The effects of restoration on biodiversity, water quality and greenhouse gas fluxes in a rich fen peatland

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SUMMARY

Rich fens are globally significant wetlands due to their high biodiversity and provision of multiple ecosystem services, such as water purification and climate mitigation. However, many U.K. rich fens have become botanically degraded. This is principally due to abandonment, following the cessation of management (mowing/grazing) and has led to a decline in plant species richness. Although the response to mowing on plant species richness has been well documented across Europe, there is no prior knowledge of this research being undertaken at U.K rich fens. Additionally, the effects of mowing on water quality are largely unquantified. Furthermore, the spatial heterogeneity of greenhouse gases across and within botanically rich and botanically poor sites is also unknown.

Two rich fen plant communities: *Cladio-Molinietum* ($n=9$) and *Scheonus nigricans - Juncus subnodulosus* ($n=8$) were examined across three sites; chosen for their conservation value and current degraded condition. A 50 % success rate was achieved following mowing to increase species richness, which meant assumptions were not met for both plant communities. Nitrate, phosphate and dissolved organic carbon concentrations did not reduce following mowing, however there was a beneficial increase in concentration of base cations at both sites. The greenhouse gas investigation revealed that the net gaseous carbon flux between both sites was comparable, which did not meet expectations that the botanically impoverished site would have higher carbon emissions, however, expected differences between plant communities were observed at both sites.

Therefore, this study shows the complexity of the botanical, hydro-chemical and greenhouse gas spatial heterogeneity at rich fens. Careful examination prior to restoration is needed to determine whether environmental/ecological barriers have been removed, so that restoration is not in any way inhibited. In addition, this study has demonstrated that objectives for biodiversity may be in conflict with objectives to manage for other ecosystem services, in these multi-functional wetlands.

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1.0 CHAPTER 1: INTRODUCTION

"Wetlands are among the most important natural resources on earth"

(Mitra *et al.* 2005).

1.1 Definition of Wetlands

Wetlands is a general term which describes ecosystems based on characteristic features; such as the presence of water (temporally variable), soil condition and organisms, particularly aquatic plants (hydrophytes), which are tolerant of water logged soils (Cowardin *et al.* 1979). Wetlands are difficult to classify, due to their wide ecological variation, particularly when they are temporally wet and/or located in transitional areas; at the interface between land and water, Figure 1.1. Spatial heterogeneity is determined by climate, hydrology and the physio-chemical environment, which subsequently affects the presence of biota, Figure 1.2 (Mitsch & Gosselink 2007).
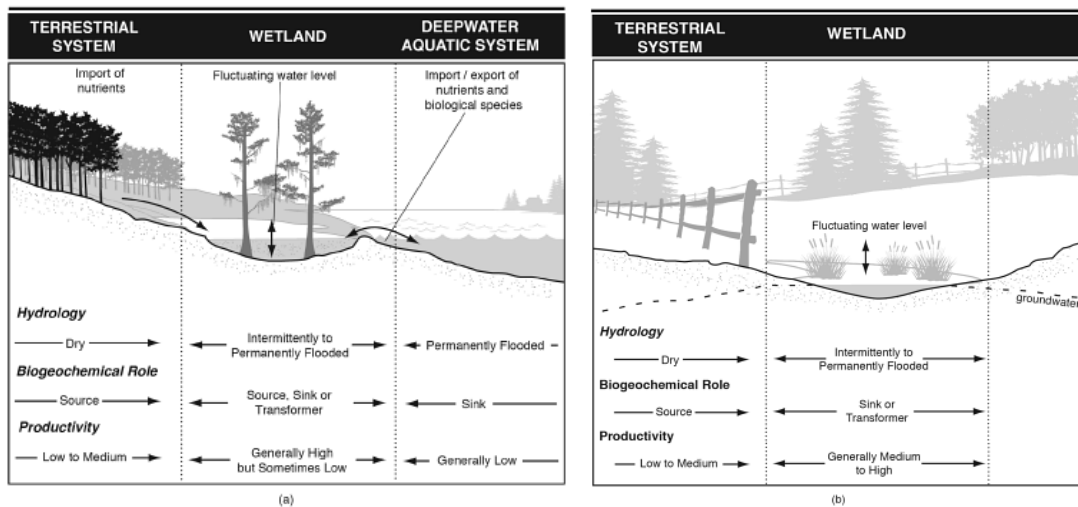
Figure 1.1   Wetland schematic diagrams showing (a) interface between terrestrial and deep water and (b) isolated basins with little outflow and no adjacent deep water (Mitsch & Gosselink 2007).

Due to their proximity to society and agriculture, wetlands are often affected by human activities, and this can lead to a decline in biodiversity and ecosystem function (Brinson *et al.* 2002; Grootjans *et al.* 2006; Smolders *et al.* 2010).

In order to protect and promote the wise use of wetlands, the convention on wetlands was held in in Ramsar, in 1971. This later led to the Ramsar Convention in 1975, and was an important step to preserve these natural resources globally (Farrier & Tucker 2000).
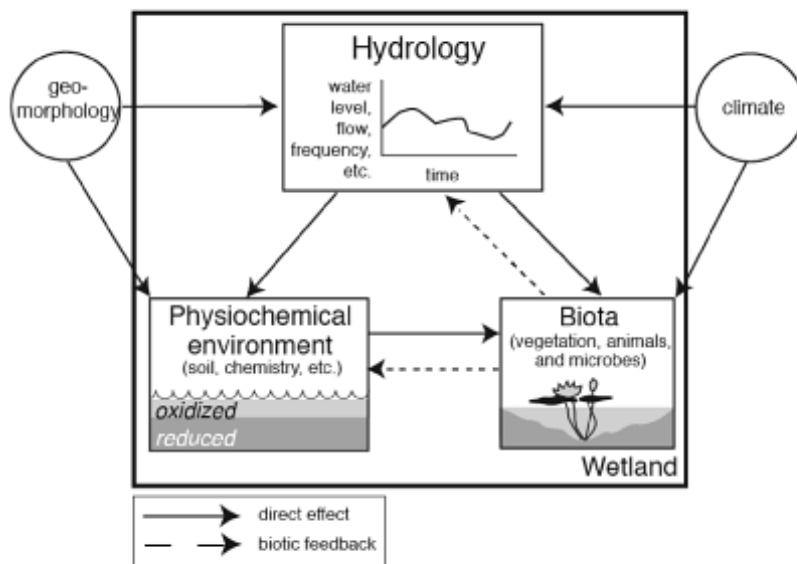
Figure 1.2 Wetland definition diagram, which shows how hydrology, physio-chemical environment and biota are interlinked (Mitsch & Gosselink 2007).

Wetlands are an essential component of the biosphere as they provision multiple ecosystem services, such as water purification, biological conservation and climate mitigation (Mitra *et al.* 2005; Mitsch & Gosselink 2007).

1.2 Peatlands

Peatlands are peat forming wetlands that occupy less than 2 % of the land surface (Bridgham 2001) but contain 1/3 of the world's soil carbon and nitrogen (Gorham 1991), and can source up to 9 % of all global methane emissions (Bartlett & Harriss 1993). Peatlands are wetlands that are defined by a minimum 30 cm depth of peat, and have specific nutrient and hydrological requirements, and are split into two categories; bogs and fens. Bogs are rain fed, acidic, and are dominated by *Sphagnum* and ericaceous shrubs, whereas fens are minerotrophic, base rich and dominated by sedges, short herbs and bryophytes, refer to chapter 2 for a detailed description (Charman 2002; Lai 2009).

In Europe, peatlands historically encompassed 20 % of the land cover (Lappalainen 1996). However, due to anthropogenic influence, 60 % of these original peatlands have now been lost. Land use change such as agricultural practice, forestry, and peat extraction, have been the cause of

habitat loss (Joosten 1997). In addition, the significant increase in growth limiting macronutrients entering the system have also deleteriously affected these wetlands (Verhoeven *et al.* 1996; Venterink *et al.* 2001). It is estimated that 5 % of all threatened species exist in pristine peatlands, however, biodiversity losses are still rising here (Rassi 2001). Botanical losses lead to a deleterious ecological shift, from a species rich, low productive wetland, to a species poor, high productive wetland (Rich & Woodruff 1996).

1.3 Characterisation of Rich Fens

Rich fens are, in the main, peat forming ecosystems, that are dependent on a supply of base rich, oligotrophic, ground water supply (Joosten & Clarke 2002). These habitats are amongst the most species rich, low production wetlands in the world (Ilomets *et al.* 2010). Many of which are of international significance (Ramsar sites), and in Europe they are protected under the European Habitat Directive as Annexe 1 habitats: Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae* (7210) and Alkaline fens (JNCC 2007). Valley and basin fens are now smaller than they were, due to agricultural encroachment; and in spite of their areal size they contribute disproportionately to ecological services and biodiversity (Lamers *et al.* 2014; Naiman & Decamps 1997). These ground water fed fens rely on mineral rich, nutrient poor water, which provisions specialist fen plant species to colonise in the absence of competitive graminoids (Boyer & Wheeler 1989; Wassen *et al.* 2005). This oligotrophic wetland is nutrient poor; defined by low concentrations of macronutrients, in particularly, where total phosphorous is between 8-10µg L^{-1} ((Environment Agency, 2002; Mitsch *et al.* 2015). In addition, rich fens are in receipt of calcium rich water with a pH range between 6.0 – 8, which also promotes low phosphorus (P) concentration (Wheeler & Shaw 1995;). These conditions promote high species richness and low stature herbs, which are light dependent (Kotowski & van Diggelen 2004; Wassen *et al.* 2005). In contrast, poor fens are species poor, acidic and dominated by Sphagnum species (Rydin *et al.* 1999).

Nutrient poor conditions are characterised by a rich abundance of bryophytes and despite the phosphorus limiting conditions found on rich fens, high frequency of moss cover is commonly paired with high density of vascular plants, which suggests bryophytes found here are facilitating phosphorus availability in shallow soil processes (Crowley 2009).

Rich fens are associated with the ecological group of "brown mosses" in the families of *Amblystegiaceae* and *Calliergonaceae* (Hedenas 2003). Brown mosses are very sensitive to elevated ammonium inputs leading to their decline and are negatively correlated with an increase in

calcifuges (acid tolerant) species such as *Sphagna* and *Polytrichum spp.,* which confound the effects of acidification (Paulissen *et al.* 2004; Paulissen *et al.* 2005).

Bryophytes are an equally important component of fen vegetation, alongside vascular plants (Mitsch & J.G. 2000) which can control abiotic conditions to facilitate herbs (Bedford & Godwin 2003). Bryophytes are an important consideration for fen restoration, as they can enable re-establishment of ecosystem functioning, such as water attenuation and nutrient cycling (Cornelissen *et al.* 2007; Graf & Rochefort 2010). Including bryophytes in fen restoration will increase vascular plant diversity, and will support transition to a rich fen trajectory (Graf & Rochefort 2010).

Figure 1.3   Photograph of Cors Bodeilio, rich fen wetland, North wales, U.K. This photograph depicts an isolated wetland located within an agricultural basin.

Furthermore, due to ground water dependency, fens are situated within intensively managed agricultural basins, Figure 1.3. This can affect the low nutrient regime fen systems depend upon, as agricultural land leaches a high concentration of nitrate into surface and ground waters, which can cause eutrophication (Smolders *et al.* 2010). Enrichment and abandonment have collectively had an increased deleterious effect on the fen, as both cause primary production to increase, which negatively affects fen species establishment (Berendse & Aerts 1984; De Kroon & Bobbink 1997).

However, in spite of these threats, some characteristic fen species are still able to persist (Koerselman *et al.* 1990; Naiman & Decamps 1997; Hald & Vinther 2000; Ilomets *et al.* 2010).

