0	0	4	2	2	2
34	0	0	13	2	0	0	1	0	0	0	0	0	0	0	1
35	0	0	0	1	0	1	1	0	0	0	0	4	0	0	0
36	0	0	9	0	0	0	1	0	0	0	0	2	1	0	0
37	0	0	8	4	0	0	3	0	0	0	0	7	0	0	0

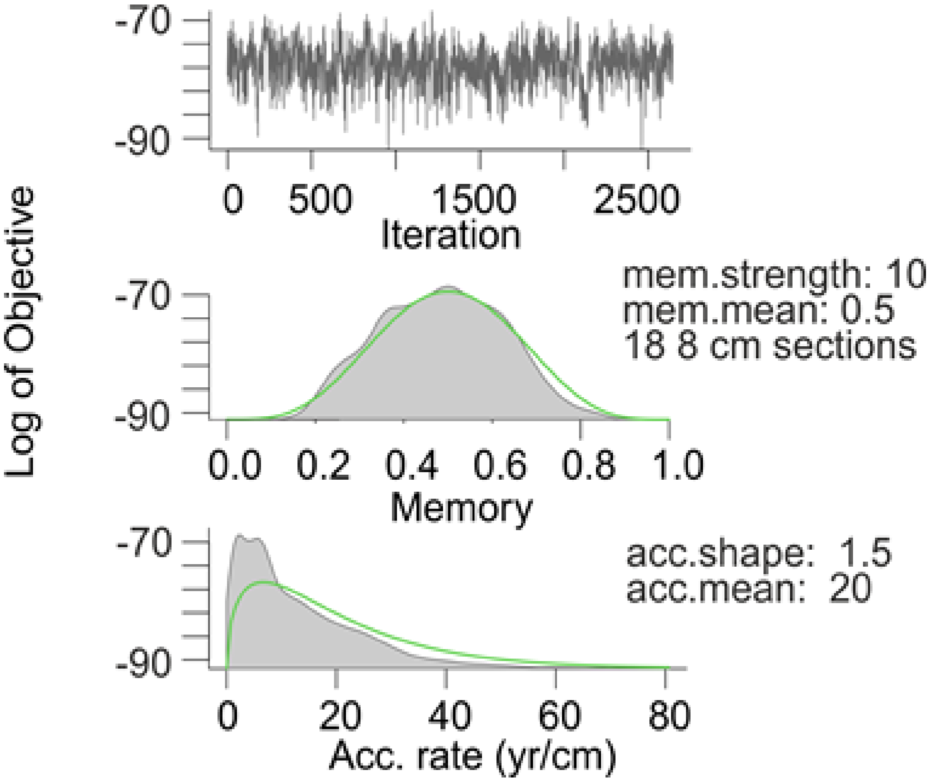
38	0	1	13	8	0	6	2	0	0	0	0	9	8	1	0
39	0	0	14	4	0	0	2	0	1	0	0	11	10	4	0
40	1	0	8	1	0	1	2	0	2	0	0	1	6	1	0
41	2	0	6	2	0	0	1	0	1	0	0	10	3	1	0
42	0	0	4	1	0	0	0	0	0	0	0	11	0	0	0
43	3	2	4	1	0	0	3	0	0	0	0	9	0	1	0
44	0	0	12	2	0	0	1	0	0	0	0	12	0	2	0
45	2	0	20	3	0	0	0	0	1	0	0	17	3	1	0
46	0	0	5	0	0	0	1	0	0	0	0	11	0	3	0
47	1	0	9	3	1	0	1	0	0	0	0	11	1	0	0
48	0	0	17	2	0	0	2	0	0	0	0	8	0	4	0
49	0	0	26	0	0	1	1	1	0	0	0	9	0	0	0
50	0	0	20	1	0	0	4	0	0	0	0	6	0	2	2
51	1	0	46	0	0	0	1	0	0	0	0	10	0	13	0
52	0	0	37	0	0	0	2	0	0	0	0	8	0	4	20
53	0	0	64	0	0	0	1	0	0	0	0	3	0	1	4
54	0	0	53	0	0	0	3	0	0	0	2	4	0	3	38
55	0	0	42	0	0	0	4	0	0	0	2	0	0	1	46
56	0	0	36	0	0	0	0	0	0	0	0	1	0	3	77
57	0	0	26	0	0	0	0	0	0	0	0	1	0	6	37
58	0	0	40	0	0	1	2	0	0	0	4	6	1	3	1
59	1	0	31	1	0	0	2	0	0	0	1	5	0	0	9
60	0	0	22	4	0	0	0	0	0	0	1	2	0	1	2
61	0	0	14	1	0	0	9	0	0	0	0	3	0	1	34
62	0	0	13	2	0	0	1	0	0	1	0	2	0	1	10
63	0	0	19	3	0	0	1	1	0	0	0	2	0	2	10
64	0	0	7	2	0	0	0	0	0	0	0	0	0	1	4
65	0	0	5	7	0	0	0	0	0	0	0	5	0	4	3

66	0	0	4	5	0	0	1	0	0	0	0	2	0	4	4
67	1	0	2	5	0	1	4	0	0	0	0	2	0	0	3
68	0	0	2	4	0	0	1	0	0	0	0	0	0	0	0
69	0	0	3	5	0	0	0	0	1	0	0	2	0	1	1
70	0	0	3	3	0	0	2	0	0	0	0	0	0	2	5
71	1	0	5	2	0	0	0	0	0	0	0	0	0	0	8
72	0	0	5	4	0	0	1	0	0	0	0	9	0	3	7
73	0	0	4	11	0	0	1	0	0	0	0	11	0	6	12
74	1	0	9	7	0	2	0	0	0	0	0	7	0	1	27
75	0	0	7	2	0	0	1	0	0	0	1	7	0	2	10
76	0	0	9	1	0	0	8	0	0	0	0	4	0	0	14
77	0	0	3	2	0	0	0	0	0	0	0	5	0	2	7
78	0	0	13	1	0	0	3	0	0	0	0	6	0	1	7
79	1	0	3	0	0	0	0	0	0	0	0	9	0	7	20
80	0	0	14	0	0	0	4	0	0	0	0	0	0	1	12
81	0	0	13	1	0	0	0	0	0	0	0	2	0	2	7
82	0	0	11	1	0	1	1	0	0	0	0	1	0	2	1
83	0	0	12	0	1	0	0	0	0	0	1	2	0	5	6
84	0	0	14	0	0	0	0	0	0	0	0	5	0	1	22
85	1	0	21	3	0	0	3	0	0	0	0	10	0	0	3
86	0	0	17	0	0	0	5	0	0	0	1	16	0	2	20
87	0	0	9	0	0	3	2	0	0	0	0	13	0	3	15
88	0	0	34	3	0	4	3	0	0	0	0	11	0	5	16
89	0	0	28	2	0	3	4	0	0	0	0	8	0	6	15
90	0	0	36	2	0	0	10	0	0	0	0	6	0	3	44
91	0	0	10	1	0	0	6	0	0	0	1	7	0	2	32
92	0	0	16	0	0	0	0	0	0	0	1	0	0	0	62
93	0	0	14	2	0	0	2	0	0	0	0	0	0	0	52

94	0	0	17	4	0	0	1	0	0	0	1	0	0	0	21
95	2	1	23	3	0	1	0	0	0	0	0	2	0	0	11
96	0	0	6	3	0	0	0	0	0	0	0	1	0	0	4
97	1	1	11	1	0	0	0	0	0	0	0	0	0	3	8
98	0	0	11	4	1	0	0	0	0	0	1	1	0	0	1
99	0	0	9	1	0	0	0	0	0	0	0	7	0	2	3
	0	0	9	2	0	0	0	0	0	0	1	10	0	0	6

Supplementary Table 1.5. Radiocarbon data from core BO17.

Depth (CM)	Lab code	Material dated	^{14}C age	^{14}C error	Calibrated age range (years CE) 95.4%	Median age (Years CE)
29	D-AMS 034826	*Sphagnum* stems and leaves	94	26	1690-1922	1837
44	D-AMS 029938	*Sphagnum* stems and leaves	427	26	1426-1613	1455
50	D-AMS 034971	*Sphagnum* stems and leaves	379	24	1449-1630	1498
60	D-AMS 034827	*Sphagnum* stems and leaves	724	29	1230-1381	1281
70	D-AMS 034972	*Sphagnum* stems and leaves	1129	25	775-994	933
75	D-AMS 029939	*Sphagnum* stems and leaves	1016	31	979-1153	1022
80	D-AMS 034828	*Sphagnum* stems and leaves	1052	27	897-1032	1002
100	D-AMS 034973	Fine fraction of bulk peat	1514	27	400-638	569
135	D-AMS 029940	*Racomitrium lanuginosum* stems and leaves	1729	33	247-408	334



Supplementary Figure 1.8. Age-depth model performance graphs, showing (from top to bottom) the MCMC iterations, the prior (green) and posterior (grey) distributions for the accumulation rate α, and memory (ω).

References for appendix I

Amesbury, M.J., Swindles, G.T., Bobrov, A., Charman, D.J., Holden, J., Lamentowicz, M., Mallon, G., Mazei, Y., Mitchell, E.A., Payne, R.J., and Roland, T.P., (2016). Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. *Quaternary Science Reviews*, *152*, 132-151.

Andrews, (2021): LA Plant community responses to experimental.xlsx. figshare. Dataset. [Online source] <https://doi.org/10.6084/m9.figshare.15395199.v1>. [Accessed 16/12/2021].

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. and White, J.S.S., (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127-135.

Guillera-Arroita, G. and Lahoz-Monfort, J.J., (2012). Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Methods in Ecology and Evolution*, *3*(5), 860-869.

Levy, E. N., and Madden, E. A. (1933). The Point Method of Pasture Analysis. *New Zealand Journal of Agriculture 46*, 267-79.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

van den Brink, P.J., Den Besten, P.J., bij de Vaate, A. and ter Braak, C.J., (2009). Principal response curves technique for the analysis of multivariate biomonitoring time series. *Environmental monitoring and assessment*, *152*(1-4), 271.

Wang, Y., Naumann, U., Wright, S., Warton, D., Wang, M.Y. and Rcpp, I., (2021). Package 'mvabund'.

Wang, Y.I., Naumann, U., Wright, S.T., and Warton, D.I., (2012). mvabund–an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, *3*(3), 471-4

Warton, D.I., (2011). Regularized sandwich estimators for analysis of high-dimensional data using generalized estimating equations. *Biometrics*, *67*(1), 116-123.

Warton, D.I., Thibaut, L., and Wang, Y.A., (2017). The PIT-trap—A "model-free" bootstrap procedure for inference about regression models with discrete, multivariate responses. *PloS one*, *12*(7), p.e0181790.

Warton, D.I., Wright, S.T. and Wang, Y., (2012). Distance-based multivariate analyses confound location nd dispersion effects. *Methods in Ecology and Evolution*, *3*(1), 89-101.

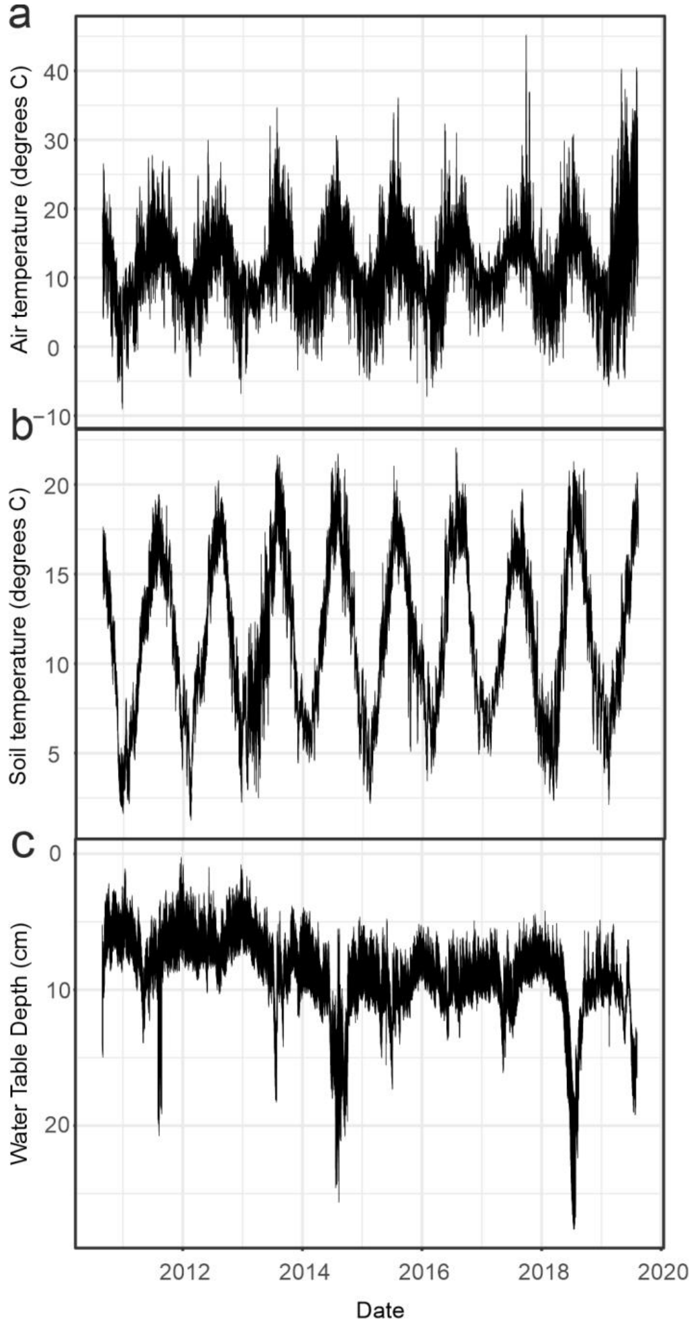
Appendix II: Chapter 4 appendices. Carbon cycle responses to experimental drought and warming in a Welsh ombrotrophic peatland in the context of late Holocene carbon accumulation

The data from this chapter have been published online and are available via: Andrews *et al.* (2021a): Carbon accumulation long-term and net ecosystem budgets Cors Fochno. figshare. Dataset. https://doi.org/10.6084/m9.figshare.17041364.v2. The c. 10 year-long 6-hourly time-series of air temperature, soil temperature and water table depth used in the modelling component of this chapter have been excluded from this appendix section but are available online as a separate file: Andrews *et al.* (2021b): CF plot WTD and temps.csv. figshare. Dataset. https://doi.org/10.6084/m9.figshare.17213561.v1

Supplementary Text 2.1. Taxa scores for Dupont Hydrological Index

The scores used to generate Dupont Hydrological Index values for each sampling interval follow those from Mauquoy *et al.* (2008), with the addition of *Sphagnum denticulatum* as a wet indicator.

Ericaceous rootlets: 8, *Calluna vulgaris:* 8, *Erica tetralix:* 8, Ericaceous wood. Undiff: 8; monocot. Undiff: 6; *Eriophorum vaginatum:* 6; *Sphagnum austinii:* 5; *Sphagnum* sect. *Acutifolia:* 4; *Sphagnum medium:* 4; *Sphagnum papillosum:* 3; *Andromeda polifolia:* 3; *Eriophorum angusticollis:* 2; *Sphagnum tenellum: 2; Sphagnum denticulatum:* 1; *Sphagnum* sect. *Cuspidata:* 1; *Sphagnum cuspidatum:* 1.



Supplementary Figure 2.1. Mean average a. air temperatures; b. soil temperatures (10 cm below ground level) and c. water table depth for all plots over the total measurement period.

Supplementary Table 2.1. Plant abundance data used to calculate Dupont Hydrological Index (DHI) scores (Dupont, 1986) and DHI scores for core BO17, generated using scores by Mauquoy *et al*. (2008) (Supplementary Text 2.1.)