1.3.1 Description of Cladio-Molinietum plant community

Cladio Molinietum (CM plant community) is a tall herb community found in base rich calcareous fens and is designated under the European Habitat Directive for its ecological importance and rarity (JNCC 2012). In the UK, this plant community is found primarily in the Norfolk Broads and on the island of Anglesey and Llyn Fens complex, North Wales. The total U.K. extent is estimated at 500 hectares and it is thought that this rare plant community has reached its potential range. Geomorphological and hydrological preferences has limited the geographical extent (Buczek & Buczek 1996; JNCC 2007). As with all lowland fens this community is commonly found within agricultural basins, which has promoted fragmentation and vulnerability to surface water pollution and further degradation (JNCC 2007).

The dominant graminoid in this plant community is *Cladium mariscus*, which is a robust, evergreen sedge, which grows to 2 m in height, and prefers oligotrophic conditions (Doren *et al.* 1997; Saltmarsh *et al.* 2006). Dense, species poor stands of *C. mariscus* can dominate large areas, due to abandonment (cessation of management), which leads to a dense canopy and thick litter cover. The ecology of this species has a vigorous growth regime, where individuals effectively and rapidly propagate vegetatively, through the production of polycorms, and can produce seed under favourable conditions (Namura-Ochalska 2005).

1.3.2 Description of Schoenus nigicans-Juncus subnodulosus

This *Schoenus nigicans-Juncus subnodulosus* (SN community) comprised of a complex, and rich assemblage of rich fen species. The current U.K. extent is estimated at 1632 hectares, of which 52 - 88 % are under conservation management (JNCC 2007). Losses here are due to agricultural gain and eutrophication (Criodain & Doyle 1997). The SN community is in contact with varying sub-communities of the CM plant community, due to a its distribution across a complex hydro-geological (soligenous/topogenous) distribution (JNCC 2007).

The dominant graminoids in this plant community are *Schoenus nigricans* and in lower frequencies *Juncus subnodulosus*; the former can be infrequent and even absent in isolated stands. *S.nigricans* is quite distinctive, due to a glaucous appearance, owing to its semi-evergreen foliage (Rodwell 1992). Sparling (1968) characterises *S. nigricans* as "caespitose" and a "hemicryptophyte" which means that it grows in dense tussocks and it is a perennial with overwintering buds. It is these physical

characteristics that make this community so diverse, as the tussocks (optimal height 40 cm) can support a host of low growing sedges, herbs and bryophytes (Rodwell 1992). A good condition community would support variations of light projection to the runnels, which may be inundated or moist year round, which is important for small herbs (10 – 30 cm) and sedge establishment. Larger tussocks can provide a richer blend of species such as calcifuges, which colonise within the tussocks, are isolated from the calcareous waters and favour drier, acidic conditions (Rodwell 1992).

1.4 Wetland Restoration

"Successful restoration of wetlands calls for interdisciplinary experimental research, in which ecology, hydrology, microbiology, and geochemistry merge into a system-ecological approach"

(Zak *et al.* 2011).

It is important to consider prior to restoration whether wetland functioning restorable and what direction the vegetation trajectory will follow after restoration intervention (Charman 2002). van Diggelen *et al.* (2001) states that it is more sensible to assess wetland potential, rather than trying to achieve an 'original' ecological condition that is not realistically achievable. Ecological restoration is costly and the most important aspect to consider is biogeochemical functioning, which is fundamental and site specific; taking account of this first can avoid unnecessary work, overspends and unpredictable outcomes (Klotzli & Grootjans 2001).

Bradshaw (1996) states that the direction of the trajectory is worthy of consideration and that progress is continuous in the absence of barriers and further states that "restoration", as defined by returning a community back to a reference state, is unrealistic and economically impossible, whereas "rehabilitation" is more viable. Although this is likely to yield a different end point community, this may be more valuable than the original. Others have also stated that restoration is a gradual process, and making predictions is difficult, given the contrasting abiotic, biotic and historical management that defines each site (Bradshaw 1996; Pfadenhauer & Grootjans 1999; Xiong *et al.* 2003; Lamers *et al.* 2014).

There are a number of ecological interventions applied when restoring peatlands such as reinstating the hydrological regime, topsoil removal and species re-introductions (Klimkowska *et al.* 2007; Malson *et al.* 2008; Klimkowska *et al.* 2010).

1.4.1 Fen restoration

Historically, where population density was high, fens were drained to increase productivity, conversely, where population density was low, they were abandoned. (Bakker & Berendse 1999). Abandonment is the largest cause of biodiversity losses due to dominant species encroachment (Middleton 2002) and litter accumulation (Middleton 2002; Peintinger & Bergamini 2006). These target fen plants are light demanding, and have a short life cycle, making them poor competitors in low light conditions (Hald & Vinther 2000; Venterink *et al.* 2009). Therefore, even if fens are inundated year round, without management, these habitats are still invaded by tall sedges. This leads to a plant composition shift to dominant graminoids, which counteracts specialist fen plant colonisation and leads to the latter becoming rare and endangered (Diemer *et al.* 2001).

No prior restoration research has been undertaken at U.K. rich fens, as far as the author is aware, as the focus has been on ditch blocking and revegetation to improve hydrology and increase water quality (Peacock *et al.* 2015; Shuttleworth *et al.* 2015). The vast majority of restoration research in lowland fens has been undertaken across other areas of Europe, where authors have focused on the botanical response to mowing (Huhta & Rautio 1998; Gusewell & Le Nedic 2004; Kolos & Banaszuk 2013; Fogli *et al.* 2014; Horak & Safarova 2015). Other fen restoration investigations have examined fen hydrology and the effects of eutrophication (Beltman *et al.* 2001; Bollens *et al.* 2001; Zak & Gelbrecht 2007), or more generally fen biogeochemistry and fen plant ecology (Boeye & Verheyen 1994; Verhoeven *et al.* 1996; Cusell *et al.* 2014).

Although rich fen restoration is not a new research discipline, there is still a dearth of knowledge surrounding the longer term implications and effects on ecosystem functioning. Furthermore, the majority of published articles only report the short term success of rehabilitation. Failures and the long term consequence of restoration (e.g. plant community trajectory) are not widely published. This is because funded research is usually undertaken over a 3-4 period, which provides little time for base time monitoring or long term evaluation. However, there are some long term studies, although they are often site or plant community specific (Fojt & Harding 1995; Gusewell *et al.* 1998; Large *et al.* 2007).

It is therefore perplexing that restoration objectives in rich fens to date, have not previously considered biodiversity and ecosystem services collectively, as these wetlands are multi-functional ecosystems, which support ecosystem services which are globally significant (Lamers *et al.* 2014).

1.5 Wetland Nutrient Cycling

Nitrogen mineralisation in fens in Europe is high (exceeding 60 - 80 kg N ha^{-1} year $^{-1}$) (Venterink *et al.* 2002) and extractable phosphorus should not exceed 25 kg P ha^{-1} year $^{-1}$ (Venterink *et al.* 2009). Higher inputs of nitrogen to fens can be attributable to nitrogen deposition, which is a major factor to the loss of species in an ecosystem that is reliant on nutrient poor conditions (Bobbink *et al.* 1998; Verhoeven *et al.* 2011). This is because elevated nitrogen deposition is positively correlated with increased nitrogen availability to plants (enhancing fertility), and this stimulates plant biomass production. Increased inputs of inorganic nitrogen compounds has been shown to be detrimental to bryophyte health and a botanical composition shift from *Carex spp.* to grasses and shrubs is likely to occur (Verhoeven *et al.* 2011).

Güsewell (2005) states that nitrogen and phosphorus concentration determines morphological plant traits whereas nitrogen : phosphorus ratio will determine the physiological traits, and for most plant species, both the nitrogen : phosphorus ratio and the availability of nitrogen will determine biomass production. Unfortunately, there is little known about morphological and physiological traits to better understand how plants perform under nitrogen, phosphorus or co-limiting conditions (De Kroon & Bobbink 1997). Phosphorus or potassium co-limited sites are controlled by various environmental factors such as iron toxicity and competition by bryophytes (Rozbrojova & Hajek 2008). Graminoids can compete in phosphorus limiting conditions as they can produce biomass with low phosphorus demands and translocate phosphorus from old plants to new ones (Verhoeven *et al.* 1996). However, this can lead to a subsequent reduction in growth rate (Gusewell *et al.* 2003). An assessment of nutrient concentrations in above ground biomass can be a good indicator of nutrients available to plants (Rozbrojova & Hajek 2008). Foliar nutrient content is an established means for depicting how different plants (with different foliar nutrient concentrations) can influence ecosystem processes (Grime *et al.* 1997) as this controls relative growth rate (Cornelissen *et al.* 1997) and nutrient use efficiency (NUE) in living plants (Aerts & Chapin 2000).

Nutrient rich litter is known to facilitate high decomposition rates, which has a positive feedback to nutrient cycling (Cornelissen & Thompson 1997). The solubility of organic compounds is dependent on biochemical composition of plant tissue, as well as litter quantity and quality, which determines decomposition processes and organic inputs to the soil pool (Olff et al. 1994; Zhang et al. 2008; Zhou et al. 2015). These effects persist long after leaf senescence as nutrient rich litter decomposition rates are high which has a positive feedback to nutrient cycling (Cornelissen & Thompson 1997). In mire plant communities foliar nutrient content will vary dependant on inter-specific differences in tissue chemistry as well as soil nutrient availability (Bombonato et al. 2010).

Garnier and Aronson (1998) found that taller herbs had lower concentrations of macronutrients in their above ground biomass allowing them to be more productive and smaller species had higher concentrations of N and P in their shoots. It was also observed that plants that could adapt to N limited sites are likely to be supported by symbiotic N_2 fixation (Tilman 1982). Furthermore, in the absence of management, plants; in particular graminoids; a deleterious dominant component of the vegetation are efficient at resorbing N and P from above-ground decomposing biomass (Aerts 1996; Aerts & Chapin 2000).

1.6 Carbon Cycling and Climate Change

Carbon dioxide (CO_2) concentrations are set to double over the next century, which is predicted to lead to an increase in temperature of between 1.5 - 5.8 °C (IPCC 2001), which is likely to have a feedback on carbon cycling in terrestrial ecosystems (Lenton & Huntingford 2003). Climate change is known to pose a threat to biodiversity and ecosystem functioning globally (Hulme 2005). The impending affects from climate change on wetlands are the direct and indirect effects of temperature, changes to hydrology and land use change (Ferrati *et al.* 2005). It is predicted that global climate change will affect the distribution of wetlands and their capacity to function (Erwin 2009). In particular, a change in hydrology is likely to lead to drier soils and carbon losses, as carbon storage is optimal under anoxic conditions (Euliss *et al.* 2006).

Wetlands cover an estimated 5 – 8 % of the terrestrial surface of the earth, yet they store 20 – 30 % of the world's carbon, and therefore contribute disproportionately to the global carbon cycle (Roulet 2000; Bridgham *et al.* 2006; Mitsch & Gosselink 2007; Lal 2008). It is still unknown what effect wetlands will have in a global changing climate, in terms of elemental cycling and atmospheric fluxes (IPCC 2001; Paul *et al.* 2006). Therefore, restoration should consider the implications to global climate change and policy makers should promote wetland restoration in support of climate mitigation (Erwin 2009).

Inundated and anoxic conditions present in wetlands can optimise carbon sequestration, reducing carbon dioxide concentration in the atmosphere and some can mitigate for climate change (Bridgham *et al.* 2006; Mitsch *et al.* 2012). Bridgham *et al.* (2006), based on his assessment of North American wetlands, suggests that currently wetlands have a zero radiative forcing on climate, due to the balance of carbon sequestration and CH_4 emissions. However, if CH_4 emissions increase, this may offset the positive carbon sequestration benefits driven by wetland plants and soils.