Depth (cm)	Ericaceous rootlets	*Calluna vulgaris*	*Erica tetralix*	Ericacous wood undiff.	Monocot undiff.	*Eriophorum vaginatum*	*Sphagnum austinii*	*Sphagnum* section *Acutifolia*	*Sphagnum medium*	*Sphagnum papillosum*	*Andromeda polifolia*	*Eriophorum angustifolium*	*Rhynchospora alba*	*Sphagnum tenellum*	*Sphagnum* section *Cuspidata*	*Sphagnum cuspidatum*	*Sphagnum denticulatum*	**Dupont Hydrological index**
1	1.5	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.6	0.4	0.0	0.0	2.9
2	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.6	0.0	0.0	2.2
3	1.5	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.6	0.0	0.0	2.7
4	1.6	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.4	0.0	0.0	3.3
5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.1	0.1	0.6	0.0	0.0	3.3
6	2.4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.3	0.2	0.4	0.0	0.0	3.4
7	2.5	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.4	0.0	0.0	3.7
8	2.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.4	0.0	0.0	3.8
9	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.4	0.0	0.0	3.8
10	3.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.4	0.3	0.0	0.0	4.4
11	3.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.3	0.4	0.0	0.0	4.2
12	4.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	4.7
13	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	4.9
14	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.3	0.4	0.0	0.0	3.8
15	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.4	0.3	0.0	0.0	4.1
16	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.1	0.4	0.3	0.0	0.0	3.8
17	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.4	0.0	0.0	3.9

18	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.0	4.4
19	2.9	0.0	0.0	0.1	0.0	0.0	0.0	0.2	0.3	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	4.2
20	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	4.0
21	3.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.1	0.4	0.0	0.0	4.3
22	3.6	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.4	0.0	0.0	4.4
23	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.5	0.0	0.0	4.3
24	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.1	0.0	0.4	0.0	0.0	4.1
25	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.5	0.0	0.0	3.6
26	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.1	0.0	0.7	0.0	0.0	2.2
27	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.8	0.0	0.0	1.4
28	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.7	0.0	0.0	1.6
29	0.3	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.0	0.7	0.0	0.1	1.7
30	0.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.1	0.1	0.6	0.1	0.2	1.4
31	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.6	0.1	0.2	1.2
32	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.6	0.0	0.2	1.4
33	0.3	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.1	0.3	0.1	0.4	1.7
34	0.1	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.5	1.4
35	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.8	1.2
36	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.2
37	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.2
38	0.4	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.6
39	1.3	0.5	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.1	0.0	0.0	0.0	0.0	0.3	3.8
40	1.0	0.0	0.4	0.1	0.0	0.0	0.0	0.0	0.1	0.9	0.0	0.3	0.1	0.0	0.3	0.0	0.0	3.2
41	1.2	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	1.5	0.1	0.0	0.0	0.0	0.2	0.0	0.0	3.4
42	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.1	0.0	0.2	0.0	0.0	3.2
43	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.1	0.0	0.2	0.0	0.0	2.9
44	1.2	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.2	0.0	0.0	3.4
45	0.8	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.1	0.1	0.0	0.1	3.2

46	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.1
47	1.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.3	2.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	3.6
48	2.8	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	1.5	0.0	0.0	0.0	0.0	0.1	0.0	0.0	4.6
49	4.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.5
50	6.1	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.0
51	7.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	7.6
52	7.5	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.8
53	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	7.6
54	7.7	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.9
55	7.1	0.0	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.6
56	6.3	0.0	0.9	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	7.6
57	7.2	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	7.8
58	6.8	0.0	0.4	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7
59	3.7	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
60	4.3	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.0
61	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	5.5
62	4.7	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	5.8
63	4.2	0.0	0.1	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.4
64	4.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	5.2
65	4.3	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.3
66	4.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	6.1
67	3.2	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.2	0.0	0.0	5.0
68	2.7	0.2	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.5
69	2.3	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	4.9
70	2.4	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	5.2
71	2.6	0.0	0.1	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	4.4
72	2.4	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	4.4
73	3.3	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.0	4.9

74	2.5	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.1	0.0	0.0	5.1
75	2.5	0.0	0.0	0.0	0.0	0.1	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9
76	3.9	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
77	4.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.0
78	3.6	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.3
79	3.3	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.7
80	2.4	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.1
81	2.7	0.0	0.0	0.0	0.0	0.0	3.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9
82	3.1	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3
83	3.2	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.5
84	2.8	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.2	0.0	0.0	4.9
85	4.4	0.0	0.2	0.0	0.0	0.0	0.7	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	5.7
86	4.5	0.0	0.3	0.0	0.0	0.0	0.8	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.1
87	5.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.1	0.0	0.0	0.2	0.0	0.0	5.9
88	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.0	0.1	0.0	0.0	6.9
89	6.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.1	0.1	0.0	0.0	0.0	0.0	6.7
90	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9
91	7.1	0.0	0.1	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5
92	7.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.4
93	5.8	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.0	0.0	6.5
94	5.1	0.0	0.3	0.2	0.0	0.0	1.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.8
95	4.2	0.0	0.0	0.1	0.0	0.0	1.6	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
96	3.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0
97	2.9	0.0	0.1	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0
98	3.2	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.9
99	3.9	0.0	0.1	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	5.9
100	3.9	0.0	0.0	0.1	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	5.7

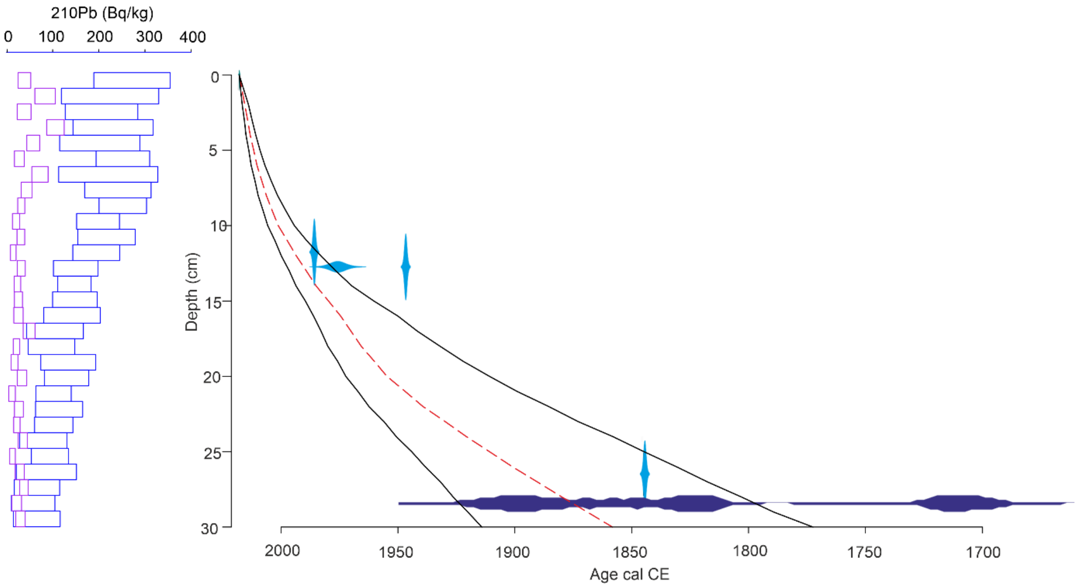
3

Supplementary Table 2.2. Radiogenic lead (^{210}Pb) activity data

labID	depth(cm)	density(g/cm^3)	210Pb(Bq/kg)	sd(210Pb)	226Ra(Bq/kg)	sd(226Ra)
BO1	1	0.02	220.83	84.887	43.17	13.79
BO2	2	0.022	272.12	82.859	38.88	13.8
BO3	3	0.019	224.38	105.671	83.62	22.31
BO4	4	0.021	205.9	78.6	38.1	14.9
BO5	5	0.021	231	86.948	106	19
BO6	6	0.027	202.12	86.913	57.88	13.79
BO7	7	0.035	252.15	58.056	27.85	10.51
BO8	8	0.021	220.62	107.57	72.38	17.6
BO9	9	0.032	241.26	72.066	43.74	11.64
BO10	10	0.031	252.02	51.431	31.98	7.67
BO11	11	0.057	198.37	46.345	20.63	7.82
BO12	12	0.048	216.95	62.437	31.05	8.4
BO13	13	0.06	194.29	50.639	14.71	6.06
BO14	14	0.046	149.91	48.229	32.09	8.66
BO15	15	0.076	147.28	36.318	23.72	7.07
BO16	16	0.048	148.15	48.232	25.85	8.64
BO17	17	0.038	142.02	61.169	25.98	10.12
BO18	18	0.045	105.12	61.703	48.88	12.72
BO19	19	0.056	97.42	50.495	21.58	7.16
BO20	20	0.047	133.82	59.548	17.18	7.35
BO21	21	0.048	130.31	47.941	33.69	10.13
BO22	22	0.064	101.96	38.346	12.04	7.11
BO23	23	0.05	114.1	51.125	26.9	9.5
BO24	24	0.06	102.46	41.438	22.54	6.85
BO25	25	0.04	79.76	51.049	35.24	9.9
BO26	26	0.06	94.2	40.24	13	6.1
BO27	27	0.04	86.39	65.276	28.61	9.75
BO28	28	0.032	66.1	49.152	37.9	9.17
BO29	29	0.036	57.79	47.067	22.21	10.39
BO30	30	0.036	65.73	50.694	30.28	10.4

Supplementary Table 2.3. Additional chronological data used in the generation of the age-depth model for core BO17. Char1986= a macrocharcoal chronohorizon that likely relates to a fire that affected the study site in 1986 CE. SCP1976= The SCP peak for 1976 CE (based upon ^{210}Pb dated horizons for north Wales and Central England by Rose and Appleby (2005). Tephra dates are based upon geochemical fingerprinting of cryptotephra horizons identified in the core stratigraphy. Ages labelled D-AMS are radiocarbon dates based upon organic plant macrofossil material from core BO17.

labID	Age (radiocarbon age BP)	Error (1σ)	depth (cm)
Char1986	-36	0.5	12
SCP1976	-26	3	13
Tephra1947	3	0.5	13
Tephra1845	105	0.5	27
D-AMS 034826	94	26	29
Tephra1510	440	0.5	38
D-AMS 029938	427	26	44
D-AMS 034971	379	24	50
D-AMS 034827	724	29	60
D-AMS 034972	1129	25	70
D-AMS 029939	1016	31	75
D-AMS 034828	1052	27	80
D-AMS 034973	1514	27	100
D-AMS 029940	1729	33	135



Supplementary Figure 2.2. ^{210}Pb results compared with other chronohorizons from the surface 30 cm of core BO17. The red dashed line is the median probability of the age-depth model generated using ^{210}Pb dates alone. the black lines indicate the 95% confidence intervals for the model derived using rplum (Aquino-López *et al.,* 2018; Blaauw *et al.,* 2021). The figure on the left shows changes in the supported (purple) and unsupported (blue) ^{210}Pb activity throughout the core. Light blue shapes are the calendar dates (Spheroidal carbonaceous particles, tephra and macrocharcoal dates). The dark blue bar at the bottom of the figure is the probability distribution function of a radiocarbon date at 29 cm.

Supplementary Table 2.4. Concentrations of pore-water dissolved organic carbon (DOC) measured from within each plot at 10 cm depth. The top row indicates the treatment type for each plot. C = Control, OTC = Warmed, D = Drought, OTCD = Combined warming and drought. Missing values are due to suspected contamination of the samples.

DOC (g l^{-1})	**OTCD**	**C**	**OTC**	**D**	**OTC**	**D**	**C**	**OTCD**	**D**	**OTC**	**C**	**OTCD**
	BO1	BO2	BO3	BO4	BO5	BO6	BO7	BO8	BO9	BO10	BO11	BO12
14/02/2018	0.0325	0.0128	0.0165	0.0156	0.0178	0.0162	0.0176	0.0338	0.0303	0.0150	0.0120	0.0305
29/05/2019	0.0382	0.0237	0.0213	0.0200	0.0204	0.0231	0.0159	0.0330	0.0239	0.0209	0.0262	0.0349
05/03/2019	0.0315	0.0202	0.0173	0.0170	0.0178	0.0218	0.0186	0.0297	0.0258	0.0188	0.0049	0.0339
21/11/2018	0.0414	0.0342	0.0281	0.0236	0.0290	0.0313	0.0266	0.0356	0.0320	0.0280	0.0309	0.0379
30/08/2018	0.0386	0.0566	0.0496	0.0523	0.0554	0.0441	0.0361	0.0450	0.0455	0.0521	0.0522	0.0402
25/07/2018	0.0182	0.0221	0.0087	0.0190	0.0120	0.0148	0.0118	0.0203	0.0228	0.0186	0.0190	0.0151
14/06/2018	0.0383	0.0335	0.0211	0.0229	0.0272	0.0304	0.0203	0.0333	0.0296	0.0253	0.0285	0.0359
03/05/2018	0.0206	0.0151	0.0155	0.0134	0.0171		0.0163	0.0283	0.0269	0.0180	0.0171	0.0215
23/12/2019	0.0269	0.0256	0.0112	0.0178	0.0270	0.0223	0.0224	0.0290	0.0301	0.0153	0.0161	0.0390
17/08/2020	0.0332	0.0238	0.0210	0.0233	0.0207	0.0112	0.0074	0.0257	0.0242	0.0218	0.0159	0.0111
19/08/2019	0.0458	0.0415	0.0395	0.0423	0.0312	0.0449	0.0251	0.0408	0.0529	0.0454	0.0403	0.0396
14/02/2020	0.0100	0.0298	0.0145	0.0129	0.0201	0.0196	0.0086	0.0096	0.0231	0.0127	0.0150	0.0141
09/08/2019	0.0446	0.0404	0.0384	0.0413	0.0301	0.0439	0.0242	0.0399	0.0520	0.0446	0.0394	0.0388
06/09/2019	0.0322	0.0440	0.0192	0.0315	0.0262	0.0288	0.0282	0.0343	0.0376	0.0307	0.0442	0.0434
13/09/2019	0.0269	0.0373	0.0342		0.0386	0.0366	0.0226	0.0372	0.0240	0.0126	0.0186	0.0453
16/08/2019	0.0357	0.0529	0.0473	0.0433	0.0179	0.0232	0.0343	0.0418	0.0508	0.0408	0.0517	0.0473
23/08/2019	0.0396	0.0491	0.0419	0.0337	0.0354	0.0452	0.0401	0.0319	0.0502	0.0434	0.0443	0.0444

Supplementary Table 2.5. Age-depth model peat accumulation rate, soil physical properties and carbon accumulation rate data for core BO17. Analyses were conducted using code in the supplementary materials of Belshe *et al*. (2019).