Phenolic compounds, largely derived from lignin (Elder & Kelly 1994) are common to humics in wetlands (Wetzel 1992) and comprises as much as 50-60 % of the peat (Clymo 1983). It is this component of the peat that has a bearing on the rate of decomposition, as lignin is highly recalcitrant and is degradable by only a discrete number of micro-organisms (Krauskopf & Bird 1995). Lignin makes up 50 – 60 % of the peat formed, which can control the rate of carbon cycling (Colberg 1988). The presence of phenolic compounds is well documented, being linked to inhibiting microbial and enzyme processes (Freeman *et al.* 1990; Wetzel 1992; Freeman *et al.* 2001b). An enzyme group, phenol oxidase, promotes decomposition where molecular oxygen is available and acts as a 'latch' to controlling carbon cycling (Freeman *et al.* 2001b). This enzyme process is an increasingly important component to carbon cycling in wetlands, given the imminent changes in climate (drier conditions) and more frequent oscillations to hydrology, and effectively acting as an on/off switch to carbon cycling, causing pulses of dissolved organic carbon (DOC) and CO_2 losses (Freeman *et al.* 2001a; Freeman *et al.* 2004).

As wetlands accumulate carbon, they also produce DOC, which is leached in to the water during decomposition (Thurman 1985). DOC production is complex, as it is mediated by the biological, physical and chemical conditions which are unique to each wetland, and exports to receiving waters are further controlled by sorption rates and UV degradation (Qualls & Richardson 2003). DOC production and export to surface waters are further complicated by climate change and associated increased temperature and elevated CO_2, all of which influence the rate of DOC release (Freeman et al. 2001a; Fisher & Acreman 2004; Fenner et al. 2007a; Fenner et al. 2007b). Lowland catchments, associated with fens are known to export significantly higher concentrations of DOC to reservoirs than highland catchments, which is associated with contrasting biogeochemical processes and plant diversity (Mettrop et al. 2014; Brooks et al. 2015).

Increased DOC concentration exported from catchments to reservoirs is associated with a change in water colour, and has been linked with halogenated disinfectant by products (DBP) which are a precursor to the formation of tri-halo-methane (THM) compounds, harmful to all living organisms (Davies et al. 2004; WHO 2011). Reduced water quality downstream is also deleterious to biodiversity, as nutrients (nitrogen and phosphorus) are exported along with dissolved organic matter (DOM), which can cause eutrophication and decrease water quality (Kalbitz et al. 2000; Kalbitz et al. 2002; Qualls & Richardson 2003).

Globally, wetlands contribute 12 % to greenhouse gas (GHG) emissions to the atmosphere (refer to Chapter 4 for detailed description of GHG flux emission pathways) (Bubier & Moore 1994). This

has led to multiple studies quantifying the environmental controls on greenhouse gas emissions (Roulet 2000; Sha *et al.* 2011; Levy *et al.* 2012). However, less focus has been given to the spatial heterogeneity and plant mediated control on carbon gas fluxes; recent studies have shown that plants have the potential to provide inexpensive proxy data, which can predict spatial distribution of gas fluxes (Dinsmore *et al.* 2009; Dias *et al.* 2010; Couwenberg *et al.* 2011; Gray *et al.* 2013; McEwing *et al.* 2015). Vegetation is considered to be a good indicator of GHG emissions as it responds to soil moisture (Ellenberg *et al.* 1992) and as water levels relate to GHG emissions, plants offer a good proxy measurement (Couwenberg *et al.* 2010; Dias *et al.* 2010; Couwenberg *et al.* 2011). Other controlling factors to GHG emissions in peatlands are pH, historical land management and nutrient availability (Couwenberg *et al.* 2011). Emissions will vary year to year dependant on variations of land-use, water level and temperature, so ideally, two or more years data collection is recommended to take account of inter annual variations (Roulet *et al.* 2007; Couwenberg *et al.* 2011).

Scientists are now trying to scale up from carbon measurements taken from wetland sites, and combine them with climate data, to determine the global potential of carbon balance (Bianchi *et al.* 1996). However, this is very difficult, due to the spatial heterogeneity across and within sites, on account of varying rates of decomposition rates and abundance of methanogenic organisms which affect CH_4 production rates (Mitra *et al.* 2005). The spatial heterogeneity presents a knowledge gap for scientists, as available data on edaphic conditions combined with plant mediated controls on carbon cycling is very limited (Weltzin *et al.* 2000). However, in addition to the temporal influence on carbon accumulation (e.g. temperature and hydrology), it is also considered that accumulation capacity is dependent on the plant functional traits found within each plant community (Aerts *et al.* 1999; Weltzin *et al.* 2000; Pastor *et al.* 2002).

1.7 Thesis Aims

The broad aims for this research were to examine the response of mowing on vegetation and pore water chemistry. A separate investigation was also undertaken to determine the spatial heterogeneity of GHGs between and within a botanically rich and botanically poor rich fen, as well as identification of plant mediated predictors for methane and carbon dioxide fluxes.

1) It was proposed that target fen species richness would increase and dominant vegetation components would decrease, within two years following the mowing treatment.

2) It was also expected that as these sites supported large quantities of accumulated biomass, biomass removal wold lead to a decrease in nitrate, phosphate and DOC concentrations, due to decomposition prevention and inhibited nutrient re-cycling. In addition, following an initial disturbance related pulse of DOC it was expected that mowing would reduce dissolved organic carbon and dissolved organic nitrogen (DON) leaching, leading to a depletion of active organic matter pools.

3) The greenhouse gas investigation proposed that the botanically rich site would support a higher gaseous carbon uptake (CO_2), and lower gaseous carbon losses (CO_2, CH_4), due to the presence of a higher number of positive plant mediated carbon traits, compared to those present at the degraded site, where it is species impoverished. In addition, it was hypothesised that there would be within site differences in CH_4 and CO_2 fluxes between plant communities.

4) It was also expected that reliable plant mediated predictors for CO_2 and CH_4 fluxes would be identified to provide further insight to the spatial heterogeneity of greenhouse gases fluxes at a temperate rich fen.

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2.0 CHAPTER 2: CONTRASTING RESPONSE TO MOWING IN TWO RICH FEN PLANT COMMUNITIES

2.1 Abstract

Globally important U.K. fens are in poor condition, principally due to abandonment, following cessation of traditional mowing and grazing in recent decades. In the absence of management, rich fen flora are displaced as a result of succession. This leads to an increase in competitive species and subsequent biomass accumulation. In order to reverse this trajectory and increase species richness, management consisting of a single mowing event was employed. Mowing was conducted in two degraded fen communities in north-west Wales, (U.K) across three sites: (i) a species rich, tussock alkaline mire, dominated by *Schoenus nigricans* and *Juncus subnodulosus* (SN community) and (ii) a species poor basin mire *Cladio-Molinietum* dominated by *Cladium mariscus* (CM community). The early vegetation responses were monitored over two years. Results show a large treatment effect on species richness in the CM community, where mean species richness increased by 51 % in the second year following mowing. Consequently, total species number across all sites increased to 74 in the treatment compared to 44 in the control. Mowing reduced vegetation height and litter cover and increased bare ground. These treatment effects combined with a reduction in graminoid and shrub cover collectively contributed to the initial stages of rehabilitation. Conversely, the SN community showed no increase in species richness, in spite of a reduction in litter cover and increased bare ground. Strong site heterogeneity and a sustained canopy height caused by rapid re-growth of the dominant graminoid *S.nigricans* may have impeded treatment effects. Therefore, increased mowing frequency in alternate years, switching between autumn and summer would be necessary to develop species richness in the SN community. Ongoing intervention in each fen

community is needed to achieve an optimal trajectory of increased rich fen and reduction of secondary succession species.

2.2 Introduction

Globally, it is estimated that fens comprise 26 % of all wetlands and 42 % of all peatlands, which equates to an area of 1.5 million km^2 (Joosten & Clarke 2002; Ramsar Convention Secretariat 2013). Fens are distributed throughout the northern hemisphere and are well represented in North America, Russia, Scandinavia and Central Europe (Lamers *et al.* 2014). The term 'rich' fen refers to minerotrophic peatlands which are base 'rich', due to a high concentration of base cations (calcium and magnesium) and are nutrient poor (oligo-mesotrophic) with pH values between 6.0 – 8.0, which subsequently leads to botanically diverse stress tolerant communities (Sjörs 1950; Wheeler 1980a; Wheeler & Proctor 2000). Furthermore, U.K. fens are quite rare and make up just 10 % of all British peatlands (JNCC 2011b). The fens which are the focus for this study, are situated off the north-west coast of Wales (U.K.) on the island of Anglesey, are internationally significant and are designated as Ramsar sites (Jones 2013). In the case of rich fens, their disjunct distribution supports their rarity, as these ground water dependent (GWD) wetlands have strict hydro-geological requirements (Joosten & Clarke 2002; Bedford & Godwin 2003; JNCC 2011b). It is these unique requirements which characterise the vegetation (Wheeler & Proctor 2000) making rich fens, amongst the most species rich, low production wetlands in the world (Ilomets *et al.* 2010). Fens also support essential ecosystem services such as water purification, flood protection and climate regulation (Gorham 1991; Zedler & Kercher 2005; Lamers *et al.* 2014) in which their contribution is disproportionate to their size (Bedford & Godwin 2003).

Historically, UK fens were economically important areas in the landscape, where agriculture, peat harvesting and biomass production for thatching ensured these systems experienced regular disturbance regimes. However, in the absence of management, rich fen plant communities have shifted from low competition/stress tolerant plant communities, with a complex assemblage of herbs, low stature sedges and bryophytes, to degraded plant communities which are dominated by graminoids and shrubs (Rodwell 1992; Billeter *et al.* 2007; JNCC 2011b). This change in trajectory from a low to high production community has also led to biomass accumulation from fast growing species, which is deleterious to maintaining fen species richness (Bergamini *et al.* 2001; White & Jentsch 2001; Hajkova & Hajek 2003; Middleton *et al.* 2006b). Abandonment also leads to litter accumulation, which covers the peat surface and impedes seedling establishment (Ruprecht *et al.* 2010). To reverse succession to an earlier sere and increase biodiversity, partial or total removal of biomass is required, which addresses the physical barrier to restoration (Brewer *et al.* 1997).

Mowing increases the space available for species to establish and increases light penetration to the peat surface (Schaffers 2002; Billeter *et al.* 2007). Successful re-colonisation by small stature fen plant species is also dependent on the proximity of the restored plant community to a seed source, seed dispersal capability of favoured species and presence of a viable seed bank (Wheeler & Shaw 1991; Billeter *et al.* 2003; Levine & Murrell 2003; Kolos & Banaszuk 2013). Therefore, rich fen species can only persist where traditional management has been maintained or is reinstated (Westhoff 1971; Tilman 1996; Middleton *et al.* 2006a; Šefferová *et al.* 2008).

This research was conducted in collaboration with the Anglesey and Llŷn fens EU LIFE project, whose main aim was to rehabilitate 751 hectares of degraded fens, in support of improving habitat quality for plants and animals, as well as enhancing recreation value to the local community. The intention for this research was to examine the botanical response to mowing in these previously abandoned fens. The focus was on two European Annexe 1 plant communities, designated for their ecological importance and rarity (Saltmarsh *et al.* 2006). The first is *Cladio-Molinietum* (CM community)*,* which is a species poor swamp community, situated within topographic depressions within valley floors and is dominated by tall sedge, *Cladium mariscus* (CM community). The second plant community is located around the fen margin, dominated by *Schoenus nigricans* and *Juncus subnodulosus* (SN community). *S.nigricans* is an ecologically important component as it produces elevated tussocks and consequential runnels (shaded channels around the tussock stools) that support a complex suite of fen species that include sedges, distinctive dicotyledonous herbs and an ecological group of "brown mosses" in the families of Amblystegiaceae and Calliergonaceae (Rodwell 1992; Bedford & Godwin 2003; Hedenas 2003).

However due to abandonment, the CM and SN communities have reduced in species richness due to an increase in cover from each of the dominant graminoid species *C.mariscus* and *S.nigricans* and so machine mowing and hand cutting was selected for each plant community respectively. These methods of management were chosen due to the sensitive nature of fen habitat (Middleton *et al.* 2006b; Van Andel & Grootjans 2006; Šefferová *et al.* 2008). In contrast to North America, burning is not common practice in U.K. fens. It is only undertaken with caution, where fire management has been used historically. This is probably due to their small areal size, which is disproportionate to high conservation value and as many species are associated with the plant litter which is being burnt (e.g. invertebrates, small mammals and amphibians) the risk to biodiversity is high (Middleton 2002; SNH 2011).

The aim of this study was to examine the response to mowing in two derelict rich fen communities employing a single mowing application. It was proposed that mowing would encourage

colonisation by calcicole (calcium-loving) rich fen plant species, which are tolerant of a low phosphate concentration, associated with the presence of calcium carbonate found in the mineral rich groundwater (Clymo 1962; Boyer & Wheeler 1989; Wassen *et al.* 2005). It was expected that following mowing, species richness would increase due to a reduction in canopy height, standing biomass and litter cover which consequently will increase exposed peat. It was also proposed that mowing would reduce dominant vegetation components, as a reduction in graminoid and shrub cover is expected to be associated with increased herb and bryophyte cover. Therefore, it is hypothesised that due to the mechanisms described above, treatment effects would produce optimum conditions to meet the conservation aim to reduce robust late succession species and increase overall species richness in each plant community.

2.3 Materials and Methods

2.3.1 Site descriptions

The study was conducted within the Anglesey fens Special Area of Conservation (SAC) which comprises 7 Sites of Special Scientific Interest (SSSI) covering 467 hectares and which form part of the Anglesey and Llŷn fens Ramsar site (Jones 2013). All experimental sites were situated on the island of Anglesey, which is located off the coast of mainland north-west Wales, United Kingdom. The three study sites comprise: (i) Cors Erddreiniog (53.3125 N, -4.29670 E), a valley head fen system, comprising three peat basins, and which is the largest of the three sites at 200 hectares (Prosser & Wallace 1995; Jones 2013), (ii) Cors Goch (53.3075 N, -4.2575 E), a basin fen comprising 67 hectares of which 25 hectares are wetland and (iii) Cors Bodeilio (53.2726 N, -4.2507 E), which is the smallest site, at 39.28 hectares, situated on shallow peat within a limestone valley (Jones 2013). These sites are influenced by an oceanic climate with a mean annual temperature of 9.4°C and total mean annual rainfall of 625 mm (calculated from the Cors Erddreiniog automated weather station (http://environmental-change.ccw.gov.uk/) from data collected between 2007 and 2013).

Paired plots were used in the CM (*n=9)* and SN (*n=8*) plant communities to ensure that hydrological and topographical conditions were as comparable as possible. One half of each paired plot (10 m^2) was randomly assigned as treatment, the other as control. Within each control and treatment plot, a set of 5 quadrats (2 m by 2 m) were established. Co-ordinates for each randomly assigned quadrat were generated, utilising an online random number generator (Random.org) and quadrats were positioned within each 10 m^2 plot. The locations of the paired 10 m^2 plots were

permanently marked by placing steel marker pegs in the peat at each corner of the plot, to allow for re-location with a metal detector after cutting. A Leica 1200 RTK digital global positioning system (dGPS) was employed to permanently locate plots and quadrat centroids and post processing was undertaken using Leica Geo Office together with RINEX data and Holyhead reference station, downloaded from the Ordinance survey GPS website (http://www.ordnancesurvey.co.uk/gps/os-net-rinex-data/). Bamboo canes were also used for ease of re-location of quadrats and plots, but were temporarily removed or pushed into the peat during mowing. Treatment and control conditions included a 5m buffer zone beyond the perimeter of each paired plot to allow for edge effects.

2.3.2 Plant communities

The *Cladio-Molinietum* (CM community) is a tall herb community found in base-rich (pH 6.0 - 7.5) peatlands, and characterised as topogenous due to its location on valley floors, where water flow is low and vertical and in summer can move below the peat surface (Wheeler 1980b; Saltmarsh *et al.* 2006; JNCC 2011a; SNH 2011). The total UK extent is estimated at 5 km^2. Its specialised hydro-geological requirements have contributed to its rapid decline (Buczek & Buczek 1996; JNCC 2007). Wheeler (1980b) describes the CM community as a swamp community owing to its location within inundated areas of the fen. The CM community is dominated by *Cladium mariscus,* a dominant perennial, sedge, which can reach a canopy height of 2 m, (Saltmarsh *et al.* 2006). In the absence of management, dense species poor communities are common, which have promoted a closed canopy. Although not monotypic, accompanying species are few and commonly include: *Phragmites australis, Menyanthes trifoliata* and *Myrica gale* (Wheeler 1980b)*.*

The second fen community occurs on peat and mineral soils and is characterised as soligenous, encountering seasonal lateral water movement. This is due to its association with springs along the fen margin, where water can be running, standing or soil remains moist, and the pH range in this community is slightly higher (pH 6.5 – 8.0) (Wheeler 1980a; SNH 2011). This community can also occur within the fen basin, where contact is maintained with calcium rich nutrient poor ground water. (Rodwell 1992; SNH 2011).

The SN community is a tussock community dominated by *Schoenus nigricans* and *Juncus subnodulosus* and is composed of a complex and rich assemblage of rich fen species; some of which are rare and the mean number of species is 27 derived from 2 m x 2 m quadrats (Rodwell 1992). Currently, the UK extent is estimated at 16.32 km^2 and 18 – 48 % of all alkaline fens are not being managed effectively, under statutory protection (JNCC 2007). Losses in this tussock community are due to agricultural gain and eutrophication (Criodain & Doyle 1997). It is the physical

characteristics that make this community so diverse as tussocks (optimal height 40 cm) and surrounding runnels can support a host of low growing sedges, herbs and bryophytes (Rodwell 1992).

2.3.3 Treatments

Management intervention in both habitats involved a single mowing event and biomass removal in both plant communities. Mowing was undertaken once in the CM community plots using a Pistenbully 100 Allseason soft tracked vehicle, modified with a 10 m^3 aluminium hopper and Mera Rabbeler forage harvester as hand cutting was not possible due to decades of biomass and litter accumulation. Harvesting was undertaken between 3 February 2012 and 28 March 2012. Live biomass and litter was cut and collected in the hopper and removed from site. The target mowing height was 5 - 10 cm, although this varied slightly depending on water table depth (WTD), peat structure and woody root density. In the SN community, one application of hand cutting was undertaken between 7 February 2012 and 29 March 2012. Due to the nature of the sensitive tussock vegetation and historical management the SN community was hand cut using strimmers (Stihl FS460C (Baden-Württemberg, Stuttgart, Germany), fitted with 3 mm nylon wire and hand raked the same day as cutting so that live biomass and litter could be removed from site. This method was chosen, as fens throughout Europe were historically mown by hand, using a scythe (cutting tool with a long curved blade) (Rowell 1986; Bartoszuk 2009).

2.3.4 Botanical surveys

Baseline plant surveys were undertaken between 26 June 2011 and 28 October 2011, and quadrats were re-surveyed post-treatment between 30 July 2012 and 20 August 2012 and 17 July 2013 and 8 August 2013. Plant surveys were undertaken by assigning all rooted taxa a percentage cover estimate, as assessed by eye. Canopy height was measured using a marked 2 m cane and 5 measurements of maximum plant height were taken to the nearest 5 cm for each vegetation component of total drooping vegetation height (the point at which the plant is no longer erect). Measurements were undertaken by placing a 2 m marking stick at the centre and 30 cm in from each quadrat corner to calculate total mean heights.

2.3.5 Biomass and nutrient content

A measurement of biomass was undertaken in December 2013 to provide an estimate of the total amount of biomass removed from the system during harvesting. Further calculations could then be undertaken to estimate the quantity of accumulated N and P tissue concentration removed in the

biomass. A 1 m^2 quadrat was randomly sampled from the control and treatment for each paired plot and plant community. The biomass was collected using secateurs, cutting to a sward height of 10 cm to ensure comparability with the mowing regime. Measurements included live and dead plant biomass combined. In the treatment plots, this included re-growth since cutting in 2011. Vegetation biomass was oven dried at 65 °C for 48 hours to remove water content, in a Riley 1250 litre HDH-OV-1250-F-250-DIG oven (West Midlands, UK). Samples were weighed immediately after drying using a Sartorius Universal balance (GMBH, Gottingen, Germany). The percentage of tissue nitrogen (N) and phosphorus (P) was derived from graminoid tissue chemistry concentrations found in the literature for rich fens (Bombonato *et al.* 2010). Calculations were only applied to control quadrat biomass weights for each plant community and further calculated to determine kg N ha^{-1}. Atmospheric N deposition loads were derived for fen habitat and the site locations from the UK Air Pollution Information System web page (www.apis.ac.uk).

2.3.6 Statistical analysis

Statistical package 'R' (R-Core-Team 2014) was employed to undertake statistical analysis of all data. Each plant community was analysed separately, using a linear mixed effect (LME) model in 'R' using the lmer function and lme4 package (Bates *et al.* 2014). The null model comprised response plus random effects ("site", "plot" and "quadrat") and the full model tested response as a function of treatment plus random effects. Analysis of variance (ANOVA) was then employed to compare differences between the variance in the null and full models to determine significance values. Treatment effects on vegetation component percentage cover, species richness, vegetation height and biomass weight. Individual species cover data (2013) were also tested.

Firstly, the models examined whether there were underlying baseline differences for the pre-treatment and control plots in 2011, to ensure the paired plots were botanically comparable prior to treatment. Percentage cover and height data were analysed using the difference between the current and base year (2012 - 2011, 2013 - 2011) to test for treatment effects in subsequent years with exception of species richness and biomass weight, which were tested using raw data. To test the significance of total number of species present in all control plots versus treatment plots in 2013; a general linear model was performed with a binomial distribution.

Multivariate analysis was undertaken to examine the relationship between plant species composition and environmental variables. Mean Ellenberg indicator values were calculated and combined with botanical data, to undertake a multivariate analysis using CANOCO (Hill *et al.* 2004; ter Braak & Šmilauer 2002). Initially, a de-trended correspondence analysis (DCA) using an

indirect gradient analysis was undertaken to assess linearity of the primary axis. As the gradient lengths were short, a linear ordination method was adopted. Indirect analysis of species data was undertaken, using principal component analysis (PCA), as a means to summarise each plant community's variation in response to treatment. Meaned Ellenberg values were used to create environmental ordination plots. The PCA ordination plots were examined to interpret results, which were best described using axes 1 and 2 for CM community and axes 2 and 3 for SN community. Axis 1 was not used for the SN community as it only showed broad site differences, not within and between environmental heterogeneity. Finally, in order to extract patterns from the explained variation and to test significance of environmental variations, a redundancy direct analysis (RDA) was performed. To test significance of environmental variables in response to treatment, Monte Carlo methods within CANOCO (ter Braak & Šmilauer 2002) were employed. This calculated the total explained variation and also assigned a percentage value to each environmental variable to indicate what proportion of explained variation was due to the species-environment relationship.