Depth (cm)	Minimum age (cal CE)	Maximum age (cal CE)	Median age (cal CE)	Mean age (cal CE)	Median sedimentation rate (cm y^{-1})	Mean sedimentation rate (cm y^{-1})	Dry bulk density (g cm^{3})	Percent Organic carbon	Organic carbon density (g cm^{3})	Mean carbon accumulation rate (g C m^{-2} y^{-1})	Median carbon accumulation rate (g C m^{-2} y^{-1})	Mean number of years / cm sampling interval
0	2018	2018	2018	2018	0.55	0.62	NA	NA	NA	167.01	148.99	1.91
1	2018	2014	2016	2016	0.52	0.57	0.08	31.84	0.03	153.41	140.08	2.01
2	2017	2011	2015	2015	0.55	0.62	0.06	28.84	0.02	110.65	99.13	1.90
3	2017	2007	2013	2013	0.55	0.61	0.05	39.35	0.02	115.40	105.02	1.90
4	2017	2003	2011	2011	0.48	0.53	0.05	39.91	0.02	98.51	89.73	2.19
5	2017	2000	2010	2009	0.40	0.44	0.04	43.06	0.02	72.83	66.34	2.61
6	2014	1999	2009	2008	0.32	0.35	0.04	41.23	0.02	57.61	52.59	3.32
7	2013	1999	2008	2007	0.33	0.37	0.05	41.41	0.02	76.20	68.16	3.22
8	2011	1998	2006	2006	0.27	0.30	0.06	43.21	0.02	70.97	63.82	3.94
9	2010	1998	2004	2004	0.22	0.24	0.07	42.87	0.03	70.97	64.48	4.87
10	2010	1996	2003	2003	0.17	0.19	0.07	49.00	0.03	64.29	58.03	6.20

11	1999	1991	1995	1995	0.15	0.17	0.08	42.75	0.03	55.59	50.00	7.10
12	1989	1985	1986	1986	0.13	0.15	0.07	43.30	0.03	45.05	39.44	8.11
13	1981	1974	1978	1978	0.13	0.15	0.07	45.03	0.03	47.59	41.02	8.25
14	1976	1963	1970	1970	0.11	0.13	0.06	42.30	0.03	33.13	28.75	9.50
15	1970	1952	1962	1961	0.11	0.13	0.05	42.96	0.02	27.66	23.51	9.90
16	1963	1941	1954	1953	0.11	0.13	0.07	43.08	0.03	39.34	33.12	9.78
17	1958	1928	1945	1944	0.11	0.13	0.06	42.50	0.02	33.29	27.94	9.75
18	1955	1914	1937	1935	0.11	0.13	0.07	42.00	0.03	37.47	31.50	10.25
19	1952	1899	1929	1926	0.10	0.12	0.09	43.70	0.04	47.57	40.86	10.62
20	1949	1884	1921	1918	0.10	0.11	0.11	43.70	0.05	53.28	45.92	11.20
21	1936	1881	1912	1910	0.10	0.11	0.07	42.91	0.03	35.68	30.65	11.27
22	1925	1879	1903	1902	0.10	0.11	0.10	44.02	0.04	48.47	41.59	11.25
23	1913	1877	1893	1894	0.10	0.11	0.10	46.17	0.04	50.09	42.71	11.45
24	1902	1874	1884	1886	0.10	0.11	0.08	44.27	0.03	39.75	33.96	11.37
25	1895	1869	1876	1878	0.10	0.11	0.07	43.69	0.03	32.19	27.76	11.53
26	1874	1857	1861	1863	0.10	0.11	0.07	43.16	0.03	35.54	30.58	11.60
27	1859	1844	1847	1848	0.09	0.11	0.06	42.68	0.03	27.06	23.73	11.87
28	1844	1823	1833	1834	0.09	0.10	0.05	41.90	0.02	19.89	17.76	12.40
29	1830	1800	1820	1819	0.08	0.09	0.03	40.89	0.01	12.95	11.51	13.37
30	1816	1777	1807	1804	0.08	0.09	0.04	43.34	0.02	16.44	14.39	14.08
31	1760	1728	1751	1749	0.08	0.09	0.06	43.33	0.03	23.83	20.84	14.34
32	1706	1676	1695	1694	0.08	0.09	0.07	43.26	0.03	27.21	24.06	14.50
33	1653	1623	1640	1640	0.08	0.09	0.07	43.41	0.03	28.07	24.26	14.56
34	1604	1570	1584	1585	0.08	0.09	0.06	44.94	0.03	25.13	22.22	14.36
35	1559	1512	1529	1531	0.08	0.09	0.05	43.71	0.02	19.17	17.01	14.40
36	1543	1511	1523	1524	0.08	0.09	0.06	43.79	0.03	22.31	19.85	14.45
37	1527	1511	1516	1517	0.08	0.09	0.06	43.57	0.02	21.28	18.99	14.54
38	1512	1509	1510	1510	0.08	0.09	0.06	41.99	0.03	23.65	21.09	14.32

39	1511	1494	1504	1504	0.08	0.09	0.07	44.51	0.03	26.49	23.54	14.69
40	1510	1478	1498	1497	0.08	0.09	0.07	46.07	0.03	28.62	25.38	14.86
41	1506	1475	1493	1492	0.08	0.08	0.06	45.73	0.03	24.74	22.35	14.97
42	1503	1471	1488	1488	0.07	0.08	0.06	45.54	0.03	21.19	19.37	15.16
43	1502	1464	1484	1483	0.07	0.08	0.06	45.95	0.03	22.21	20.37	15.20
44	1500	1454	1479	1479	0.07	0.08	0.08	46.55	0.04	28.13	25.79	15.98
45	1498	1444	1475	1474	0.07	0.08	0.08	48.21	0.04	29.39	26.74	16.54
46	1494	1441	1472	1471	0.07	0.07	0.07	47.46	0.03	23.23	21.36	16.77
47	1490	1438	1469	1468	0.07	0.07	0.07	47.38	0.03	22.60	20.82	17.08
48	1487	1434	1465	1465	0.07	0.07	0.08	48.49	0.04	26.42	24.43	17.20
49	1485	1430	1463	1462	0.07	0.07	0.06	48.80	0.03	21.49	19.77	17.83
50	1484	1425	1460	1459	0.06	0.07	0.08	47.73	0.04	25.93	24.15	18.91
51	1471	1407	1442	1441	0.06	0.06	0.07	49.27	0.04	22.64	21.42	19.31
52	1464	1382	1425	1424	0.06	0.06	0.09	49.71	0.04	26.67	25.42	19.39
53	1458	1350	1408	1407	0.06	0.06	0.09	50.78	0.05	29.03	27.86	19.45
54	1454	1316	1391	1390	0.06	0.06	0.11	50.89	0.06	34.96	33.70	19.56
55	1450	1282	1375	1372	0.06	0.06	0.11	51.02	0.05	33.46	32.08	19.64
56	1422	1275	1357	1354	0.06	0.06	0.09	50.63	0.05	29.59	28.60	19.64
57	1404	1267	1338	1336	0.06	0.06	0.10	49.50	0.05	30.23	29.35	19.40
58	1394	1256	1319	1318	0.06	0.06	0.12	49.05	0.06	36.51	34.69	19.62
59	1385	1242	1300	1300	0.06	0.07	0.12	48.32	0.06	38.33	36.19	19.19
60	1377	1223	1282	1282	0.06	0.07	0.11	49.20	0.05	35.10	32.71	19.05
61	1343	1188	1254	1254	0.06	0.07	0.10	49.04	0.05	32.27	30.04	18.57
62	1320	1147	1226	1226	0.07	0.07	0.09	49.38	0.05	32.75	30.17	18.15
63	1296	1098	1200	1198	0.07	0.07	0.08	47.98	0.04	28.40	26.46	17.91
64	1284	1043	1173	1170	0.07	0.07	0.07	48.83	0.03	23.99	22.71	18.17
65	1278	988	1147	1142	0.07	0.07	0.07	47.46	0.03	23.20	21.65	17.83
66	1243	981	1118	1115	0.07	0.07	0.07	47.58	0.03	22.80	21.53	18.01

67	1212	972	1088	1088	0.07	0.07	0.06	47.49	0.03	19.14	17.88	17.94
68	1189	962	1055	1061	0.07	0.07	0.06	47.74	0.03	19.39	18.27	17.85
69	1169	950	1025	1033	0.07	0.07	0.04	47.14	0.02	15.01	14.17	17.89
70	1151	927	992	1006	0.07	0.07	0.05	47.18	0.02	15.88	15.14	17.25
71	1136	923	987	999	0.07	0.07	0.05	46.99	0.02	18.02	17.28	17.14
72	1120	919	983	992	0.07	0.08	0.06	48.28	0.03	20.19	19.19	16.72
73	1112	915	979	986	0.07	0.08	0.05	47.96	0.02	18.63	17.73	16.57
74	1104	910	974	979	0.07	0.08	0.05	47.68	0.02	18.04	17.13	16.57
75	1096	902	970	972	0.07	0.08	0.07	49.09	0.03	25.17	23.73	16.60
76	1078	894	960	964	0.07	0.08	0.07	48.05	0.03	24.41	23.15	16.85
77	1060	882	950	956	0.07	0.07	0.07	48.27	0.03	24.11	23.21	17.04
78	1043	870	939	948	0.07	0.07	0.08	48.78	0.04	28.83	27.72	17.01
79	1028	856	927	939	0.07	0.07	0.07	48.83	0.04	25.62	24.66	17.38
80	1018	837	916	931	0.07	0.07	0.08	49.31	0.04	26.98	25.87	18.19
81	1000	826	903	914	0.07	0.07	0.06	49.12	0.03	19.07	18.42	18.35
82	991	807	891	897	0.07	0.07	0.08	48.96	0.04	26.32	25.48	18.61
83	985	773	878	880	0.07	0.07	0.10	49.11	0.05	34.47	33.41	18.91
84	979	744	865	862	0.07	0.07	0.11	46.80	0.05	35.41	34.25	18.68
85	974	708	851	845	0.07	0.07	0.08	49.14	0.04	27.80	27.14	18.70
86	951	698	833	827	0.07	0.07	0.09	49.24	0.04	28.17	27.41	18.94
87	932	687	812	809	0.07	0.07	0.10	48.45	0.05	31.53	30.71	18.84
88	921	670	791	791	0.07	0.07	0.09	42.49	0.04	25.49	24.92	18.88
89	908	648	772	774	0.07	0.07	0.08	50.49	0.04	28.76	28.15	18.60
90	900	625	754	756	0.07	0.07	0.09	48.12	0.05	30.98	30.13	18.68
91	878	619	737	739	0.07	0.07	0.09	48.25	0.05	30.38	29.85	18.91
92	857	610	719	722	0.07	0.07	0.09	49.93	0.05	30.30	29.95	18.81
93	842	601	701	706	0.07	0.07	0.11	49.55	0.05	36.43	35.73	18.76
94	829	590	684	689	0.07	0.07	0.11	48.98	0.06	37.43	36.51	19.09

95	817	571	665	673	0.07	0.07	0.09	48.96	0.04	29.65	29.07	18.97
96	775	565	651	656	0.07	0.07	0.10	48.08	0.05	32.90	32.32	18.84
97	735	558	635	639	0.07	0.07	0.10	48.69	0.05	31.26	31.09	18.96
98	698	551	619	622	0.07	0.07	0.07	47.41	0.03	21.77	21.82	19.08
99	667	543	602	604	0.07	0.07	0.08	49.08	0.04	27.73	27.35	19.10
100	645	524	586	587	0.07	0.07	0.07	50.31	0.04	24.34	23.78	19.65

Supplementary Table 2.6. Modelled annual carbon fluxes and net ecosystem carbon budgets for each experimental plot. Annual modelled rates of CH_4 emissions, gross primary productivity (GPP), net ecosystem respiration (NER), net ecosystem exchange (NEE) and dissolved organic carbon (DOC) flux. Estimates for 2010 and 2019 were not used in this study because these estimates were generated from environmental time-series data that did not cover the entire duration of these years. Treatments: 1 = Control, 2 = Warming, 3 = Drought, 4 = Combined warming and drought.

Year	**Treatment**	**Plot**	**Block**	**CH_4 (g CH_4 m^{-2} y^{-1})**	**CH_4 (g C m^{-2} y^{-1})**	**GPP (g CO2 m^{-2} y^{-1})**	**GPP (g C m^{-2} y^{-1})**	**NER (g CO_2 m^{-2} y^{-1})**	**NER (g C m^{-2} y^{-1})**	**NEE (g CO_2 m^{-2} y^{-1})**	**NEE (g C m^{-2} y^{-1})**	**DOC (g C m^{-2} y^{-1})**
2010	4	1	1	0.654	0.490	-48.5	-13.2	110.6	30.2	62.2	17.0	18.1
2010	4	8	2	1.376	1.032	-67.8	-18.5	68.7	18.7	0.9	0.2	18.7
2010	4	12	3	0.827	0.620	-73.9	-20.1	90.3	24.6	16.5	4.5	19.5
2010	1	2	1	1.306	0.980	-52.2	-14.2	47.6	13.0	-4.6	-1.3	19.1
2010	1	7	2	1.292	0.969	-55.0	-15.0	41.6	11.4	-13.4	-3.7	12.8
2010	1	11	3	1.401	1.051	-80.8	-22.0	49.6	13.5	-31.1	-8.5	16.2
2010	3	4	1	1.565	1.174	-46.5	-12.7	30.4	8.3	-16.0	-4.4	15.5
2010	3	6	2	1.225	0.919	-62.3	-17.0	80.8	22.0	18.5	5.1	16.5

2010	3	9	3	2.023	1.517	-86.5	-23.6	61.7	16.8	-24.8	-6.8	19.8
2010	2	3	1	1.366	1.024	-54.4	-14.8	52.4	14.3	-2.0	-0.6	15.1
2010	2	5	2	1.147	0.860	-94.6	-25.8	104.8	28.6	10.2	2.8	15.1
2010	2	10	3	0.868	0.651	-70.8	-19.3	57.4	15.6	-13.4	-3.6	15.8
2011	4	1	1	2.680	2.010	-321.8	-87.8	369.0	100.6	47.3	12.9	22.5
2011	4	8	2	4.906	3.680	-351.9	-96.0	270.5	73.8	-81.4	-22.2	23.2
2011	4	12	3	2.873	2.155	-425.7	-116.1	356.3	97.2	-69.4	-18.9	24.2
2011	1	2	1	4.806	3.604	-294.4	-80.3	148.5	40.5	-146.0	-39.8	23.8
2011	1	7	2	4.536	3.402	-335.1	-91.4	140.3	38.3	-194.8	-53.1	15.9
2011	1	11	3	4.334	3.251	-464.2	-126.6	148.4	40.5	-315.8	-86.1	20.1
2011	3	4	1	6.166	4.624	-283.1	-77.2	122.4	33.4	-160.7	-43.8	19.3
2011	3	6	2	4.432	3.324	-371.3	-101.3	250.0	68.2	-121.3	-33.1	20.5
2011	3	9	3	6.382	4.787	-451.7	-123.2	207.0	56.5	-244.8	-66.8	24.6
2011	2	3	1	5.281	3.961	-334.1	-91.1	195.5	53.3	-138.6	-37.8	18.8
2011	2	5	2	3.801	2.850	-487.0	-132.8	380.5	103.8	-106.4	-29.0	18.8
2011	2	10	3	3.042	2.281	-377.6	-103.0	113.8	31.0	-263.8	-71.9	19.6
2012	4	1	1	2.565	1.924	-326.0	-88.9	322.3	87.9	-3.7	-1.0	35.9
2012	4	8	2	3.863	2.897	-319.3	-87.1	226.1	61.7	-93.2	-25.4	37.0
2012	4	12	3	4.405	3.304	-461.7	-125.9	330.6	90.2	-131.1	-35.8	38.6
2012	1	2	1	4.244	3.183	-276.3	-75.4	135.6	37.0	-140.7	-38.4	37.9
2012	1	7	2	4.459	3.344	-348.8	-95.1	128.3	35.0	-220.5	-60.1	25.3
2012	1	11	3	5.404	4.053	-593.1	-161.8	173.3	47.3	-419.9	-114.5	32.1
2012	3	4	1	6.679	5.009	-311.8	-85.0	101.5	27.7	-210.3	-57.4	30.8
2012	3	6	2	4.374	3.280	-382.0	-104.2	225.3	61.4	-156.8	-42.8	32.8
2012	3	9	3	6.721	5.041	-493.7	-134.6	188.6	51.4	-305.0	-83.2	39.2
2012	2	3	1	4.658	3.494	-313.7	-85.5	191.9	52.3	-121.7	-33.2	30.0
2012	2	5	2	3.893	2.919	-500.1	-136.4	330.8	90.2	-169.3	-46.2	29.9
2012	2	10	3	3.146	2.359	-399.4	-108.9	108.7	29.6	-290.7	-79.3	31.3

2013	4	1	1	3.095	2.321	-343.9	-93.8	376.2	102.6	32.3	8.8	21.2
2013	4	8	2	4.425	3.319	-327.0	-89.2	276.5	75.4	-50.5	-13.8	21.9
2013	4	12	3	5.316	3.987	-498.7	-136.0	394.5	107.6	-104.2	-28.4	22.9
2013	1	2	1	5.731	4.298	-300.7	-82.0	184.9	50.4	-115.9	-31.6	22.4
2013	1	7	2	6.353	4.765	-393.1	-107.2	135.0	36.8	-258.1	-70.4	15.0
2013	1	11	3	5.672	4.254	-608.3	-165.9	186.1	50.8	-422.2	-115.1	19.0
2013	3	4	1	7.049	5.286	-303.9	-82.9	139.1	37.9	-164.8	-44.9	18.2
2013	3	6	2	5.407	4.055	-432.1	-117.8	256.2	69.9	-175.9	-48.0	19.4
2013	3	9	3	7.005	5.254	-477.3	-130.2	215.4	58.7	-261.9	-71.4	23.2
2013	2	3	1	5.455	4.092	-326.0	-88.9	223.6	61.0	-102.4	-27.9	17.8
2013	2	5	2	4.891	3.668	-509.2	-138.9	480.5	131.0	-28.7	-7.8	17.7
2013	2	10	3	3.485	2.614	-393.7	-107.4	117.8	32.1	-276.0	-75.3	18.5
2014	4	1	1	3.129	2.347	-329.4	-89.8	438.7	119.6	109.2	29.8	21.2
2014	4	8	2	4.906	3.680	-342.5	-93.4	362.4	98.8	19.9	5.4	21.9
2014	4	12	3	5.072	3.804	-561.0	-153.0	481.2	131.2	-79.8	-21.8	22.9
2014	1	2	1	6.241	4.681	-319.2	-87.1	183.9	50.2	-135.3	-36.9	22.4
2014	1	7	2	7.308	5.481	-473.8	-129.2	144.7	39.5	-329.1	-89.8	15.0
2014	1	11	3	4.941	3.706	-624.9	-170.4	209.8	57.2	-415.1	-113.2	19.0
2014	3	4	1	7.382	5.536	-319.4	-87.1	186.1	50.7	-133.3	-36.4	18.2
2014	3	6	2	5.729	4.296	-440.3	-120.1	305.4	83.3	-134.9	-36.8	19.4
2014	3	9	3	7.310	5.482	-508.6	-138.7	240.3	65.5	-268.3	-73.2	23.2
2014	2	3	1	5.466	4.099	-328.8	-89.7	319.7	87.2	-9.1	-2.5	17.8
2014	2	5	2	5.049	3.786	-533.0	-145.4	542.3	147.9	9.3	2.5	17.7
2014	2	10	3	3.885	2.913	-429.0	-117.0	127.0	34.6	-302.0	-82.4	18.5
2015	4	1	1	2.977	2.233	-339.5	-92.6	450.5	122.9	111.0	30.3	31.4
2015	4	8	2	3.882	2.911	-304.1	-82.9	305.9	83.4	1.8	0.5	32.4
2015	4	12	3	3.905	2.929	-489.6	-133.5	401.0	109.4	-88.6	-24.2	33.8
2015	1	2	1	5.414	4.061	-286.2	-78.0	176.0	48.0	-110.2	-30.0	33.2