2.4. Results

2.4.1 Percentage cover of vegetation components

There were no significant differences observed in the baseline vegetation survey for each plant community for vegetation components and species richness. This confirmed that control and pre-treatment plots were botanically comparable. There were also no significant differences in DGPS elevations between treatments for the CM community (P, 0.14) and SN community (P, 0.67), suggesting topography was also equivalent.

Significant reductions were observed in the percentage cover of vegetation components for mown plots, compared with the control plots in the CM community for each year following mowing, Figure 2.1a. Reductions were evident following comparisons between the treatment and control mean percentage cover for each vegetation component, reported here with ± 1 s.e.: (i) graminoid cover in the treatment plots reduced by 46 % in 2012 (50.2 % ± 2.7) compared to the control (93.5 % ± 2.8) and by 28 % in the treatment (51.3 % ± 2.5) in the following year, compared to the control (71.48 % ± 3.9), (ii) ericoid/sub-shrub cover also reduced by 45% in the treatment (15.3 % ± 1.4) compared to the control (27.6 % ± 2.8) in 2012 and by 33 % in the treatment (24 % ± 2) compared to the control in the following year (36 % ± 3.1) and (iii) litter cover was significantly reduced by 46 % in treatment plots in 2012 (50.3 % ± 5.5) compared to the control (93.3 ± 2.7) and by 50% in treatment plots in the following year (47.9 % ± 5.9) compared to the control (95.3 % ± 3.1). Bare

ground was absent in both control and treatment plots in 2011 (0 %). However, in 2012 bare ground was 14 % higher in treatment plots in 2012 (14.2 % ± 2.1) compared to the control (0 %), and treatment plots further increased by 16 % in 2013 (16.2 % ± 2.4) compared to control plots (0.2 % ± 0.2).

Herb cover showed no difference (*P*, 0.64) between treatment (1.1 % ± 0.3) and control plots (2.7 ± 0.9) in the first year, however by the second year, herb cover increased by 79 % in treatment plots (3.9 % ± 0.7) compared to the control plots (2.2 % ± 0.5). In addition, a reduction in the dominant sedge was also observed; *C.mariscus* cover decreased by 63 % (*P*<0.001) in treatment plots in 2012 (30.4 % ± 3) compared to the control plots which remained high (81.9 % ± 4.1). A smaller reduction, 55 % was observed in the treatment plots in the following year (*P*<0.001, 25.8 % ± 2) compared to the control (57.6 % ± 4.2). Bryophyte cover was the only vegetation component to be unaffected by treatment in the CM community.
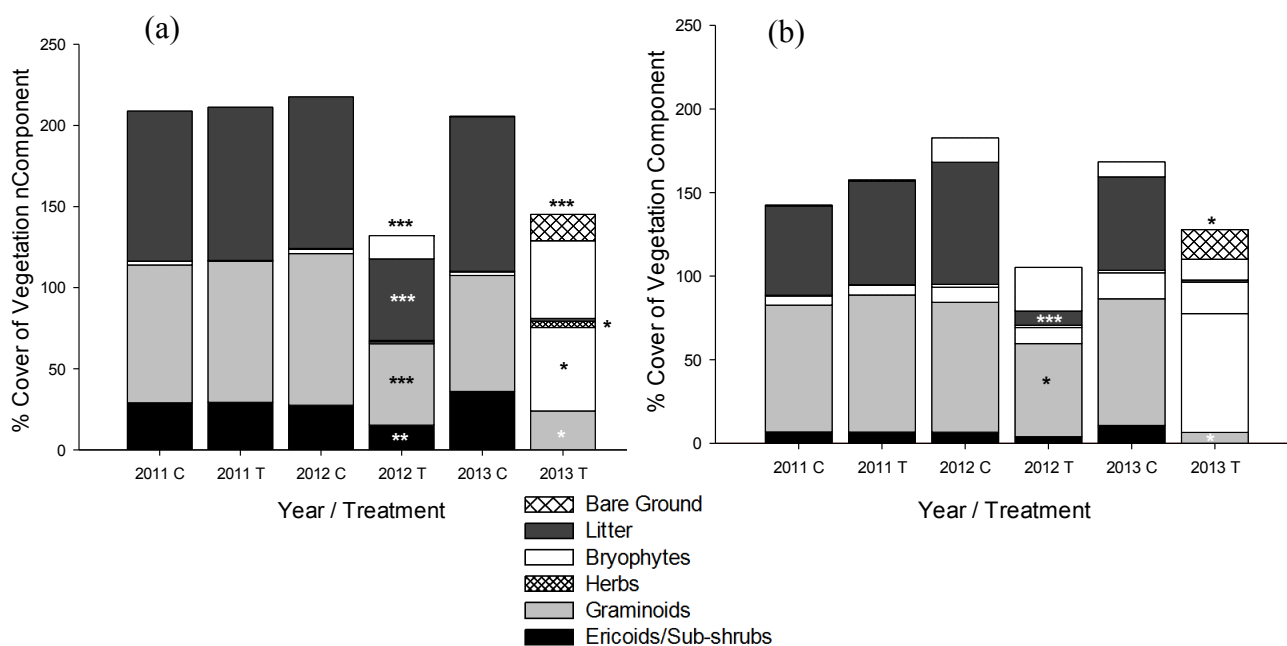
Figure 2.1. Mean percentage cover for each vegetation component for the CM community (a) and SN community (b) across all sites for the paired plots control (C) and treatment (T) for each year. Statistical analysis of treatment effects was undertaken on differenced data (T/C year minus T/C baseline) for each vegetation component and applied to LME model to test significant differences between the control and treatment for each year. Statistical codes used: '***' *P*<0.001 '**' *P*<0.01 '*' *P*<0.05 and no symbol, *P* >0.05.

The SN community, Figure 2.1b did not show a reduction in the majority of vegetation components which is in contrast to the CM community. Graminoid cover reduced by 28 % in 2012 in treatment plots (55.7 % ± 3.3) compared to control plots (77.7 % ± 4.6); however this reduction was not

sustained in 2013. A temporary reduction was also reflected in the percentage cover of dominant graminoid *S.nigricans,* which reduced by 49 % in treatment plots (18.83 % ± 2.146) in the first year following mowing, compared to the control (40.65 % ± 4.717), only to become comparable to the control plots once again in the subsequent year.

Ericoid/sub-shrub cover showed no treatment reduction following mowing in the first year, but did show a 39% reduction in treatment plots (6.6 % ± 1.5) in the second year compared to the control (10.7 % ± 2.8). Litter cover reduced by 88 % in treatment plots (8.5 % ± 1.7) in 2012 compared to control plots (73.1 % ± 4.6) and sustained a 78 % reduction by 2013 in treatment plots (12.4 % ± 1.9) compared to control plots (55.9 % ± 4.7). Furthermore, no difference in bare ground was observed in the first year, although in the following year, treatment plots (17.8 % ± 2) increased compared to control plots (8.9 % ± 1.5); the controls appeared to exhibited surveying disturbance. In spite of the sustained reduction in litter cover; the temporary reduction in graminoid cover is likely to be attributable to the unaffected cover in the treatment compared to the control for the herbs (18.8 % ± 1.48, 15.56 % ± 1.16) and bryophytes (1.37 % ± 0.6, 1.49 % ± 0.5) respectively in 2013.

2.4.2 Vegetation height
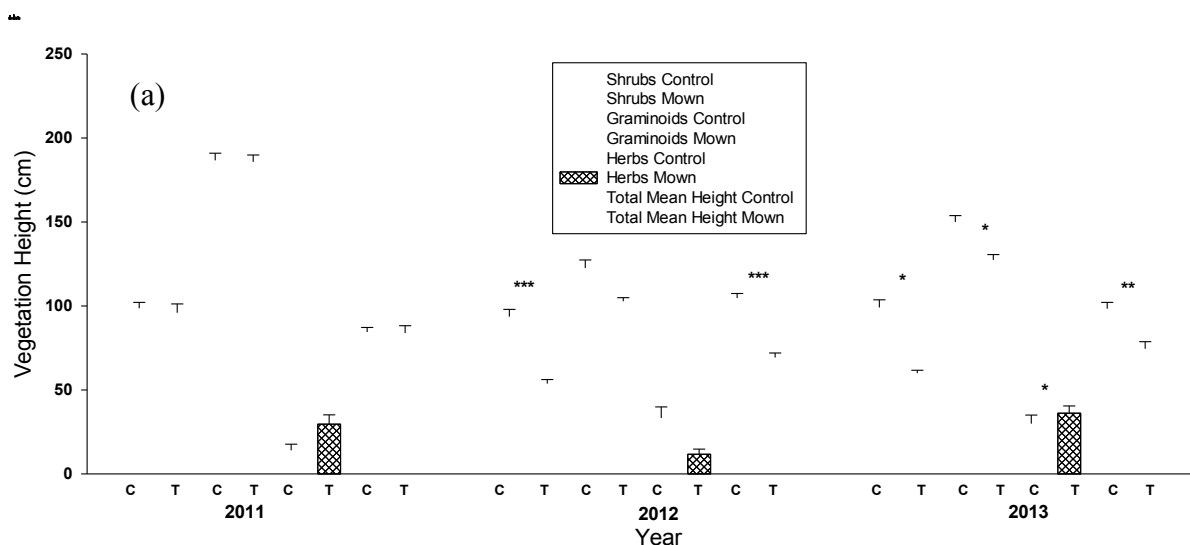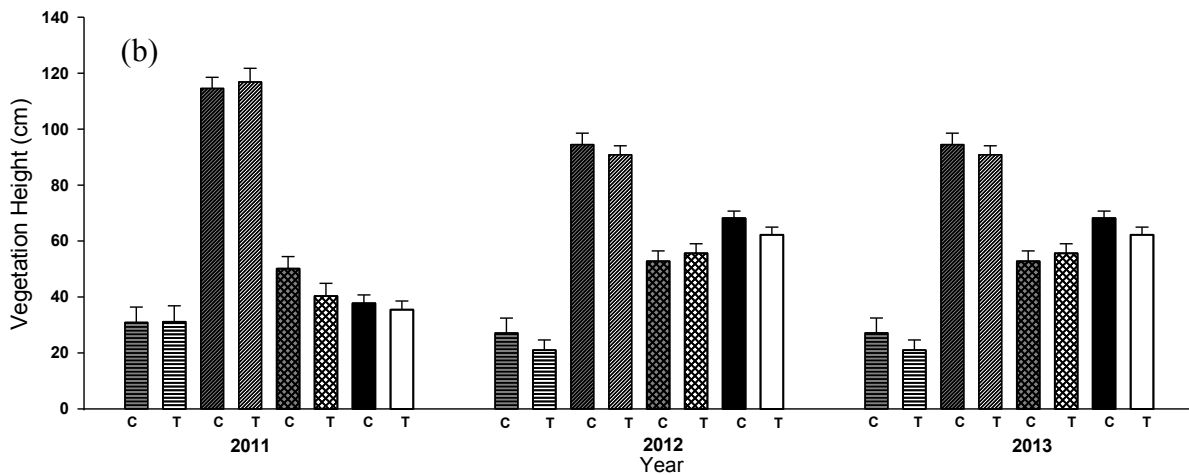
Figure 2.2. Vegetation height for CM community (a) and SN community (b) across all sites for the paired plots control (C) and treatment (T). Mean maximum for each vegetation components and overall mean maximum for all sites is illustrated. Statistical analysis of treatment effects was undertaken on differenced data (T/C year minus T/C baseline) for each vegetation height component and applied to LME model to test significant differences between the control and treatment for each year. Statistical codes used: '***' $P<0.001$ '**' $P<0.01$ '*' $P<0.05$ and no symbol, $P > 0.05$.

In the CM community, Figure 2.2a, mowing reduced the overall mean vegetation height between the treatment and the control in 2012 and 2013 by 34 % and 24 % respectively. Ericoid/sub-shrub cover reduced by 66 %, and 67 % and graminoid cover reduced by 35 % and 41 % with no observed difference in herb height. No treatment effect was observed for the SN community heights, Figure 2.2b.

2.4.3 Biomass and nutrient removal

Standing biomass and litter in the CM community, Figure 2.3a was reduced by 75 % compared to the control, which was comparable across all sites. Mean biomass weight removed was calculated as 1396.4 g m^2. N removal was calculated as 240.18 kg N ha^{-1} and equated to 15 years of N in annual atmospheric deposition, which is 16.1 kg N ha^{-1} year^{-1} for fen habitat at these sites (APIS 2014) and P removal was calculated as 13.27 kg P ha^{-1}.

In contrast, Figure 2.3b illustrates that the overall amount of biomass removed in the SN community was much lower (41 %) and it was not comparable across sites, owing to large error bars caused by site heterogeneity. Cors Goch was the only site with a significant reduction. However, biomass contained 57.04 kg N ha^{-1}, which equates to 3.5 years of atmospheric N being removed and 3.15 kg P ha^{-1}.
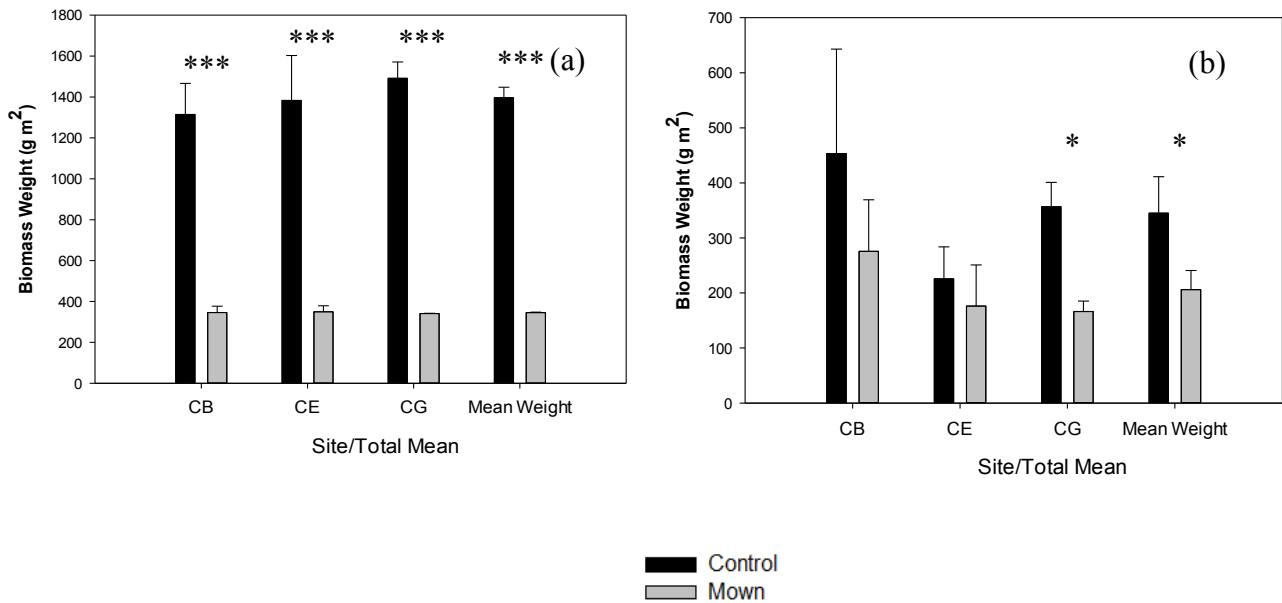
Figure 2.3 Biomass weight for CM community (a) and SN community (b) showing mean weight for all control and treatment plots for each site and overall mean biomass weight for all sites: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Black bars indicate the control plots and grey bars indicate the mown plots. Each bar shows +/- 1 standard error and statistical codes used are: '***' $P<0.001$ '**' $P<0.01$ '*' $P<0.05$, no symbol, $P >0.05$.

2.4.4 Species richness

In the CM community, following the initial disturbance caused by mowing in 2012, a 51 % increase in species richness was observed in 2013, Figure 2.4a. The positive change in species richness was driven by an increase in the number of herbs. By 2013 the mean number of herbs were 2.31 ($\pm$ 0.328) in the treatment plots versus 0.95 ($\pm$ 0.174, $P<0.05$) in the control plots. Also, by 2013 there were 2.16 ($\pm$ 0.208) bryophyte species per treatment plot versus 0.56 ($\pm$ 0.148, $P<0.001$) per control plot. Differences between sites were also apparent, Figure 2.4b, where Cors Erddreiniog and Cors Bodeilio both increased in species richness and Cors Goch showed no response to treatment (P, 0.55).

Overall the SN community showed no change in species richness, Figure 2.4 (c) in response to treatment. However, Cors Goch, which was the least species rich site, exhibited a weak positive response to treatment (P, 0.06) which was not significant, Figure 2.4d. In 2013, it was observed that the mean number of species remained low at 17.38 $\pm$ 0.532 species per treatment plot and 16.30 $\pm$ 0.710 species per control plot. This was 36 % lower than the constant mean number of species for this community (Rodwell 1992), as referred to in the methods.
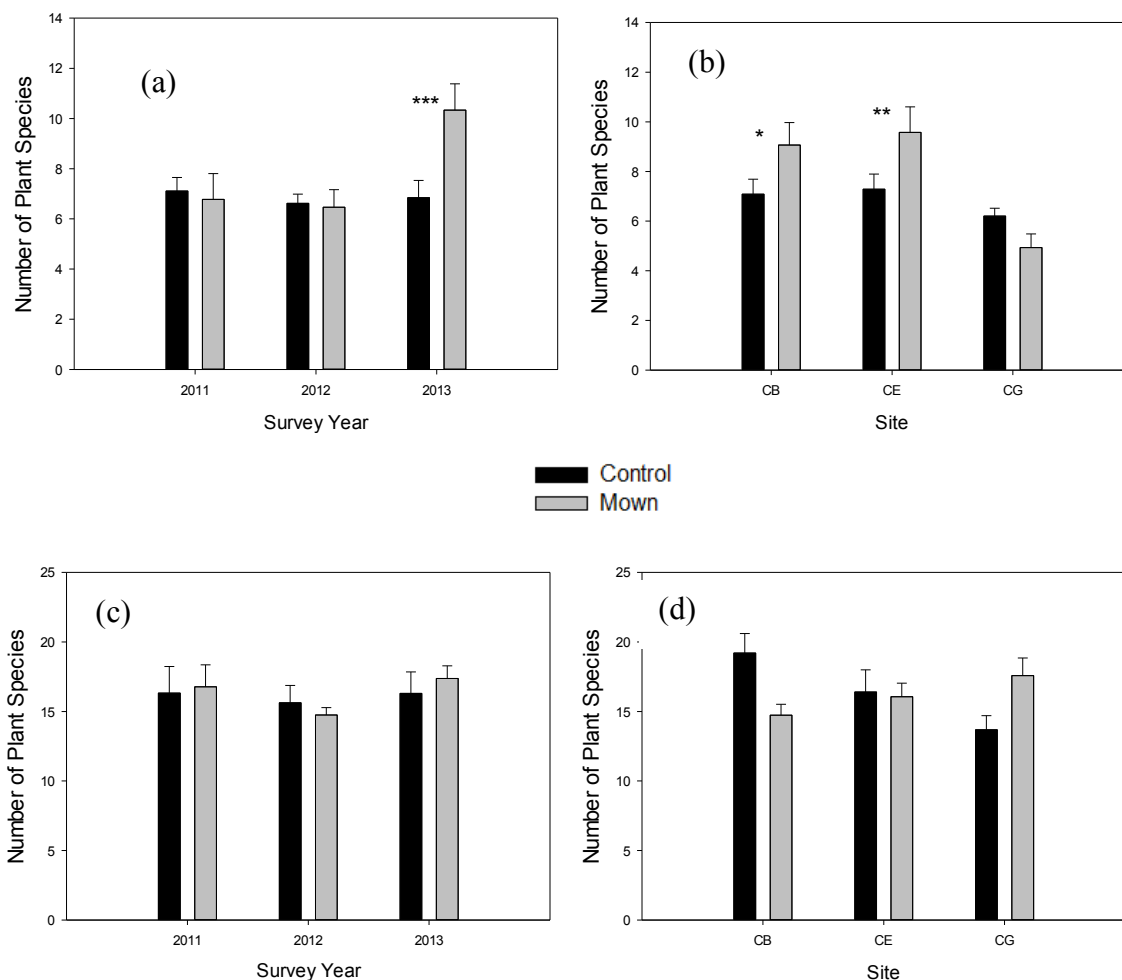
Figure 2.4 CM community species richness for: (a) all sites over time and species richness and for (b) each site in 2013. SN community species richness for (c) all sites over time and species richness for (d) for each site in 2013. Site codes: Cors Bodeilio (CB), Cors Erddreiniog (CE), Cors Goch (CG). Black bars indicate the control plots and grey bars indicate the mown plots. Each bar shows +/- 1 standard error and statistical codes used are: '***' $P<0.001$ '**' $P<0.01$ '*' $P<0.05$, no symbol, $P>0.05$.

2.4.5 Multivariate analysis for CM community

All environmental variables (EV), Table 2.1, tested highly significant ($P<0.001$) using the Monte Carlo permutation test, which showed that EN, ER, and *C.mariscus* cover made a considerable contribution to total species variation.

In the CM community, the PCA showed that the first 4 axes explained 78.3 % of the species environment relationships and explained 52.3 % of percentage variance for species data for axes 1 and 2 is 36.6 % and the largest effect size was derived from site.

Table 2.1 List of CM community environmental variables (EV) and associated

abbreviations shown in the following environmental ordination plot, figure 5 (c), which depicts percentage of total species variation explained within RDA and significance tested for each variable independently. *** '*P,* 0.001'.

Environmental Variables [EV]	Variance (%)
Site	12.6 %***
EllenbergN – nitrogen [EN]	12.2 %***
EllenbergR – acidity [ER]	10 %***
C.Mariscus cover [Cl]	7.7 %***
Species richness [Spp]	7.6 %***
Litter cover [L]	6 %***
EllenbergF – moisture [EF]	5.8 %***
Bare ground [B]	3 %***
EllenbergL – light [EL]	2.6 %***
Year [Y]	2.2%***
Vegetation Height [H]	2.3%***
Treatment [T]	1.8%***

two sites based on environmental gradients.

This is evident from the distinct spatial heterogeneity in species distribution, Figure 2.5a. In the CM community, the PCA showed that the first 4 axes explained 78.3 % of the species environment relationships and explained 52.3 % of the total species variance. The cumulative percentage variance for species data for axes 1 and 2 is 36.6 % and the largest effect size was derived from site. This is evident from the distinct spatial heterogeneity in species distribution, Figure 2.5b.