2015	1	7	2	5.210	3.908	-372.7	-101.7	148.7	40.6	-224.0	-61.1	22.2
2015	1	11	3	4.473	3.354	-538.2	-146.8	190.6	52.0	-347.6	-94.8	28.1
2015	3	4	1	7.136	5.352	-293.8	-80.1	154.1	42.0	-139.7	-38.1	27.0
2015	3	6	2	4.733	3.550	-369.7	-100.8	250.8	68.4	-118.9	-32.4	28.7
2015	3	9	3	6.789	5.092	-451.3	-123.1	219.2	59.8	-232.1	-63.3	34.3
2015	2	3	1	5.306	3.980	-308.1	-84.0	263.4	71.8	-44.8	-12.2	26.3
2015	2	5	2	4.383	3.288	-476.7	-130.0	439.1	119.7	-37.6	-10.3	26.2
2015	2	10	3	3.442	2.582	-385.2	-105.1	123.9	33.8	-261.4	-71.3	27.4
2016	4	1	1	2.977	2.233	-274.4	-74.8	417.0	113.7	142.5	38.9	24.7
2016	4	8	2	4.729	3.547	-276.2	-75.3	293.5	80.0	17.2	4.7	25.5
2016	4	12	3	4.623	3.467	-404.7	-110.4	437.3	119.3	32.7	8.9	26.6
2016	1	2	1	6.477	4.858	-247.8	-67.6	160.5	43.8	-87.4	-23.8	26.1
2016	1	7	2	6.738	5.054	-380.7	-103.8	147.2	40.1	-233.5	-63.7	17.5
2016	1	11	3	5.016	3.762	-459.3	-125.3	183.5	50.0	-275.8	-75.2	22.1
2016	3	4	1	7.726	5.794	-257.1	-70.1	160.7	43.8	-96.5	-26.3	21.2
2016	3	6	2	5.987	4.490	-393.4	-107.3	265.7	72.5	-127.7	-34.8	22.6
2016	3	9	3	7.119	5.339	-398.0	-108.5	221.3	60.4	-176.7	-48.2	27.0
2016	2	3	1	5.601	4.201	-261.7	-71.4	261.7	71.4	0.0	0.0	20.7
2016	2	5	2	5.189	3.892	-414.9	-113.2	460.8	125.7	45.9	12.5	20.6
2016	2	10	3	3.456	2.592	-321.5	-87.7	121.4	33.1	-200.1	-54.6	21.6
2017	4	1	1	2.500	1.875	-248.0	-67.6	449.7	122.6	201.7	55.0	33.2
2017	4	8	2	3.626	2.720	-245.9	-67.1	292.1	79.7	46.3	12.6	34.2
2017	4	12	3	3.690	2.767	-376.1	-102.6	438.2	119.5	62.1	16.9	35.7
2017	1	2	1	4.556	3.417	-225.3	-61.4	170.0	46.4	-55.3	-15.1	35.1
2017	1	7	2	4.713	3.535	-267.0	-72.8	146.4	39.9	-120.6	-32.9	23.5
2017	1	11	3	4.539	3.404	-407.1	-111.0	179.7	49.0	-227.5	-62.0	29.7
2017	3	4	1	6.476	4.857	-231.6	-63.2	154.1	42.0	-77.5	-21.1	28.5
2017	3	6	2	4.801	3.601	-316.9	-86.4	249.1	67.9	-67.8	-18.5	30.3

2017	3	9	3	6.636	4.977	-366.7	-100.0	205.0	55.9	-161.7	-44.1	36.3
2017	2	3	1	4.896	3.672	-250.1	-68.2	244.6	66.7	-5.5	-1.5	27.8
2017	2	5	2	4.194	3.145	-407.7	-111.2	420.6	114.7	12.9	3.5	27.7
2017	2	10	3	3.393	2.544	-315.1	-85.9	127.9	34.9	-187.2	-51.1	28.9
2018	4	1	1	2.880	2.160	-247.8	-67.6	381.7	104.1	133.8	36.5	24.8
2018	4	8	2	4.845	3.633	-278.0	-75.8	311.1	84.8	33.1	9.0	25.6
2018	4	12	3	4.103	3.077	-414.7	-113.1	468.3	127.7	53.6	14.6	26.7
2018	1	2	1	5.440	4.080	-222.9	-60.8	169.7	46.3	-53.2	-14.5	26.3
2018	1	7	2	7.086	5.315	-394.8	-107.7	152.8	41.7	-242.0	-66.0	17.6
2018	1	11	3	4.388	3.291	-411.9	-112.3	185.2	50.5	-226.7	-61.8	22.2
2018	3	4	1	7.910	5.932	-279.2	-76.1	158.1	43.1	-121.1	-33.0	21.3
2018	3	6	2	6.075	4.557	-404.1	-110.2	303.4	82.8	-100.7	-27.5	22.7
2018	3	9	3	6.826	5.120	-387.4	-105.7	242.5	66.1	-144.9	-39.5	27.2
2018	2	3	1	6.415	4.811	-326.5	-89.0	339.3	92.5	12.9	3.5	20.8
2018	2	5	2	4.794	3.595	-411.0	-112.1	724.4	197.6	313.3	85.5	20.7
2018	2	10	3	3.435	2.576	-329.3	-89.8	129.8	35.4	-199.4	-54.4	21.7
2019	4	1	1	1.574	1.181	-208.3	-56.8	212.3	57.9	4.0	1.1	31.4
2019	4	8	2	2.317	1.737	-208.2	-56.8	208.0	56.7	-0.3	-0.1	32.4
2019	4	12	3	2.016	1.512	-327.1	-89.2	321.7	87.7	-5.4	-1.5	33.8
2019	1	2	1	2.906	2.180	-188.4	-51.4	101.0	27.6	-87.4	-23.8	33.2
2019	1	7	2	2.727	2.046	-216.6	-59.1	81.3	22.2	-135.3	-36.9	22.2
2019	1	11	3	2.311	1.733	-301.4	-82.2	115.2	31.4	-186.2	-50.8	28.1
2019	3	4	1	4.120	3.090	-211.9	-57.8	95.6	26.1	-116.3	-31.7	27.0
2019	3	6	2	3.399	2.549	-303.8	-82.8	148.2	40.4	-155.5	-42.4	28.7
2019	3	9	3	3.904	2.928	-306.3	-83.5	129.3	35.3	-177.0	-48.3	34.3
2019	2	3	1	3.070	2.303	-225.1	-61.4	175.7	47.9	-49.4	-13.5	26.3
2019	2	5	2	2.499	1.874	-327.0	-89.2	326.5	89.0	-0.6	-0.2	26.2
2019	2	10	3	1.872	1.404	-253.6	-69.2	43.0	11.7	-210.6	-57.4	27.4

Supplementary Table 2.7. Estimates and significance of the fixed effects and co-variants in the generalised mixed effects linear models for each measured carbon flux. Values for Gross Primary Productivity (GPP), Net Ecosystem Exchange (NEE), Net Ecosystem Respiration (NER) are in g CO_2 M^{-2} h^{-1}. CH_4 values are in g CH_4 M^{-2} h^{-1}. Dissolved Organic Carbon (DOC) concentration values are g l^{-1}. All values are multiplied by 1000 due to the low values of many variables. Model covariates were determined by manual first-term deletion until only significant covariates remained. Fixed factor (treatment) estimates are the mean effect of the fixed factor upon the measured variable, with CI showing the 95% confidence interval for this estimate. For covariates, the estimate is the amount that an increase of the value of that covariant by 1 will have on the measured variable.

	Net Ecosystem Exchange (g CO_2 m^{-2} h^{-1}) *1000				**Gross Primary Productivity (g CO_2 m^{-2} h^{-1}) *1000**				**Net Ecosystem Respiration (g CO_2 m^{-2} h^{-1}) *1000**				**NER CH_4 (g CH_4 m^{-2} h^{-1}) *1000**				**Dissolved organic carbon (g l^{-1}) *1000**			
Treatment	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**
Control (Intercept)	-123.5	-157.5 – -89.6	-7.1	**<0.001**	-135.6	-236.9 – -34.3	-2.6	**0.009**	-40.5	-114.6 – 33.6	-1.1	0.284	-0.6	-1.2 – 0.0	-1.8	0.067	20.3	10.1 – 30.5	3.9	**<0.001**
Warmed	77.8	40.8 – 114.7	4.1	**<0.001**	55.6	-23.4 – 134.6	1.4	0.168	23.9	-52.8 – 100.6	0.6	0.542	-0.145	-0.579 – 0.290	-0.7	0.514	-1.9	-7.8 – 4.0	-0.6	0.524
Drought	34.3	-3.2 – 71.9	1.8	0.073	8.4	-70.6 – 87.4	0.2	0.835	58	-18.7 – 134.7	1.5	0.138	0.347	-0.085 – 0.780	1.6	0.116	1.8	-4.1 – 7.6	0.6	0.554
Combined	71.8	34.5 – 109.0	3.8	**<0.001**	32.4	-46.6 – 111.4	0.8	0.421	60.2	-16.4 – 136.9	1.5	0.124	-0.222	-0.656 – 0.213	-1.0	0.317	2.2	-3.7 – 8.1	0.7	0.465
PAR	-0.04	-0.05 – -0.03	-9.3	**<0.001**	-0.1	-0.1 – -0.03	-6.5	**<0.001**					<0.001	-0.001 – <-0.001	-2.8	**0.006**				
Air Temp					-3.1	-5.4 – -0.8	-2.6	**0.008**	6.5	5.1 – 7.8	9.1	**<0.001**								
WTD	3.9	3.0 – 4.8	8.8	**<0.001**																
Soil temp													0.127	0.091 – 0.164	6.8	**<0.001**	0.7	-0.01 – 1.4	1.9	0.052
Warmed	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**
Control (Intercept)	-107.5	-137.3 – -77.7	-7.1	**<0.001**	-131.8	-223.9 – -39.7	-2.8	**0.005**	-11.3	-75.1 – 52.6	-0.3	0.729	-0.4	-1.0 – 0.2	-1.4	0.177	21.2	11.4 – 30.9	4.3	**<0.001**
OTC present	57.7	29.4 – 86.0	4.0	**<0.001**	44.6	-6.0 – 95.2	1.7	0.084	14.2	-40.3 – 68.7	0.5	0.61	-0.4	-0.7 – -0.0	-2.1	**0.033**	-0.7	-5.0 – 3.5	-0.3	0.728
PAR	<0.01	-0.1 – <-0.0	-9.3	**<0.001**	-0.1	-0.1 – <-0.0	-6.6	**<0.001**					<0.01	<-0.01 – <-0.01	-2.7	**0.006**				
Air temp					-3.7	-6.0 – -1.4	-3.1	**0.002**	7.7	6.2 – 9.2	10.2	**<0.001**								

WTD	4.0	3.1 – 4.8	9.2	**<0.001**	2.6	1.4 – 3.8	4.3	**<0.001**					<0.01	<-0.01 – <0.01	-0.9	0.386				
Soil temp													0.1	0.1 – 0.2	6.8	**<0.001**	0.7	<-0.0 – 1.4	1.9	0.053
Drought	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**P**
Control (intercept)	-84.7	-120.3 – -49.1	-4.7	**<0.001**	-107.4	-200.6 – -14.2	-2.3	**0.024**	-28.1	-90.1 – 33.9	-0.9	0.374	-0.6	-1.2 – -0.0	-2.0	**0.047**	19.5	9.7 – 29.4	3.9	**<0.001**
Pumping	14.2	-33.4 – 61.7	0.6	0.56	-26.3	-83.4 – 30.7	-0.9	0.365	44.9	-0.9 – 90.7	1.9	0.055	0.2	-0.2 – 0.6	0.9	0.35	2.9	-0.9 – 6.8	1.5	0.131
PAR	<0.01	-0.1 – <-0.0	-9.3	**<0.001**	-0.1	-0.1 – <-0.01	-6.6	**<0.001**					<0.01	<-0.0 1– <-0.01	-2.7	**0.007**				
Air temp					-3.7	-6.0 – -1.4	-3.2	**0.001**	7.7	6.2 – 9.2	10.1	**<0.001**								
WTD	3.9	3.0 – 4.8	8.8	**<0.001**	2.7	1.5 – 3.9	4.4	**<0.001**					<0.01	<-0.0 – <0.0	-1.1	0.261				
Soil temp													0.1	0.1 – 0.2	6.7	**<0.001**	0.7	< - 0.0 – 1.4	1.9	0.057

Supplementary Table 2.8. Estimates and significance of the fixed effects in the linear mixed effect models for each component of the modelled carbon budget, at all experimental levels. Fixed factor (treatment) estimates are the mean effect of the fixed factor upon the measured variable, with CI showing the 95% confidence interval for this estimate. OTC = all plots with OTCs. Droughted = all plots subjected to episodic seasonal groundwater pumping.