The ordination plot for the CM community, Figure 2.5 (a) clearly illustrates that Cors Goch (CG), (diamonds) differs from the other

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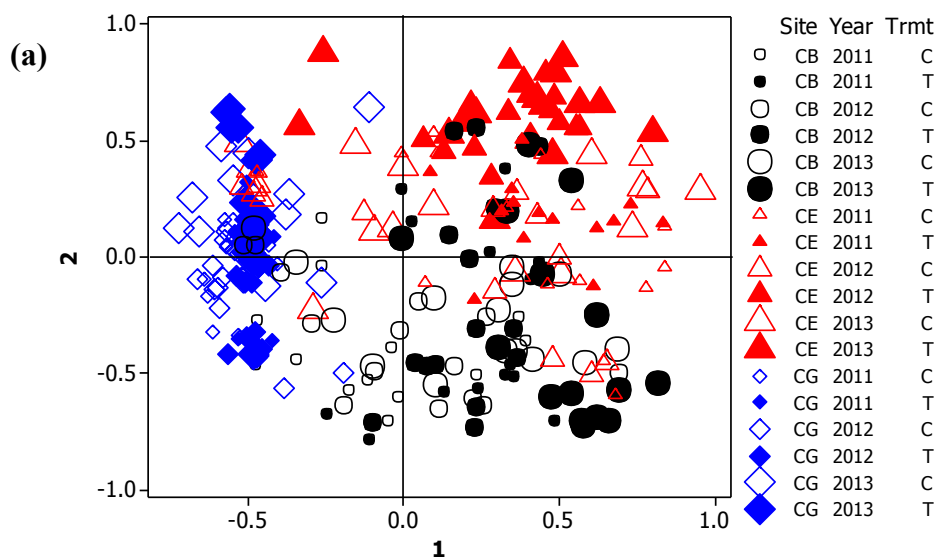
Figure 2.5. PCA sample ordination plot for CM community (a) for all sites and all years. Site abbreviations are: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Open symbols represent control (C) and solid symbols represent treatment (T) and symbol size depicts time (years), (b) Species ordination plot (PCA) for all years depicts species weighting >0.05 as well as enforced significant species shown below this threshold. Statistical codes for species indicate treatment effect in 2013: '***' $P<0.001$ '**' $P<0.01$ '*' $P,0.05$ where + indicates a significant increase in cover and − indicates a significant reduction in cover as a result of treatment, (b) the environmental ordination plot (c) is applicable to both diagrams and also derived from the PCA.

This is a possible cause for the unaltered change in species richness [Spp] (as reported earlier), shown by the low position on axis 1, which is associated with higher moisture, Figure 2.5c. Species impoverishment is also evident by the low position on axis 1 in Figure 2.5 (b) and close association with *C.mariscus, Salix cinerea* and aquatic specie *Equisetum palustre,* suggesting that these species' requirements for N and moisture are higher here, Figure 2.5c. CG has higher levels of moisture, and nitrogen, as evident from its position on the Ellenberg N - nitrogen [EN]/Ellenberg F – moisture [EF] gradient. CG is also associated with increased vegetation height [H], litter cover [L] and *C.mariscus* cover [Cl]. At Cors Bodeilio [CB], (circles), Figure 2.5 (a), samples move from left to right across axis 1 over time, consistent with an increase in species richness. This trajectory is negatively associated with increased moisture, EllenbergL - light [EL] and vegetation height, as indicated by the opposing gradient of [EN], EllenbergR - pH [ER], moisture, light and vegetation height.

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There is also a divergence along axis 2, suggesting within site heterogeneity is high. This site also demonstrates more acidic conditions and reduced light as demonstrated by species (*Calluna vulgaris, S.subnitens* and *Erica tetralix*) present in bottom right axes in Figure 2.5b. Finally, Cors Erddreiniog (CE), (triangles) is moving up axis 2 and across axis 1, demonstrating a strong positive response to treatment in regard to species richness. This site's trajectory is more progressed than CB and CG as this is the most species rich of all three sites as a result of treatment. This site is also associated with less litter, lower canopy height and lower cover of *C.mariscus* which are negatively associated with treatment, Figure 2.5c.

By 2013 in the CM community, a total of 74 species were recorded in treatment plots across all sites versus 44 in the control (*P*<0.001). Treatment effect was evident in 13 species with the majority increasing in percentage-abundance; in particular, *Phragmites australis,* which increased by 78 % in mown plots. However, notable reductions were observed in other graminoids and sub-shrubs such as: *C.mariscus, C. vulgaris* and *Myrica gale*. Two new species colonised: *Hypericum pulchrum* and C*ampylopus flexuosus,* refer to Figure 2.5b for other significantly affected species.

2.4.6 Multivariate analysis for SN community

The percentage variance for species data for axes 2 and 3 is 20.9 % and the largest effect size was derived from EllenbergF - moisture [EF], site, *C.mariscus* cover [Cl] and EllenbergN – nitrogen [EN]. All environmental variables (EV) tested highly significant (*P*<0.001) using the Monte Carlo permutation test, Table 2.2. In the SN community, the PCA showed that the first 4 axes explained 74.4 % of the species environment relationships and explained 46.5 % of the total species variance. Axes 2 and 3 are presented for the SN community which best describes the species environment relationships as axis 1 mainly illustrated site differences.

The PCA shows a clear divergence between sites' individual trajectory in response to treatment, Figure 2.6a. Axis 3 displays a species richness [Spp], year [Y] and treatment [T] gradient, which is negatively associated with [EF], litter [L] and vegetation height [H]. Axis 2 exhibits increasing EllenbergR – acidity [ER], EN, *C. mariscus* cover and bare ground, which is negatively associated with EL.

**Table 2.2** List of SN community environmental variables (EV) and associated abbreviations shown in following environmental ordination plot, figure 6 (c), which depicts percentage of total species variation explained within RDA and significance tested for each variable independently. ***P, 0.001'.
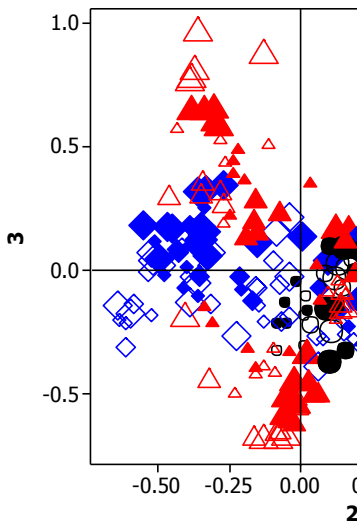
Environmental Variables [EV]	Variance (%)
EllenbergF – moisture [EF]	10 %***
Site	9.6 %***
C.Mariscus cover [Cl]	7.6 %***
EllenbergN – nitrogen [EN]	7.2 %***
EllenbergR – acidity [ER]	6.7 %***
EllenbergL – light [EL]	5 %***
Species richness [Spp]	3 %***
Year [Y]	2.2 %***
Litter cover [L]	2.1 %***
Vegetation Height [H]	1.3 %***
Bare Ground [B]	1.3 %***

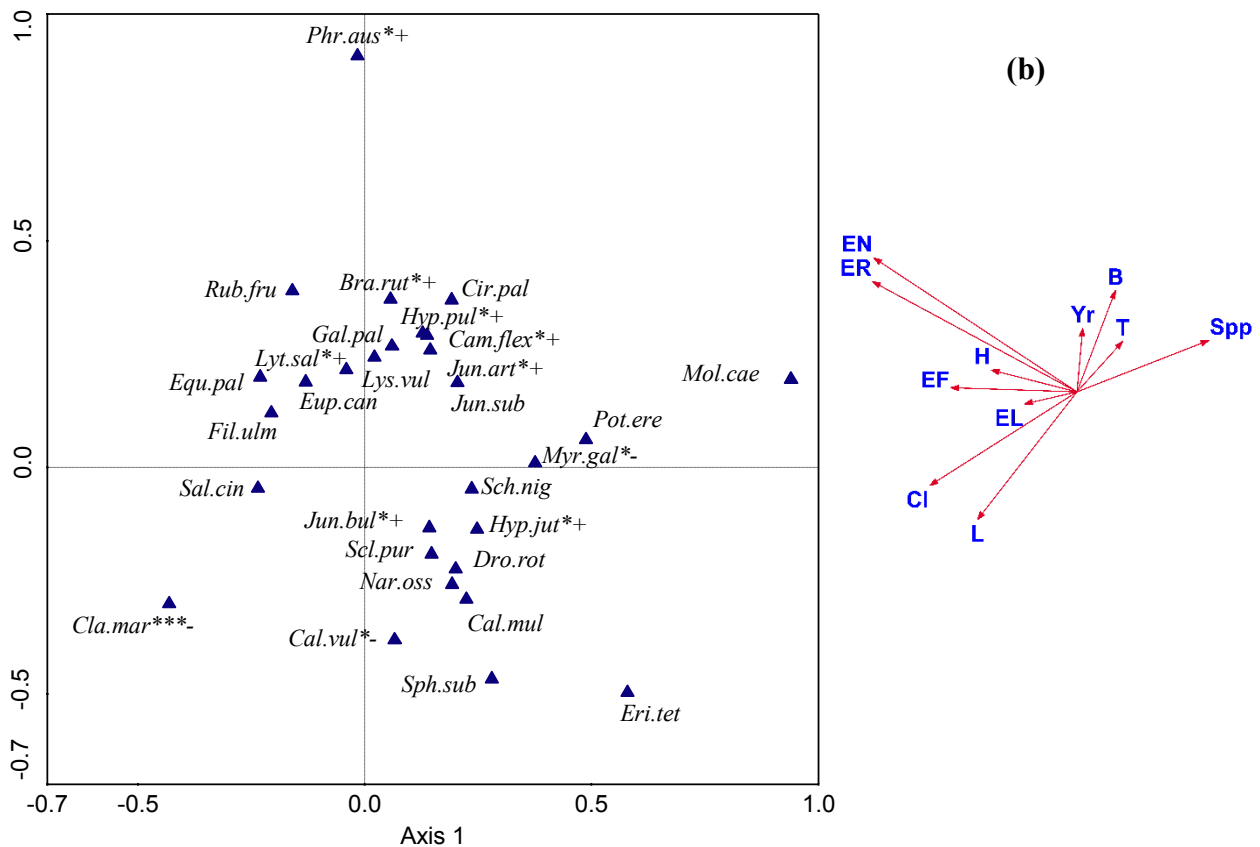**(a)**

(b)
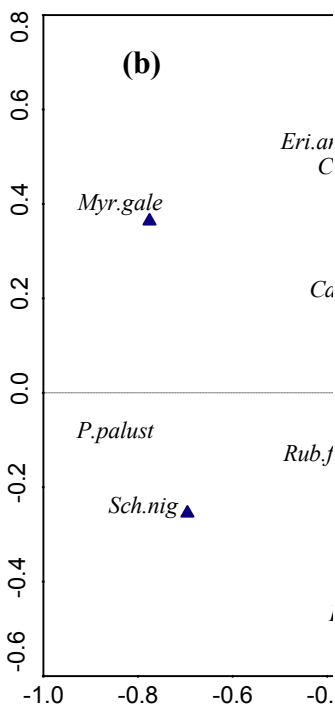
(c)
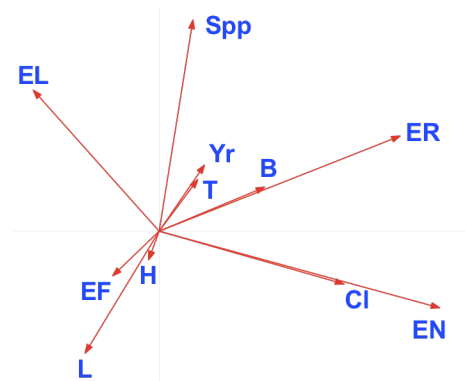
Figure 2.6 PCA sample ordination plot for SN community (a) for all sites and all years. Site abbreviations are: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Open

symbols represent control (C) and solid symbols represent treatment (T) and symbol size depicts time (years), (b) species ordination plot (PCA) for all years depicts species weighting >0.05 as well as enforced significant species shown below this threshold. Statistical codes for species indicate treatment effect in 2013: '***' *P*<0.001 '**' *P*<0.01 '*' *P*, 0.05 where + indicates a significant increase in cover and − indicates a significant reduction in cover, as a result of treatment. The environmental ordination plot (c) is applicable to both diagrams and also derived from the PCA

CG (diamonds) is the only site that exhibits a positive shift up axis 3, Figure 2.6a, which is consistent with species richness (*P*, 0.06) data reported earlier and appears to be associated with increased bare ground, reduced litter cover and negative association with nitrogen. CB (circles) is moving across axis 2 and up axis 3 towards increased bare ground [B] and acidity [ER], with a more gradual shift towards species richness. Finally, CE (triangles) demonstrates a strong divergence between plots which appear to be distributed based on a moisture/litter/canopy height gradient which is negatively associated with species richness. Species in wetter samples included *Menyanthes trifoliata*, *P.australis* and *E.tetralix,* Figure 2.6b. Overall, species richness at this site remained constant and exhibited no treatment effect.