	Net Ecosystem Exchange (g CO$_2$ m^{-2} y^{-1})				**Primary Productivity (g CO$_2$ m^{-2} y^{-1})**				**Net Ecosystem Respiration (g CO$_2$ m^{-2} y^{-1})**			
Treatments	**Estimates**	**CI**	**Statistic**	**p**	**Estimates**	**CI**	**Statistic**	**P**	**Estimates**	**CI**	**Statistic**	**P**
Control (Intercept)	-221.5	-338.3 – -104.8	-3.7	<0.001	-385.2	-495.1 – -275.4	-6.9	<0.001	163.7	49.2 – 278.2	2.8	0.005
Warmed	123.6	29.6 – 217.6	2.6	**0.01**	4.4	-94.7 – 103.5	0.1	0.93	119.2	-40.1 – 278.5	1.5	0.143
Drought	58.9	-35.1 – 152.9	1.2	0.219	13.4	-85.7 – 112.5	0.3	0.791	45.5	-113.8 – 204.8	0.6	0.575
Combined	235.8	141.8 – 329.8	4.9	**<0.001**	30.7	-68.4 – 129.8	0.6	0.543	205.1	45.7 – 364.4	2.5	**0.012**
OTC	Estimates	CI	Statistic	p	Estimates	CI	Statistic	P	Estimates	CI	Statistic	P
Control (Intercept)	-192.1	-302.1 – -82.1	-3.4	**0.001**	-378.5	-475.3 – -281.8	-7.7	**<0.001**	186.5	106.5 – 266.5	4.6	**<0.001**
Warming	150.3	65.6 – 234.9	3.5	**0.001**	10.9	-51.5 – 73.3	0.3	0.732	139.4	30.0 – 248.8	2.5	**0.013**
Droughted	Estimates	CI	Statistic	p	Estimates	CI	Statistic	P	Estimates	CI	Statistic	p
Control (Intercept)	-159.7	-277.8 – -41.7	-2.7	**0.008**	-383.0	-479.6 – -286.4	-7.8	**<0.001**	223.3	126.8 – 319.7	4.5	**<0.001**
Pumped	85.6	-34.8 – 205.9	1.4	0.164	19.8	-41.5 – 81.2	0.6	0.526	65.7	-67.6 – 199.0	1	0.334

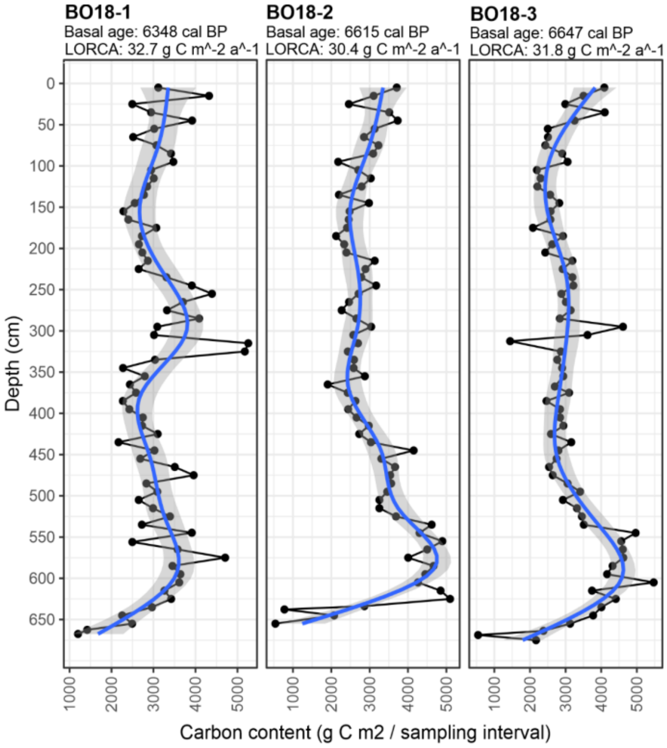
	CH_4 emissions (g CH_4 m^{-2} y^{-1})				Net ecosystem carbon budget (+ CO_2 equivalent CH_4) (g C m^{-2} y^{-1})				Net Annual Ecosystem Carbon budget (g C m^{-2} y^{-1})			
Treatments	Estimates	CI	Statistic	p	Estimates	CI	Statistic	P	Estimates	CI	Statistic	p
Control (intercept)	5.3	4.3 – 6.4	10.2	**<0.001**	-72.1	-196.1 – 51.9	-1.1	0.254	56.4	24.5 – 88.4	3.5	**0.001**
Warmed	-0.9	-2.3 – 0.5	-1.3	0.204	98.5	-3.2 – 200.2	1.9	0.058	33	58.6 – 7.4	-2.5	**0.011**
Drought	1.0	-0.4 – 2.4	1.5	0.144	87.8	-13.9 – 189.5	1.7	0.09	16.8	42.4 – -8.8	-1.3	0.197
Combined	-1.5	-2.9 – -0.1	-2.1	**0.033**	193.7	92.0 – 295.3	3.7	**<0.001**	63.2	88.8 – 37.6	-4.8	**<0.001**
OTC presence	Estimates	CI	Statistic	P	Estimates	CI	Statistic	p	Estimates	CI	Statistic	p
Control (intercept)	5.9	5.1 – 6.6	14.6	**<0.001**	-28.2	-144.3 – 87.8	-0.5	0.634	48.0	17.9 – 78.1	3.1	**0.002**
Warmed	-1.7	-2.7 – -0.7	-3.3	**0.001**	102.2	13.3 – 191.1	2.3	**0.024**	-39.7	62.8 – 16.6	-3.4	**0.001**
Drought	Estimates	CI	Statistic	P	Estimates	CI	Statistic	p	Estimates	CI	Statistic	p
Control (intercept)	4.9	3.8 – 6.0	8.8	**<0.001**	-22.9	-140.0 – 94.3	-0.4	0.702	39.9	7.8 – 72.0	2.4	**0.015**
Pumping	0.2	-1.3 – 1.7	0.3	0.777	91.5	-2.8 – 185.8	1.9	0.057	-23.5	55.5 – -8.5	-1.4	0.15

Supplementary Table 2.9. Basal radiocarbon ages and depths for the long cores BO18-1 – BO18-3.

Lab ID	Core	Material	Radiocarbon age (age BP)	Error (1σ)	Depth (cm)	Cal. Age BP (95 % CI, Median age)
D-AMS 034974	BO18_1	Bulk peat	5563	29	665.0	6399-6297, 6348
D-AMS 034975	BO18_2	Bulk peat	5811	36	637.5	6729-6497, 6615
D-AMS 034976	BO18_3	Bulk peat	5833	33	667.5	6741-6505, 6647

Supplementary Table 2.10. Calculation of long-term average apparent rate of carbon accumulation for each long core (BO18-1 – BO18-3).

	BO18-1	**LORCA** (g C m^{-2} y^{-1})	**BO18-2**	**LORCA** (g C m^{-2} y^{-1})	**BO18-3**	**LORCA** (g C m^{-2} y^{-1})	**Average LORCA**	**Error (2σ)**
Total mass of carbon (g)	207675	32.4	200911	30.1	211305.4	31.5	31.3	2.1
Basal Depth (cm)	665		637.5		667.5			
Median basal date (cal yr BP)	6348		6615		6647			
Mean accumulation rate (g C m^{-2} y^{-1})	1.05		0.96		1.00			



Supplementary Figure 2.3. Carbon content throughout each of the cores BO18-1:3. The Long-Term Rate of Carbon Accumulation (LORCA) and basal ^{14}C dates are included for each core. A GAM smooth and 95% CI if fitted each core to show similarity in the trends between each plot.

References for appendix II

Andrews, L., O., Rowson, J; . Caporn, S; Dise, N. B; Payne, R. J.; Gehrels, W R; *et al.* (2021a, Carbon accumulation long-term and net ecosystem budgets Cors Fochno. figshare. Dataset. https://doi.org/10.6084/m9.figshare.17041364.v2

Andrews., L., O., Rowson, J; Caporn, S; Dise, N. B; Payne, R. J.; Gehrels, W R; *et al.,* (2021b), CF plot WTD and temps.csv. figshare. Dataset. https://doi.org/10.6084/m9.figshare.17213561.v1

Aquino-López, M.A., Blaauw, M., Christen, J.A., and Sanderson, N.K., (2018). Bayesian Analysis of ^{210}Pb Dating. *Journal of Agricultural, Biological and Environmental Statistics*, *23*(3), 317-333.

Belshe, E.F., Sanjuan, J., Leiva-Dueñas, C., Piñeiro-Juncal, N., Serrano, O., Lavery, P. and Mateo, M.A., (2019). Modelling organic carbon accumulation rates and residence times in coastal vegetated ecosystems. *Journal of Geophysical Research: Biogeosciences*, *124*(11), 3652-3671.

Blaauw, M., Christen, J. A. and Aquino-López, M. A. (2021). rplum: Bayesian Age-Depth Modelling of Cores Dated by Pb-210. R package version 0.2.2.

Dupont, L.M., (1986). Temperature and rainfall variation in the Holocene based on comparative palaeoecology and isotope geology of a hummock and a hollow (Bourtangerveen, The Netherlands). *Review of Palaeobotany and Palynology*, *48*(1-3), 71-159.

Mauquoy, D., Yeloff, D., van Geel, B., Charman, D.J. and Blundell, A., (2008). Two decadally resolved records from north-west European peat bogs show rapid climate changes associated with solar variability during the mid–late Holocene. *Journal of Quaternary Science: Published for the Quaternary Research Association*, *23*(8), 745-763.

Rose, N.L. and Appleby, P.G. (2005). Regional applications of lake sediment dating by spheroidal carbonaceous particle analysis I: United Kingdom. *Journal of Paleolimnology*, *34*(3), 349-361. https://doi.org/10.1007/s10933-005-4925-4

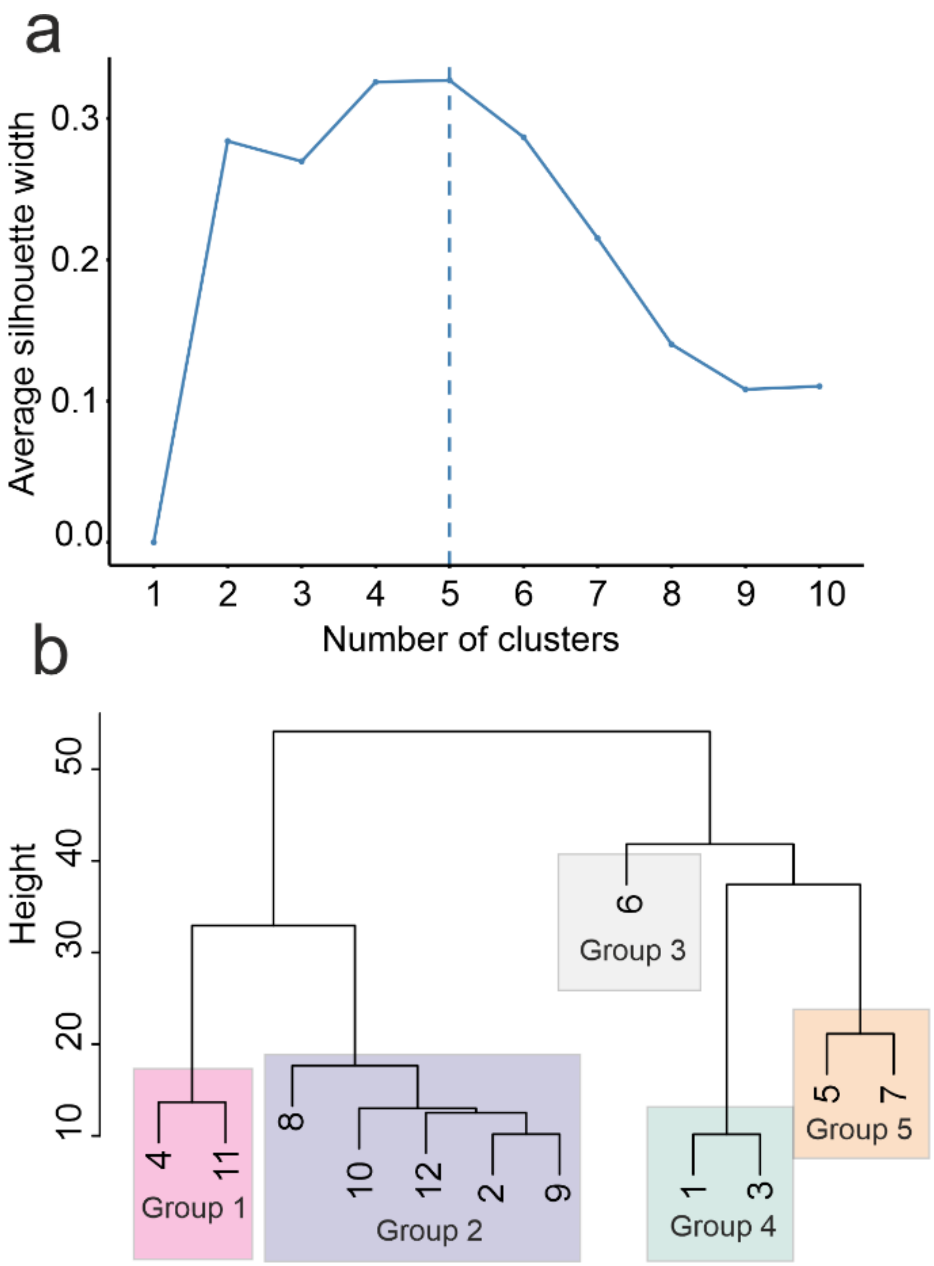
Appendix III: Chapter 5 appendices. Testing the sensitivity of palaeoecological decay proxies and litter decomposition to experimental warming and drought in a Welsh ombrotrophic peatland: Implications for peatland palaeoecological studies

Supplementary Table 3.1. Tea bag index (Keuskamp *et al.,* 2013) parameters (Stabilisation factor *S,* decomposition rate *k;* percentage mass loss of green and rooibos tea) and palaeoecological decomposition proxies (loss on ignition (LOI %), C/N ratios (as well as % carbon and nitrogen content of the decayed green tea) and % light transmission (as a proxy for the degree of humification). Treatments: 1 = Control, 2 = Warmed, 3 = Drought, 4 = Combined warming and drought. Missing values relate to some samples being lost following the experimental incubation. Others were recovered but there was either insufficient material remaining for all the analyses.

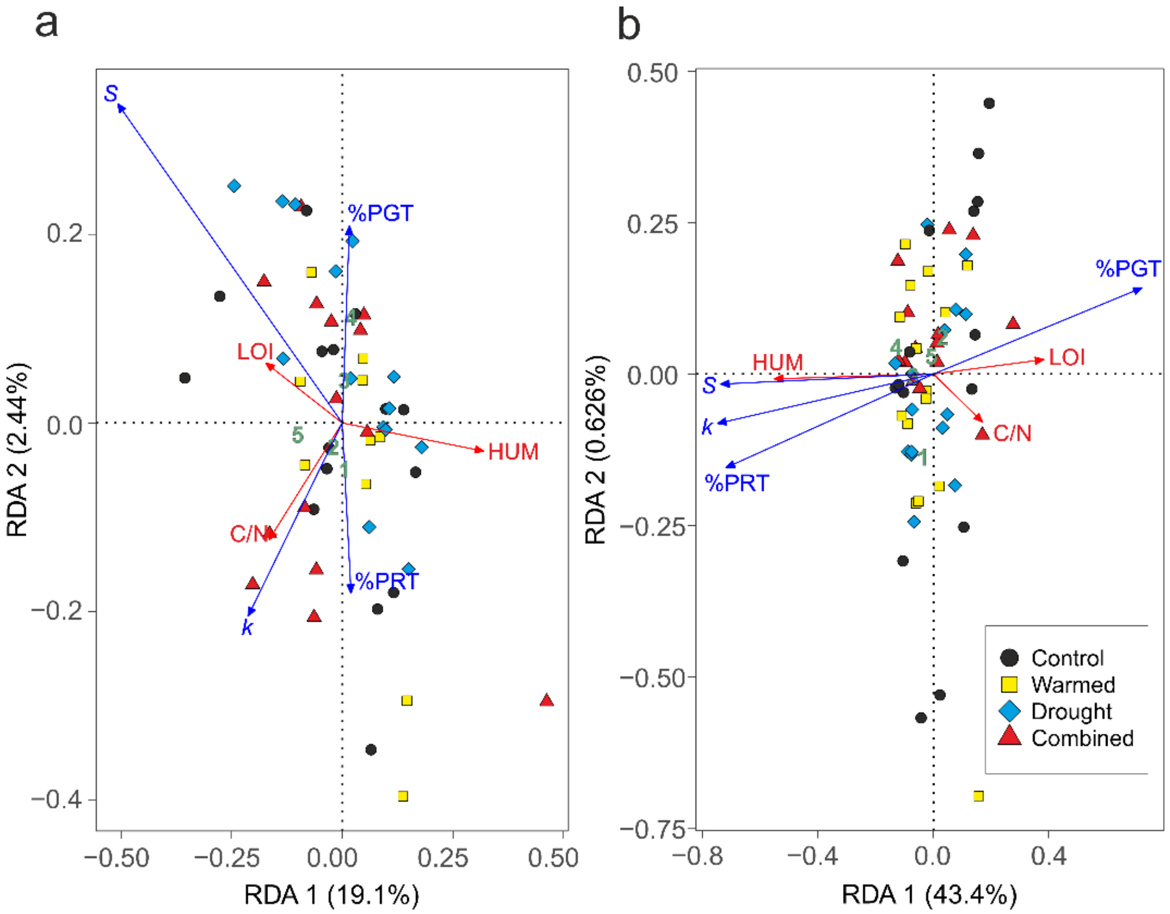
Plot	**Buried**	**Treatment**	***S***	***k***	**LOI %**	**C/N ratio**	**% Light transmission**	**%C**	**%N**	**% Mass loss (green tea)**	**% Mass loss (rooibos tea)**
BO1	S	4	0.2210	0.0107	96.4	8.4	49.7	52.3	6.2	65.6	26.7
BO1	S	4	0.2216	0.0111	95.9	8.6	46.8	48.3	5.6	65.5	27.3
BO1	S	4	0.2502	0.0118	95.5	8.3	43.5	50.7	6.1	63.1	27.2
BO1	S	4	0.2076	0.0146	95.6	9.0	47.7	50.4	5.6	66.7	32.2
BO1	S	4	0.2406	0.0138	96.2	8.3	49.8	49.7	6.0	63.9	30.0
BO2	S	1	0.1810	0.0109	96.1	9.4	47.6	51.2	5.5	69.0	28.4
BO2	S	1	0.1905	0.0119	95.9	8.7	55.5	47.4	5.5	68.2	29.5
BO2	S	1	0.1539	0.0129	96.3	8.5	54.1	48.4	5.7	71.2	32.2
BO2	S	1	0.2695	0.0230	96.4	8.6	52.5	49.9	5.8	61.5	35.4
BO2	S	1	0.1806	0.0122	95.8	9.6	54.3	50.5	5.3	69.0	30.3
BO3	S	3	0.2243	0.0155	96.4	8.8	49.2	50.5	5.7	65.3	32.4
BO3	S	3	0.2367	0.0116	96.2	8.0	48.3	51.4	6.4	64.3	27.5
BO3	S	3	0.2344	0.0116	96.2	8.5	56.1	50.9	6.0	64.5	27.6
BO3	S	3	0.2279	0.0105	95.9	8.3	52.8	50.5	6.1	65.0	26.2
BO3	S	3	0.2593	0.0126	96.1	8.3	47.0	50.2	6.0	62.4	27.9
BO4	S	2	0.1665	0.0227	95.5	10.7	56.6	52.4	4.9	70.2	40.2
BO4	S	2	0.2408	0.0271	96.1	9.3	44.8	50.8	5.5	63.9	38.4
BO4	S	2	0.1797	0.0104	95.8	9.7	45.6	51.7	5.3	69.1	27.7
BO4	S	2	0.1712	0.0159	95.8	10.1	56.5	50.1	5.0	69.8	35.0
BO4	S	2	0.2250	0.0123	96.2	9.2	51.1	49.2	5.3	65.3	28.8
BO5	S	3	0.1700	0.0112	96.5	9.5	51.9	52.6	5.5	69.9	29.3
BO5	S	3	0.2421	0.0130	97.6	8.5	43.9	50.7	6.0	63.8	29.0
BO5	S	3	0.1561	0.0112	95.2	9.2	55.2	51.3	5.6	71.1	29.8
BO5	S	3	0.1711	0.0126	96.0	8.7	52.2	51.1	5.9	69.8	31.2

BO5	S	3	0.2262	0.0115	96.0	8.8	38.5	51.3	5.8	65.2	27.7
BO6	S	2	0.2084	0.0105	96.2	8.6	45.0	51.1	6.0	66.6	26.9
BO6	S	2	0.1849	0.0123	98.0	9.0	53.1	49.8	5.5	68.6	30.3
BO6	S	2	0.2212	0.0101	96.2	8.6	50.0	50.4	5.9	65.6	25.8
BO6	S	2	0.2710	0.0130	96.1	8.7	50.0	50.5	5.8	61.4	27.9
BO6	S	2	0.2372	0.0114	96.2	9.0	51.2	49.9	5.6	64.2	27.2
BO7	S	1	0.1700	0.0112	95.7	10.8	53.3	51.7	4.8	69.9	29.3
BO7	S	1	0.1984	0.0141	96.2	9.6	38.2	51.1	5.3	67.5	32.0
BO7	S	1	0.2028	0.0128	95.7	9.8	46.5	49.9	5.1	67.1	30.2
BO7	S	1	0.1862	0.0114	95.9	9.5	47.5	48.8	5.1	68.5	29.0
BO7	S	1	0.1468	0.0105	96.2	10.4	36.1	51.0	4.9	71.8	28.9
BO8	S	4	0.2581	0.0168	96.4	8.7	45.7	48.8	5.6	62.5	32.0
BO8	S	4	0.2063	0.0139	95.8	9.0	41.2	50.1	5.6	66.8	31.5
BO8	S	4	0.2407	0.0140	96.0	8.7	71.8	50.7	5.8	63.9	30.2
BO8	S	4	0.2110	0.0119	95.9	8.9	50.7	49.5	5.6	66.4	28.8
BO8	S	4	0.2173	0.0149		8.8	41.6	50.1	5.7	65.9	32.1
BO10	S	3	0.2425	0.0163	96.1	9.3	43.3	50.2	5.4	63.8	32.3
BO10	S	3	0.2649	0.0152	95.0	8.3	41.8	49.6	5.9	61.9	30.4
BO10	S	3	0.2217	0.0134	95.9	8.6	52.5	49.5	5.8	65.5	30.2
BO10	S	3	0.2182	0.0141	95.5	9.3		50.6	5.5	65.8	31.2
BO10	S	3	0.2019	0.0149	96.2	8.7	52.5	50.0	5.7	67.2	32.7
BO11	S	1	0.1834	0.0121	95.2	9.8	52.6	50.8	5.2	68.8	30.1
BO11	S	1	0.1813	0.0128	96.6	8.8	47.6	51.4	5.8	68.9	31.1
BO11	S	1	0.2446	0.0122	97.8	8.5	49.8	48.8	5.7	63.6	28.0
BO11	S	1	0.1855	0.0179	96.6	8.9	46.6	51.7	5.8	68.6	36.1
BO11	S	1	0.2271	0.0124	96.5	8.3	44.4	49.8	6.0	65.1	28.9
BO12	S	4	0.2003	0.0054	94.7	9.8	45.3	49.2	5.0	67.3	17.1
BO12	S	4	0.3229	0.0172	94.9	10.1	46.8	47.2	4.7	57.0	29.6
BO12	S	4	0.3421	0.0181	93.1	10.6	40.9	47.8	4.5	55.4	29.3
BO12	S	4	0.4403	0.0185	94.5	10.3	42.6	47.3	4.6	47.1	25.1
BO12	S	4	0.2627	0.0115	94.3	10.3	46.6	48.5	4.7	62.1	26.5
BO1	D	4	0.3153	0.0127	98.1	9.1	70.1	52.1	5.7	57.7	25.9
BO1	D	4	0.2927	0.0137	98.2	9.1	73.9	52.7	5.8	59.6	27.8
BO1	D	4	0.3185	0.0140	98.1	8.9	72.6	52.2	5.9	57.4	27.1
BO1	D	4	0.3107	0.0155	98.1	9.3	63.1	51.8	5.6	58.0	28.7
BO1	D	4	0.3175	0.0153	97.9	9.1	76.0	51.3	5.7	57.5	28.3
BO2	D	1	0.2140	0.0122	97.3	8.5	50.2	52.1	6.2	66.2	29.1
BO2	D	1	0.1305	0.0107	95.5	10.2	54.6	51.1	5.0	73.2	29.9
BO2	D	1	0.1780	0.0119	95.8	9.3	51.0	52.7	5.7	69.2	30.0
BO2	D	1	0.1612	0.0102	97.3	8.7	50.6	52.9	6.1	70.6	28.1
BO2	D	1	0.1900	0.0130	97.6	8.3	47.5	51.9	6.3	68.2	31.0
BO3	D	3	0.1745	0.0110	97.1	9.6	72.7	52.7	5.5	69.5	28.9
BO3	D	3	0.2222	0.0116	97.9	9.1	77.2	52.7	5.8	65.5	28.0
BO3	D	3	0.1927	0.0099	97.9	9.2	71.2	53.4	5.8	68.0	26.5
BO3	D	3	0.2479	0.0131	98.2	9.7	72.2	51.3	5.3	63.3	28.9
BO3	D	3	0.1498	0.0106	97.5	8.5	65.2	51.2	6.0	71.6	29.1
BO4	D	2	0.3102	0.0130	99.1	8.9	66.4	50.7	5.7	58.1	26.4
BO4	D	2	0.2733	0.0121	97.8	9.4	66.5	51.0	5.4	61.2	26.7

BO4	D	2	0.2912	0.0129	98.1	10.1	63.0	50.5	5.0	59.7	27.0
BO4	D	2	0.3139	0.0135	97.9	9.1	60.3	50.6	5.5	57.8	26.8
BO4	D	2	0.3241	0.0137	97.6	10.0	70.4	49.8	5.0	56.9	26.5
BO5	D	3	0.1311	0.0105	96.0	9.3	70.0	51.9	5.6	73.2	29.4
BO5	D	3	0.1561	0.0109	97.6	9.1	57.1	53.4	5.8	71.1	29.4
BO5	D	3	0.1531	0.0101	92.6	9.2	57.0	53.3	5.8	71.3	28.0
BO5	D	3	0.1612	0.0115	95.6	9.1	53.2	51.9	5.7	70.6	30.1
BO5	D	3	0.1563	0.0113	96.6	10.1	57.5	52.3	5.2	71.0	29.9
BO6	D	2	0.3062	0.0136	96.2	9.3	71.9	51.5	5.5	58.4	27.2
BO6	D	2	0.2614	0.0114	98.0	9.0	54.0	52.6	5.8	62.2	26.3
BO6	D	2	0.3158	0.0148	97.8	9.4	75.2	51.1	5.4	57.6	28.0
BO6	D	2	0.2724	0.0114	97.7	9.5	66.6	52.4	5.5	61.3	25.9
BO6	D	2	0.3189	0.0123	97.7	9.1	69.6	51.7	5.7	57.4	25.4
BO7	D	1	0.2979	0.0138	98.2	9.3	74.6	50.5	5.4	59.1	27.7
BO7	D	1	0.2363	0.0116	98.2	9.2	77.6	50.2	5.4	64.3	27.5
BO7	D	1	0.1862	0.0114	98.2	8.6	65.1	51.6	6.0	68.5	29.0
BO7	D	1	0.2215	0.0110	98.2	9.1	72.3	51.4	5.6	65.6	27.2
BO7	D	1	0.2515	0.0129	98.3	9.2	76.4	50.7	5.5	63.0	28.6
BO8	D	4	0.1688	0.0111	98.3	8.7	59.1	54.2	6.2	70.0	29.1
BO8	D	4	0.2469	0.0146	98.1	8.5	75.9	52.9	6.2	63.4	30.6
BO8	D	4	0.1516	0.0105						71.4	28.8
BO8	D	4	0.1583	0.0108	95.6	8.7	51.1	52.8	6.1	70.9	29.1
BO8	D	4	0.1408	0.0102	95.9	9.9	49.5	52.5	5.3	72.3	28.8
BO9	D	2	0.2794	0.0152	97.5	8.8	75.0	52.1	5.9	60.7	29.8
BO9	D	2	0.2030	0.0109	97.7	12.3	52.8	52.9	4.3	67.1	27.7
BO9	D	2	0.2521	0.0121	95.9	8.5	69.9	52.4	6.1	63.0	27.5
BO9	D	2	0.1804	0.0115	97.8	10.0	69.8	54.0	5.4	69.0	29.4
BO9	D	2	0.2269	0.0115	98.3	8.5	73.2	53.1	6.3	65.1	27.7
BO10	D	3	0.2471	0.0132	97.9	8.9	54.3	51.8	5.8	63.4	29.0
BO10	D	3	0.2141	0.0143	98.2	10.2	71.7	50.6	5.0	66.2	31.6
BO10	D	3	0.2039	0.0127	98.2	9.7	72.1	53.1	5.5	67.0	30.1
BO10	D	3	0.1546	0.0110	98.1	9.2	60.8	52.0	5.6	71.2	29.6
BO10	D	3	0.1629	0.0117	98.3	9.8	61.9	52.2	5.3	70.5	30.3
BO11	D	1	0.1765	0.0116	98.4	11.4	64.1	52.4	4.6	69.3	29.6
BO11	D	1	0.2449	0.0135	98.1	10.3	75.7	49.9	4.8	63.6	29.5
BO11	D	1	0.2428	0.0132	98.1	9.8	53.3	54.1	5.5	63.8	29.2
BO11	D	1	0.1623	0.0100	98.1	8.8	52.1	52.8	6.0	70.5	27.6
BO11	D	1	0.2243	0.0122	98.1	11.5	70.2	51.7	4.5	65.3	28.8
BO12	D	4	0.3179	0.0155	98.1	9.4	63.2	50.1	5.3	57.4	28.5
BO12	D	4	0.1523	0.0089	95.6	9.4	41.8	52.0	5.5	71.4	26.0
BO12	D	4	0.3290	0.0153	97.8	9.3	70.8	50.6	5.5	56.5	27.9
BO12	D	4	0.3202	0.0148	97.4	9.3	68.4	50.7	5.4	57.2	27.8
BO12	D	4	0.2370	0.0107	97.8	9.2	62.6	50.8	5.5	64.2	26.2



Supplementary Figure 3.1. a. average silhouette method for determining the total number of clusters b. Cluster analysis of vegetation relative abundance data for the year 2019, showing the groupings of plots (plot numbers are given as identifiers, groups are identified by coloured squares).



Supplementary Figure 3.2. Redundancy analysis showing the relationships between palaeoecological proxies (red vectors) and tea bag index parameters (Keuskamp *et al.,* 2013, blue vectors) for surface (a) and buried (b) samples. Points represent the position of individual samples, with colours and shapes representing the different treatments (control, warmed, drought and combined warmed and drought). Centroids for vegetation groups (1-5) are shown as green numbers. C/N= C/N ratio; LOI= Loss on ignition; HUM= % light transmission; %PGT= Percentage mass green tea loss; %PRT= Percentage mass rooibos tea loss; *k*= decomposition rate; *S*= stabilisation factor.

Supplementary Table 3.2. Description of the stratigraphy of core BO17. Sediment descriptions follow Troels-Smith (1955). Colour description is based upon the Munsell soil colour chart (Munsell Color 2010).

Depth (cm)	Age cal CE (basal)	Troel-Smith	Colour (Munsell)	Notes
0.0-13	2017-1978	Tb2Th1Tl1+Sh	HUE10YR 3/3 Dark brown	Living layer. *Sphagnum* peat, primarily *S. pulchrum.* Woody roots and some *Rhynchospora alba* present. Some humification apparent.
13-26	1847	Tb1Th1Sh2+Tb	HUE10YR 2/2 Very dark brown	Well-humified peat, containing remains of herbaceous plants and *Sphagnum* remains, as well as occasional ligneous material. Branches of *Myrica gale* at 24cm.
26-36	1523	Tb2Th2	HUE10YR 3/4 Dark yellowish brown	A highly humified layer of *Sphagnum,* monocot remains and the remains of *Menyanthes trifoliata.* Notable absence of ligneous material and roots.
36-67	1008	Th2Sh1Tl1	HUE 7.5YR 2.5/1 Black	A highly humified peat containing many monocot roots. *Eriophorum angustifolium* remains visible.
67-76	960	Tb3Tl1+Th	Hue 2.5 YR 2.5/1 Reddish black	Poorly humified *Sphagnum austinii* layer.
76-100	586	Tb2Th1Tl1+Sh	HUE 7.5YR 2.5/1 Black	As before, with a higher proportion of the peat composed of monocot remains.

References for Appendix III

Keuskamp, J.A., Dingemans, B.J., Lehtinen, T., Sarneel, J.M. and Hefting, M.M., (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods in Ecology and Evolution*, *4*(11), 1070-1075.

Munsell Color (2010). *Munsell Soil Color Charts : with Genuine Munsell Color Chips*. Grand Rapids,

Troels-Smith, J., (1955). Karakterisering af løse jordarter. *Danmarks Geologiske Undersøgelse IV. Række*, *3*(10), 1-73.

Appendix IV. Testate amoebae as non-pollen palynomorphs in pollen slides: usefulness and application in palaeoenvironmental reconstruction

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Author contributions

LOA: writing – original draft (lead)

RJP: supervision (equal)

GTS: writing – review and editing (supporting).

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Data availability Data sharing is not applicable to this article as no datasets were generated or analysed.

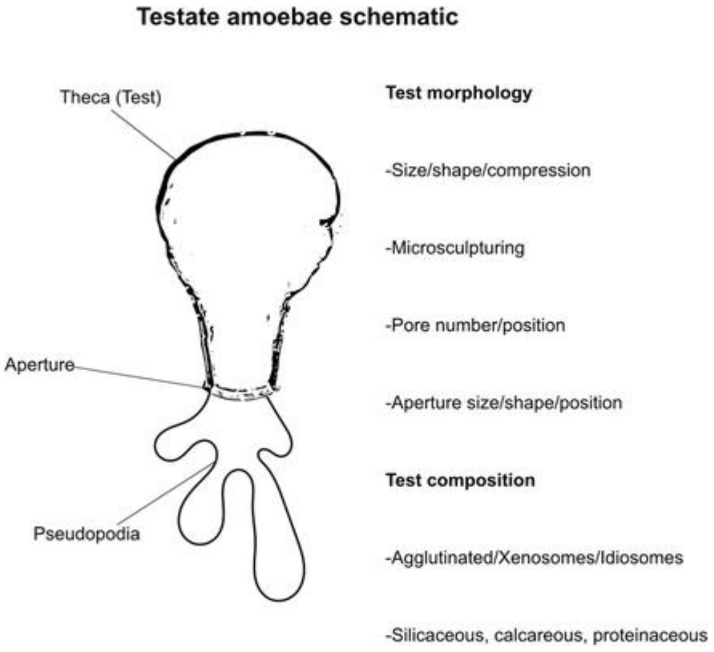
4.1. Abstract

Testate amoebae are a frequently used palaeoecological proxy for reconstructing changes in palaeohydrological conditions, particularly in studies of Sphagnum-dominated peatlands. Their use in palaeoecological studies has increased following the development of transfer functions, allowing for the quantitative reconstruction of water table depth changes through time. Increasingly, they are included in non-pollen palynomorph (NPP) studies alongside a wide range of other proxies, representing a valuable tool, particularly in multi-proxy studies. Testate amoebae have been used for qualitative assessment of palaeohydrology in NPP studies and may aid the verification of environmental interpretations of conditions inferred from curves of NPP with unknown ecology and taxonomy. Their usefulness in such studies is limited by the destruction of tests owing to harsh chemical treatments used in pollen preparation methods. This makes community distribution data of testate amoebae derived by these methods largely unsuitable for quantitative assessment of water table depth. Furthermore, many palynological studies combine testate amoebae as one single curve, losing further ecological detail. Patterns of change of surviving species, most commonly of *Assulina, Archerella, Arcella, Hyalosphenia* and *Archerella flavum*, remain relatively unaffected and therefore can still be useful for interpreting qualitative changes in hydrological conditions through time, particularly when coupled with other proxies.

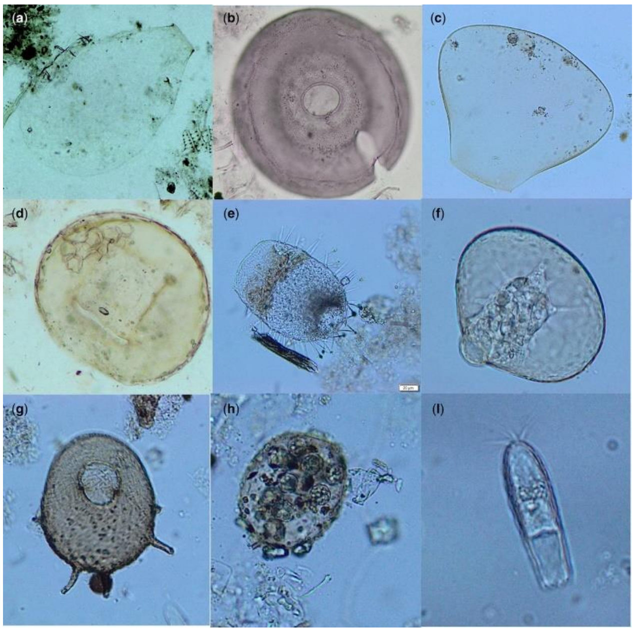
The authors would like to dedicate this paper to the memory of the late Dr Richard John Payne.

4.2. Testate amoebae

Testate amoebae are a polyphyletic group of eukaryotic micro-organisms, belonging to a minimum of three different taxonomic phyla (Mitchell *et al.,* 2008; Ruggiero *et al.,* 2015). The term 'testate amoebae' itself has no specific taxonomic meaning, but instead refers collectively to the wide variety of eukaryotic micro-organisms that build shells (tests). Conservative estimates suggest there are around 2500 species of testate amoebae globally (Mitchell *et al.,* 2008). The small size of most species allows for their dispersal across great distances, limited only by the narrow ecological tolerances exhibited by some species (Charman *et al.,* 2000). Testate amoebae are highly abundant in moist habitats such as lakes, wetlands, and soils (103 – 104 individuals per g^{-1} dry weight peat) (Mitchell *et al.,* 2008). Each taxonomic group develops their own tests differently, with some tests composed of endogenous plates (idiosomes) or secretions, with or without agglutinated environmental particles (xenosomes) (Charman *et al.,* 2000). The chemical composition of these tests also varies greatly, being either siliceous, calcareous, or organic (Charman *et al.,* 2000). Species exhibit a large amount of morphological variability, ranging in size between 4 and 400 µm and exhibiting a diverse range of body plans and surface ornamentations (Payne *et al.,* 2012) (Appendix Figures 4.1 and 4.2). Testates are easily identified to species level, mostly cosmopolitan, are often abundant in sediments, have specific environmental preferences and are often well preserved in Quaternary sediments for thousands of years (Charman *et al.,* 2000). These features make testate amoebae useful proxies in palaeoecological studies.



Appendix Figure 4.1. Testate amoebae schematic showing the various features which can be used to identify a test to the highest possible taxonomic resolution.



Appendix Figure 4.2. A selection of tests demonstrating the range of morphologies, test features and surface ornamentations possessed by testate amoebae. (a) *Longinebela tubulosa* (Kosakyan *et al.,* 2016); (b) *Arcella artocrea* (Leidy, 1876); (c) *Hyalosphenia papilio* (Leidy, 1874); (d) *Bullinularia indica* (Penard, 1907); (e) *Placocista spinosa* (f) *Nebela flabellulum* Leidy, 1874; (g) *Centropyxis aculeata* type Ehrenberg, 1832; (h) *Amphitrema wrightianum* Archer, 1869; (i) *Euglypha cristata Leidy*, 1874. Photographs taken by author (LA).

4.3. Testate amoebae in palaeoecology

Scientific interest in testate amoebae has increased in the last 20 years, increasing from an annual average of five papers involving testate amoebae during the 1990s to over 50 in 2015 (Kosakyan *et al.,* 2016). Testate amoebae have also been increasingly adopted as research tools by a range of disciplines, with studies in over 150 scientific journals between 1996 and 2015, an increase from 40 journals between 1976 and 86 (Kosakyan *et al.,* 2016). In palaeoecology, testate amoebae have most commonly been applied in studies of *Sphagnum* dominated peatlands in the Northern Hemisphere (Hendon and Charman 1997; Mitchell *et al.,* 2008). The waterlogged, acidic conditions of peat allow for the preservation of archives of environmental change through time, spanning the time since their initiation after the beginning of the Holocene to the present day (Blackford and Chambers 1991; Chambers and Charman 2004). The potential of testate amoebae as palaeoecological indicators was first recognized during the early to the middle of the twentieth century (e.g., Harnisch 1926, 1927; Grospietsch 1953; Aaby 1976). The abundance of certain taxonomic groups was known to correspond with specific environmental gradients, particularly moisture and water table depths (Tolonen 1986). This knowledge allowed for the subjective evaluation of changes in peatland water table levels, based upon changes in testate amoebae community structure. Recent developments have moved to make testate amoebae-derived reconstructions of palaeohydrology quantitative, using advanced statistical techniques examining the relationships between community structure and specific environmental variables. The development of large ecological datasets relating testate amoebae community structure to ecological gradients has allowed for the development of statistical transfer functions (Birks 1995; Amesbury *et al.,* 2016). These statistical models describe the relationships between species and environmental variables of interest. In testate amoebae studies, water table depth is the most significant factor affecting testate amoebae community structure, although pH and the availability of micro-nutrients are also important (Tolonen *et al.,* 1992). Once the present-day ecological preferences of testate communities are known, these can then be applied to fossil assemblages, allowing quantitative estimates of changes in ecological gradients through time to be derived (Warner and Charman 1994). Since this development, the use of testate amoebae in palaeoenvironmental studies has increased exponentially (Charman *et al.,* 2000; Payne *et al.,* 2012). Transfer functions have been developed from various sites around the world (e.g., Lamentowicz and Mitchell 2005; Payne and Mitchell 2007; Amesbury *et al.,* 2016) and have been applied in a large number of studies (e.g., Warner and Charman 1994; Booth and Jackson 2003; Swindles *et al.,* 2007). Testate amoebae are frequently used to augment other proxies for hydrological variability, such as plant macrofossil and peat humification analysis (Blackford and Chambers 1991; Payne *et al.,* 2012).

4.4. Testate amoebae as non-pollen palynomorphs in palynological slides

The purpose of this article is to discuss the potential usefulness of testate amoebae as indicators of palaeohydrological change in palynological studies. Several methods have been used for the extraction of testate amoebae from sediments (Tolonen 1986; Hendon and Charman 1997; Booth *et al.,* 2010). These techniques tend to fall into two categories: preparations for the specific removal of testate amoebae analysis generally based upon a combination of dispersal in boiling water and sieving (Hendon and Charman 1997), and preparations based upon pollen preparation methods. The latter undergo a sequence of chemical treatments for the removal of unwanted mineral and organic detritus (Faegri and Iversen 1989). In such studies, testate amoebae are typically categorized along with other non-pollen remains that survive the harsh chemical pre-treatments used to create pollen slides. These sub-fossils are collectively termed non-pollen palynomorphs (NPPs) and include a vast range of micro-organism remains including those of fungi, cyanobacteria, rotifers, and algae (van Geel, 2002). These remains of aquatic animals, plants and fungi tend to be autochthonous, and are therefore likely to be more sensitive to local ecological changes than pollen (Payne *et al.,* 2012). Their inclusion in palynological studies can therefore enhance the richness of interpretations derived from palaeoecological studies with limited additional investment of effort, expense, or time (van Geel 2002; Mighall *et al.,* 2006). Many palynological studies incorporate testate amoebae into their NPP counts. NPP data are typically used in conjunction with other palaeoecological proxies (e.g., pollen, peat humification, plant macrofossils). Specific examples include Lacourse and Davies (2015), who inferred changes in relative water table depth by comparing the testate amoebae assemblages within the pollen slides with fungal remains, identifying a hydrological shift coincident with the transition from forested to bog conditions. Huntley *et al.* (2013) compared declines of *Arcella artocrea* with concurrent declines in copepod spermatophores, interpreting this change as reflecting a hydrological shift from standing water to the development of a *Sphagnum* moss lawn, triggered by drainage prior to modern road construction. van der Linden *et al.* (2008) in a multi-proxy study of anthropogenic and climate changes from a Swedish bog, counted testate amoebae as NPPs in both pollen and plant macrofossil samples. However, despite including these in the resultant diagrams, these curves were not used in the interpretations, as specific analysis of testate amoebae using water-based methods was also undertaken in this study. Most studies of this type are from peat or similar organic soils, with a smaller number from lacustrine sediments and few from archaeological contexts (Payne *et al.,* 2012). Testate amoebae offer an obvious interpretive benefit in non-pollen palynomorph studies, as unlike many NPPs for which little known taxonomic or ecological knowledge exists; these are reasonably well established for testate amoebae (van Geel, 2002). Trends in community distributions of testate amoebae may be used to independently verify if changes in water table predicted by other NPPs, most notably fungal spores, reflect hydrological changes in peatland studies (Yeloff *et al.,* 2007).

4.5. Limitations

4.5.1. Differential preservation due to chemical preparation methods

It is well documented that certain species of testate amoebae are vulnerable to the harsh chemical treatments associated with pollen preparation (e.g., acetolysis) due to their fragility in comparison with more resistant pollen grains (Aaby, 1976; Tolonen, 1986; Payne *et al.,* 2012). A range of different methods are used to prepare palynological slides; however, it is currently unknown whether certain methods are more-or-less destructive towards tests (Payne *et al.,* 2012). A study by van der Molen and Hoekstra (1988) subjected samples from the same cores to both palynological and water-based methods, to compare differences in the types and number of tests preserved by each method. Their results showed that whilst 11 species were identified from the samples prepared by water-based methods, only two species were identified in slides prepared using pollen type preparations. One of the common preparatory steps in pollen analysis requires sieving the sample through a 100–125 µm mesh sieve, which may have the effect of separating the larger tests from the pollen sample (van der Linden *et al.,* 2008). These factors may account for the differential preservation and severely reduced concentration of tests in palynological slides compared with water-based methods (Hendon and Charman 1997; Payne *et al.,* 2012). Species whose tests are composed of organic secretions (e.g., *Archerella, Arcella, Hyalosphenia* sp.) or organic coated idiosomes (e.g., *Assulina* sp.) are more common in pollen slides, owing to their resistance to the strong acid treatments associated with pollen studies (Payne *et al.,* 2012). *Archerella flavum* are the most frequently encountered species, whereas species with agglutinated tests are the least resistant to destruction (Hendon and Charman 1997; Payne *et al.,* 2012). However, some species with xenosomic-type tests, including *Centropyxis* and *Phryganella*, are reasonably well represented in pollen slides (Payne *et al.,* 2012). A review of the available literature of palynological studies identifying testate amoebae showed that only 20 species were represented, with the most represented genus being the *Arcella*, with eight species (Payne *et al.,* 2012). Most of the taxa identified within pollen preparations were relatively cosmopolitan, although some relatively rare taxa, such as *Arcella stellaris* and *Phryganella nidulus* were preserved (Payne *et al.,* 2012). Despite the loss of subtle changes in abundance due to the artificial absence of rare species, changes in species composition within palynological slides may still reflect ecologically meaningful changes that more-or-less mirror the results of water-based methods. However, the loss of these species gives artificial weighting to those that survive; therefore, these assemblages are not accurate representations of the fossil record (Payne *et al.,* 2012). Despite this, patterns of change remain relatively intact between samples from different preparations, such that the ecological information of these taxa may be retained (Payne *et al.,* 2012). The effects of low-count totals may be addressed in NPP studies by simply increasing the number of individuals counted (e.g., Muller *et al.,* 2003). Payne *et al.* (2012) tested the suitability of testate community structures derived from palynological methods for generating transfer function-based reconstructions of water table depth. Testate data derived from water-based manipulations were manipulated (loss of taxa not recorded in NPP studies, lower test count totals, loss of rarer taxa). The resultant transfer function derived estimates of water table depth showed that the combined manipulations effectively 'destroyed' the palaeoecological signal apparent from the original, water-based reconstructions. Whilst the effects of low-count totals could be addressed, the loss of individual tests cannot be accounted for (Payne *et al.,* 2012). It is therefore unlikely that transfer functions applied to palaeoecological data can be used to derive accurate reconstructions. However, Amesbury *et al.* (2016) argue that such reconstructions should be considered with caution in any case, recommending that reconstructions be considered as directional rather than an accurate reconstruction of water table depths. This argument was corroborated by the comparison of testate amoebae-based water table depths from modern samples with instrumental measurements from the same location by Swindles *et al*. (2015). Their results indicated that whilst reflecting directional changes, testate amoebae-based water table depths gave inaccurate estimations of either the mean or median recorded depths. It could therefore be argued that whilst accuracy and ecological detail is lost, the overall direction of the curves remains similar and may offer some benefits in aiding ecological qualitative interpretations. Payne *et al*. (2012) also recommend plotting ordination scores in the same manner as Rull *et al*. (2008) to integrate this information.

4.5.2. Lack of taxonomic detail

In addition to the above caveats, palynological studies often lack taxonomic detail (Payne *et al.,* 2012). Identification in palaeoecological studies remains largely based upon shell morphologies, which at lower taxonomical levels is often unresolved (Mitchell *et al.,* 2008). Payne *et al*. (2012) note that some of the highest number of taxa identified in palynological studies were analysed by trained testate amoebae analysts (e.g., Wheeler *et al.,* 2010). Palynologists in studies using NPPs are infrequently specialists in testate amoeba analysis, therefore the degree of taxonomic resolution in NPP studies can be expected to be lower than in testate-amoeba specific studies. Uncertainties at the higher taxonomic levels have minimal impact upon the usefulness of testate amoebae in palaeoecological studies (Mitchell *et al.,* 2008). However, common species which survive palynological preparation are often easily identified with confidence using the number of available guides, keys and monographs (e.g. Leidy, 1879; Ogden and Hedley, 1980; Charman *et al.,* 2000; Meisterfeld, 2002; Clarke, 2003; Mazei and Tsyganov, 2006; Mazei and Warren, 2012, 2014). Despite most tests being readily identifiable to at least the genus level, in some palynological studies testates are merely represented as curves of their total counts (e.g., Wood and Wilmshurst, 2012). Such approaches severely limit meaningful interpretation of the testate amoebae assemblages. For example, Miehe *et al.* (2009) counted total testate amoebae, claiming that their increased presence was indicative of nutrient enrichment from anthropogenic activities, despite the well-known negative impact of experimental nutrient addition upon the abundance of testate amoebae (Gilbert *et al.,* 1998). Wood and Wilmshurst (2012) similarly represented testate amoebae as a single curve, interpreted as indicators of ‘wetter’ conditions, although this interpretation was derived in conjunction with data from other proxies. Some studies identify testate amoebae to the genus level. For example, since *Assulina* sp. are both easily identified and well represented in pollen preparations (Charman 2001), percentage values of this genus are frequently represented as single curves in NPP studies. However, this taxon is represented by at least three distinct species (*Assulina muscorum, A. seminulum* and *A. scandinavica*), each with their own specific ecological preferences. Similarly, Borromei *et al.* (2010) interpreted samples with increased percentage concentrations of undifferentiated *Arcella* species as representing shallow, mesoeutrophic or mesotrophic freshwater pools. This interpretation is contestable because *Arcella* is a large genus, containing species occupying a range of environmental situations, and is therefore likely to be too general (Payne *et al.,* 2012).

4.6. Conclusions

Testate amoebae are useful indicators of palaeohydrology and are being increasingly included in NPP studies along with a wide range of other microfossils and proxies, particularly in studies of Sphagnum-dominated peatlands. They represent a valuable tool in palaeoecological studies, particularly in multi-proxy studies. Testate amoebae have been used effectively in several NPP studies. They are useful for the qualitative assessment of palaeohydrological change, particularly when used in conjunction with other NPPs. In addition, testate amoebae have an advantage over most NPPs in that they form a group of NPPs where the taxonomy and ecology of species frequently identified are relatively well known, and therefore may aid in the verification of environmental interpretations of trends exhibited by NPPs for which their ecology and taxonomy is currently unknown. However, the usefulness of testate amoebae as a proxy for palaeohydrological conditions is hindered by the loss of tests in both number and disproportionately by species. This limitation is likely to result from the loss or destruction of the tests during pollen preparation methods. This means that community structures of testate amoebae from palynological studies do not accurately represent the fossil record. However, patterns of change remain relatively unchanged, due to the survival of many cosmopolitan species and the disproportionate loss of rarer species. In spite of this, the surviving fossil communities cannot be expected to provide accurate reconstructions of water table depth when applied to transfer functions, although it is argued in this article that the directional changes that survive in the reconstructions may be used as qualitative guides to aid interpretation. A further caveat in many palynological studies involving testate amoebae is that they often lack taxonomic detail, unnecessarily grouping testates in one single curve for the total sum of tests counted. This curve is less ecologically meaningful than deriving an individual curve for each species identified.

4.7. Acknowledgements

We thank numerous colleagues, with special mention given to Roland Gehrels for his advice. We thank the useful and constructive comments of two anonymous reviewers on an earlier draft of this manuscript.

4.8. References for appendix IVhttps://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=B+Aaby&title=Cyclic+climatic+variations+in+climate+over+the+past+5,500+yr+reflected+in+raised+bogs&publication_year=1976&journal=Nature&volume=263&pages=281-284

Aaby, B. (1976). Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. *Nature,* 263*,* 281–284.

Amesbury, M.J.*,* Swindles, G.T. *et al.* (2016). Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology*. Quaternary Science Reviews,* 152*,* 132–151.

Archer, W. (1869). On some freshwater Rhizopoda, new or little-known. *Quarterly Journal of Microscopical Science, New Series,* 9*,* 250–271*,* 322–324*,* 386–397.

Birks, H.J.B. (1995). Quantitative Palaeoenvironmental reconstructions. *In:* Maddy D. *and* Brew J.S. (*eds) Statistical Modelling of Quaternary Science Data.* Quaternary Research Association Technical Guide No. 5. Cambridge University Press, Cambridge, 161–254.

https://sp.lyellcollection.org/content/511/1/151?hwshib2=authn%3A1639837164%3A20211217%253A1308348b-f329-4fba-a7e1-ede9e88c434d%3A0%3A0%3A0%3A9GFqV07JPIqANy8hMhsTyQ%3D%3D - xref-ref-5-1Blackford, J.J. *and* Chambers, F.M. (1991). Proxy records of climate from blanket mires: evidence for a Dark Age (1400 BP): climatic deterioration in the British Isles. *The Holocene,* 1*,* 63–67*.*

Booth, R.K. *and* Jackson, S.T. (2003). A high-resolution record of late-Holocene moisture variability from a Michigan raised bog, USA*. The Holocene,* 13*,* 863–876*.*

Booth, R.K., Lamentowicz, M. *and* Charman, D.J. (2010). Preparation and analysis of testate amoebae in peatland palaeoenvironmental studies. *Mires and Peat,* 7, 1–7.

Borromei, A.M., Coronato, A. *et al.* (2010). Multiproxy record of Holocene paleoenvironmental change, Tierra del Fuego, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 286, 1–16.

Chambers, F.M. *and* Charman, D.J. (2004). Holocene environmental change: contributions from the peatland archive. *The Holocene,* 14, 1–6.

Charman, D.J. (2001). Biostratigraphic and palaeoenvironmental applications of testate amoebae. *Quaternary Science Reviews,* 20, 1753–1764, https://sp.lyellcollection.org/content/511/1/151?hwshib2=authn%3A1639837164%3A20211217%253A1308348b-f329-4fba-a7e1-ede9e88c434d%3A0%3A0%3A0%3A9GFqV07JPIqANy8hMhsTyQ%3D%3D - xref-ref-11-1Charman, D.J., Hendon, D., *and* Woodland, W.A. (2000). *The Identification of Testate Amoebae (Protozoa: Rhizopoda) in Peats.* Technical Guide No. 9, Quaternary Research Association, London.

Clarke, K.J. (2003). *Guide to the Identification of Soil Protozoa-Testate Amoebae.* Freshwater Biological Association (FBA).

Ehrenberg, C.G. (1832). Über die Entwickelung und Lebensdauer der Infusionsthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. *Abhandlungen der Königlichen Akademie Wissenschaften zu Berlin, Physikalische Klasse,* 1831, 1–154.https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=C.G.+Ehrenberg&title=%C3%9Cber+die+Entwickelung+und+Lebensdauer+der+Infusionsthiere;+nebst+ferneren+Beitr%C3%A4gen+zu+einer+Vergleichung+ihrer+organischen+Systeme&public

ation_year=1832&journal=Abhandlungen+der+K%C3%B6niglichen+Akademie+Wissenschaften+zu+Berlin,+Physikalische+Klasse&volume=1831&pages=1-154

Faegri, K. *and* Iversen, J. (1989). *Textbook of Pollen Analysis.* Caldwell.https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&q_txt=Faegri+K.+and+Iversen+J.+1989.+Textbook+of+Pollen+Analysis.+Caldwell.

Gilbert, D., Amblard, C., Bourdier, G. *and* Francez, A.J. (1998). Short-term effect of nitrogen enrichment on the microbial communities of a peatland. *Hydrobiologia,* 373, 111–119.

Grospietsch, T. (1953). Die Untersuchung von Mooren mit Hilfe der Rhizopodenanalyse. *Mikrokosmos,* 42, 101–106.https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=T.+Grospietsch&title=Die+Untersuchung+von+Mooren+mit+Hilfe+der+Rhizopodenanalyse&publication_year=1953&journal=Mikrokosmos&volume=42&pages=101-106

Harnisch, O. (1926). Studien zur Okologie und Tiergeographie der Moore. *Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Thiere,* 51, 1–166.https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=O.+Harnisch&title=Studien+zur+Okologie+und+Tiergeographie+der+Moore&publication_year=1926&journal=Zoologische+Jahrbucher.+Abteilung+fur+Systematik,+Geographie+und+Biologie+der+Thiere&volume=51&pages=1-166

Harnisch, O. (1927). Einige Daten zur rezenten und fossilen testaceen Rhizopodenfauna der Sphagnen. *Archiv für Hydrobiologie,* 18, 245.https://sp.lyellcollection.org/lookup/googlescholar?link_type=googlescholar&gs_type=article&author%5b0%5d=O.+Harnisch&title=Einige+Daten+zur+rezenten+und+fossilen+testaceen+Rhizopodenfauna+der+Sphagnen&publication_year=1927&journal=Archiv+f%C3%BCr+Hydrobiologie&volume=18

Hendon, D., *and* Charman, D.J. (1997). The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene,* 7*,* 199–205.

Huntley, M.J., Mathewes, R.W. *and* Shotyk, W. (2013). High-resolution palynology, climate change and human impact on a late Holocene peat bog on Haida Gwaii, British Columbia, Canada. *The Holocene,* 23*,* 1572–1583.

Kosakyan, A., Gomaa, F., Lara, E., and Lahr, D.J. (2016). Current and future perspectives on the systematics, taxonomy, and nomenclature of testate amoebae. *European Journal of Protistology,* 55*,* 105–117. https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=A.+Kosakyan&author%5b1%5d=F.+Gomaa&author%5b2%5d=E.+Lara&author%5b3%5d=D.J.+Lahr&title=Current+and+future+perspectives+on+the+systematics,+taxonomy+and+nomenclature+of+testate+amoebae&publication_year=2016&journal=European+Journal+of+Protistology&volume=55&pages=105-117https://sp.lyellcollection.org/content/511/1/151?hwshib2=authn%3A1639837164%3A20211217%253A1308348b-f329-4fba-a7e1-ede9e88c434d%3A0%3A0%3A0%3A9GFqV07JPIqANy8hMhsTyQ%3D%3D - xref-ref-22-1

Lacourse, T. and Davies, M.A. (2015). A multi-proxy peat study of Holocene vegetation history, bog development, and carbon accumulation on northern Vancouver Island, Pacific coast of Canada. *The Holocene,* 25*,* 1165–1178.

Lamentowicz, M. and Mitchell, E.A. (2005). The ecology of testate amoebae (Protists) in *Sphagnum* in north-western Poland in relation to peatland ecology. *Microbial Ecology,* 50, 48–63.

Leidy, J. (1874). Notice of some new freshwater rhizopods. *Journal of Natural History,* 14(83*),* 383–385.https://sp.lyellcollection.org/lookup/google-scholar?link_type=googlescholar&gs_type=article&author%5b0%5d=J.+Leidy&title=Notice+of+some+new+freshwater+rhizopods&publication_year=1874&journal=Journal+of+Natural+History&volume=14&pages=383-385

Leidy, J. (1876). Remarks on Arcella, Etc. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 54–58.

Leidy, J. (1879). Fresh water rhizopods of North America. *United States Geological Survey of the Territories Report,* 12, 1–324.

https://sp.lyellcollection.org/content/511/1/151?hwshib2=authn%3A1639837164%3A20211217%253A1308348b-f329-4fba-a7e1-ede9e88c434d%3A0%3A0%3A0%3A9GFqV07JPIqANy8hMhsTyQ%3D%3D - xref-ref-27-1Mazei, Y. and Tsyganov, A.N. (2006). *Freshwater Testate Amoebae.* KMK, Moscow.

Mazei, Y. and Warren, A. (2012). A survey of the testate amoeba genus *Difflugia* Leclerc, 1815 based on specimens in the E. Penard and CG Ogden collections of the Natural History Museum, London. Part 1: species with shells that are pointed aborally and/or have aboral protuberances. *Protistology,* 7, 121–171.

Mazei, Y. and Warren, A. (2014). A survey of the testate amoeba genus *Difflugia* Leclerc, 1815 based on specimens in the E. Penard and CG Ogden collections of the Natural History Museum, London. Part 2: species with shells that are pyriform or elongate. *Protistology,* 8, 133–171.

Meisterfeld, R. (2002). Order Arcellinida Kent, 1880. *The Illustrated Guide to the Protozoa,* 2*,* 827–860.

Miehe, G.*,* Miehe S.*,* Kaiser K.*,* Reudenbach C.*,* Behrendes L.*,* Duo L., and Schlütz F. (2009). How old is pastoralism in Tibet? An ecological approach to the making of a Tibetan landscape*. Palaeogeography, Palaeoclimatology, Palaeoecology,* 276*,* 130–147.

Mighall, T.M.*,* Cortizas A.M.*,* Biester H., and Turner S.E. (2006). Proxy climate and vegetation changes during the last five millennia in NW Iberia: pollen and non-pollen palynomorph data from two ombrotrophic peat bogs in the North Western Iberian Peninsula*. Review of Palaeobotany* and *Palynology,* 141*,* 203–223.

Mitchell, E.A.*,* Payne R.J., and Lamentowicz M. (2008). Potential implications of differential preservation of testate amoeba shells for paleoenvironmental reconstruction in peatlands*. Journal of Paleolimnology,* 40*,* 603–618.

Muller S.D.*,* Richard P.J.H. and Larouchel A.C. (2003). Holocene development of a peatland (southern Quebec): a spatio-temporal reconstruction based on pachymetry, sedimentology, microfossils, and macrofossils*. The Holocene,* 13*,* 649–664*,*

Ogden G.G. and Hedley R.H. (1980). An atlas of freshwater testate amoebae*. Soil Science,* 130*,* 176*,*

Payne, R., and Mitchell, E.A.D. (2007). Ecology of testate amoebae from mires in the central Rhodope Mountains, Greece, and development of a transfer function for palaeohydrological reconstruction*. Protist,* 158*,* 159–171.

Payne, R.J., Lamentowicz, M., van der Knaap, W.O., van Leeuwen, J.F., Mitchell, E.A. and Mazei, Y. (2012). Testate amoebae in pollen slides. *Review of Palaeobotany and Palynology,* 173*,* 68–79.

Penard, E. (1907). VII. – On Some Rhizopods from the Sikkim Himalaya. *Journal of the Royal Microscopical Society,* 27(3*),* 274–278.

Ruggiero M.A., Gordon D.P. *et al.,* 2015. A Higher Level Classification of All Living Organisms. *PLoS ONE,* 10*,* e0119248.

Rull, V., López-Sáez, J.A. and Vegas-Vilarrúbia, T. (2008). Contribution of non-pollen palynomorphs to the paleolimnological study of a high-altitude Andean lake (Laguna Verde Alta, Venezuela). *Journal of Paleolimnology,* 40*,* 399.

Swindles, G.T., Holden, J. *et al.* (2015). Testing peatland water table depth transfer functions using high-resolution hydrological monitoring data. *Quaternary Science Reviews,* 120*,* 107–117.

Swindles, G.T., Plunkett, G. and Roe, H.M. (2007). A delayed climatic response to solar forcing at 2800 cal. BP: multiproxy evidence from three Irish peatlands. *The Holocene,* 17*,* 177–182.

Tolonen, K. (1986). Rhizopod analysis. *In:* Bergglund B. (*ed.) Handbook of Holocene Palaeoecology and Palaeohydrology,* John Wiley and Sons Ltd*,* 645–666.

Tolonen, K., Warner, B.G. and Vasander, H. (1992). Ecology of testaceans (Protozoa: Rhizopoda) in*: Mires in southern Finland: I. Autecology. Archiv für Protistenkunde,* 142*,* 119–138.

van der Linden, M., Barke, J., Vickery, E., Charman, D.J. and van Geel, B. (2008). Late Holocene human impact and climate change recorded in a North Swedish peat deposit. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 258*,* 1–27.

van der Molen, P.C., and Hoekstra, S.P. (1988). A palaeoecological study of a hummock-hollow complex from engbertsdijksveen, in the Netherlands. *Review of Palaeobotany and Palynology,* 56*,* 213–274.

van Geel B. (2002). Non-pollen palynomorphs. *In:* Smol J.P., Birks H.J. and Last W.M. (*eds) Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators.* Springer*,* Dordrecht*,* 99–119.

Warner, B.G. and Charman, D.J. (1994). Holocene changes on a peatland in northwestern Ontario interpreted from testate amoebae (Protozoa) analysis. *Boreas,* 23*,* 270–279.

Wheeler, J.*,* Swindles, G.T. and Gearey, B.R. (2010). Finding Bosworth Battlefield: a multiproxy palaeoenvironmental investigation of lowland sediments from Dadlington, Leicestershire, England. *Journal of Archaeological Science,* 37*,* 1579–1589.

Wood, J.R. and Wilmshurst, J.M. (2012). Wetland soil moisture complicates the use of *Sporormiella* to trace past herbivore populations. *Journal of Quaternary Science,* 27*,* 254–259.

Yeloff, D.*,* Charman, D.*,* van Geel, B. and Mauquoy, D. (2007). Reconstruction of hydrology, vegetation and past climate change in bogs using fungal microfossils. *Review of Palaeobotany* and *Palynology,* 146*,* 102–145.