Species response across all SN community sites showed that in the first year following mowing *Myrica gale* reduced (*P*<0.05) and *Angelica sylvestris* (*P*<0.05) increased, although neither species sustained this treatment effect. In 2013 *Oenanthe lachenalii* (*P*<0.01) reduced and there was an increase in *Carex flacca* (*P*, 0.055) and *Lythrum salicaria* (*P*, 0.053), as observed by a weak positive treatment effect. However no new species colonised following treatment. Across all sites,

total number of species were 103 in the control, and 98 in the treatment in the baseline year. By 2013, total number of species were recorded as 97 in both the control and treatment.

2.5 Discussion

This research demonstrates how a single mowing event can have contrasting effects on two botanically different vegetation communities and that the disparity observed is complex. Variation in response to restoration is complicated by ecological gradients between and within sites, which include historical management and plant community dynamics (Turner *et al.* 1998; Wheeler & Proctor 2000; White & Jentsch 2001). Inherent conditions such as nutrient availability, hydrology, peat depth and buffering capacity (Cusell *et al.* 2014; Lamers *et al.* 2014) (not examined here) are also likely to be mechanisms which are driving the positive and negative response to restoration.

In the CM community, a large increase in species richness was achieved through mechanised mowing, due to a modification to vegetation structure and peat disturbance. This has led to botanical recovery in the short term. Hypotheses were confirmed due to biomass and litter removal, disturbance to the soil and subsequent peat exposure. This resulted in a reduced canopy and reduction in graminoid and shrub cover, which collectively contributed to the strong treatment response observed. Biomass removal changed the physical structure in the CM community, causing subsequent changes which have eliminated pre-existing ecological barriers (created by secondary succession) and supported rehabilitation for early succession species to colonise. Conversely, although the SN community vegetation components responded to treatment initially; this was short lived. However, species richness remained constant throughout.

Biomass removal has the potential to reduce available N and P from each plant community in the long term, which would be a beneficial treatment response at these co-limited sites (Venterink *et al.* 2003; Bombonato *et al.* 2010). If biomass is not removed, 50-60 % of N and 80-90 % of P is resorbed from decaying above-ground biomass, in which graminoids are particularly efficient at resorbing P (Aerts 1996; Aerts & Chapin 2000). Therefore, if nutrient cycling can be inhibited following routine biomass removal over time; this will benefit the low nutrient requirements of target fen species, which subsequently will support target fen community rehabilitation. Limiting the availability of N and P in a fen is an important component in restoration but nutrient recovery will need repeated intervention (Grime *et al.* 1988; Venterink *et al.* 2009; Bombonato *et al.* 2010).

2.5.1 CM community

In the short term, the CM community has responded rapidly to intervention, where moisture and nitrogen levels are low. Therefore, this community has achieved the conservation aim of increasing species richness. Removal of physical barriers (biomass and litter) and peat exposure, combined with a reduction in graminoid and ericoid/sub-shrub cover are likely to be the principle causes for species recovery. In particular, mowing reduced the cover of dominant graminoid and woody species: *C.mariscus, M.gale* and *C.vulgaris.* Prior to mowing, these species dominated the canopy and outcompeted small stature species for all available resources. Reduced cover from these species and optimised environmental conditions has permitted new herbs and bryophytes to colonise. However, due to coppiced shrubs such as *M.gale* and clonal growth of late succession graminoids such as *C.mariscus;* these two vegetation components began to recover, in spite of sustaining a significant reduction overall. Therefore, for this community to progress along a trajectory of increased herbs and reduced graminoids and shrubs, ongoing management is needed to control dominant species expansion, biomass accumulation and vegetation height (Middleton *et al.* 2006b; Rasran *et al.* 2007).

The displacement of robust species and reduced competition has led to the total number of species in the control and treatment significantly increasing from 44 to 74 respectively. Reduced competition has supported the colonisation of previously absent small stature species such as *Hypericum pulchrum* and *Campylopus flexuosus.* However, in spite of these species' contribution to increased species richness, their ecology suggests they are not target rich fen species (Stace 2010). Their presence may be more indicative of the presence of non-target species within the seed bank (Kiehl *et al.* 2010). However, some target species did increase by the second year, as demonstrated by a significant increase in target brown moss *Campylium stellatum var. stellatum.* Bryophytes are an important component of rich fens and an increase in the number of species from this vegetation group will further facilitate vascular plant recovery. This is due to their influence on biogeochemical processes, such as P acquisition, as bryophytes can oxidise soils, which subsequently leads to increased phosphatase activity (Crowley & Bedford 2011). Other species which have increased due to mowing include: *L.salicaria, J.articulatus* and *J.bulbosus* which are pioneers, owing to their high light requirements (Hill *et al.* 2004). New species colonisation suggests propagule availability is not limited for these species and seed/spore bank viability is good, as ameliorated conditions have supported seedling establishment (Stroh *et al.* 2012). However, if target wetland species do not increase in subsequent years through natural re-colonisation, species re-introduction should be considered via hay, plant or bryophyte fragment transfer from botanically

characteristic sites (Van Groenendael *et al.* 1998; Cobbaert *et al.* 2004; Graf & Rochefort 2010; Hedberg *et al.* 2012). Ho and Richardson (2013) suggest that *Juncus and Carex spp.* seed reintroduction can facilitate restoration, as these native perennials are considered to protect against invasions from more competitive species.

Although litter cover was reduced, it remained higher than expected. During harvesting, shredded litter was blown from the Pistenbully's open auger, adhering to the inundated peat surface. Therefore, harvesting should not be undertaken when the wetland is heavily inundated or during high winds, as this appears to inhibit litter removal rates. Litter cover has been shown (in both plant communities) to be negatively associated with species richness and is a known barrier to low growing species establishment (Jensen & Meyer 2001).

Although mowing has been beneficial for the CM community, mowing in the winter has exposed some deleterious effects to species composition. *P.australis* exhibited stimulated growth and increased in cover as a result of mowing. This is due to winter mowing, which allows translocation and storage of resources to rhizomes at the end of the growth season (Asaeda *et al.* 2006). Carbon translocation and vigorous expansion can be minimised if mowing takes place in late summer. (Fogli *et al.* 2014).

2.5.1.1 CM community site response

CG was the only site in which the CM community did not increase in species richness, which is considered to be caused by inherent site conditions. For this site, higher nitrogen [EN] and moisture [EF] values were observed, which are negatively associated with species richness. Wetter sites favour dominant graminoid species, such as *C. mariscus* and *P. australis*; the former thrives on a high water table year round (Saltmarsh *et al.* 2006), which limits species richness. If the wetland is too wet, limited species can germinate (Kennedy et al. 1992) and target species may be precluded. Bryophyte distribution is also deleteriously affected by a high water table, becoming less frequent in inundated areas of the fen (Ilomets *et al.* 2010). Wetter conditions and higher nitrogen availability are thought to have contributed to the poor treatment response at this site. Therefore, further attempts of restoration at this site are less likely to be successful, until the water level and nitrogen availability is reduced.

Conversely, CE exhibited better conditions for fen restoration, which is evident from increased species richness and a good ecological trajectory in response to mowing. This site's trajectory is positively directed towards increased species richness, which is associated with increased bare

ground and a lower canopy height. CB also demonstrated an increase in species richness, however its trajectory is not as strong as CE. However, due to this site's strong association with *C.mariscus* and litter cover; it is suggested that these ecological barriers will prevent continuing increased species richness, unless a mowing regime is established.

Finally, ongoing monitoring is needed to determine when species richness stops increasing and begins to decline, to ensure timely and cost-effective mowing can be reinstated on rotation. Modern fen management follows a 3-5 year rotation as tracked machines can cause large scale disturbance, such as pooling on the peat surface; furthermore a flexible mowing date will support the conservation of wetland fauna (McDougall 1972; SNH 2011; Kotowski *et al.* 2013). Mowing on rotation will also manage biomass and litter accumulation (Diemer *et al.* 2001; Valko *et al.* 2012), which are the primary physical inhibitors for small stature herbs (Kolos & Banaszuk 2013). Furthermore, timing and frequency should be site dependent. Autumn mowing is optimum in this community, as this can alleviate internal eutrophication, inhibit *P.australis* expansion and maintain a low shrub cover; however this would need to be repeated routinely (Aerts & Chapin 2000; Hovd & Skogen 2005; Sundberg 2011).

2.5.2 SN community

The response to a single treatment in the SN community did not confirm all the hypotheses, in terms of increasing species richness, reducing dominant species and reducing canopy height. In spite of this, positive treatment effects included a reduction in litter cover and biomass and an increase in bare ground.

Overall, fewer treatment effects were evident in this plant community, owing to the inhibitory physical constraints imposed by graminoids and high within and between site spatial heterogeneity, evident by differing species richness and biomass weights (Valko *et al.* 2012; Lamers *et al.* 2014). Therefore, the SN community would benefit from a more intense, frequent mowing regime that is also site specific.

Mowing reduced graminoid cover initially, however graminoids regained their pre-treatment cover in the second year, reinstating competition against smaller herbs for nutrients and space. Other studies have shown that seed banks become depleted exponentially with succession, which may have contributed to the absence of new species following management (Jensen 1998; Bakker & Berendse 1999; Hald & Vinther 2000; Donath *et al.* 2007). The mean number of species in the control (16.3) and treatment (17.3) was constant two years after treatment. However, a reference SN

community has 27 constant species present (Rodwell 1992). This indicates that the SN community remains degraded following a single mowing application.

The fast re-establishment of graminoid cover is probably due to the dominant sedge, *S. nigricans;* its cover reduced temporarily in year one, but was comparable to the control in year two. It is not known to be clonal; although the semi-evergreen foliage produces large quantities of persistent biomass each growth season, which contributed to the unchanged canopy height, two years following mowing (Wheeler & Shaw 1991; Rodwell 1992). High percentage cover of *Schoenus nigricans* was also negatively associated with species richness. This is because it is tolerant of low nutrients, as well as forming drier microhabitats (tussocks) which are raised from waterlogged conditions (Rodwell 1992). However, this graminoid provides essential physical structure to this plant community, contributing to the species richness. Future management needs to control biomass accumulation so that runnels remain open and a light canopy is provided for low stature herbs and bryophytes to colonise.

Furthermore, shrubs exhibited a delayed response to mowing, reducing only by the second year. Reduced shrub cover in 2013 was not being driven by dominant shrub *M. gale* as presumed, as this species renewed its cover in the same year. Therefore the overall change in shrub cover was driven by Ericoids which are less likely to pose a threat to herb colonisation as they support a smaller canopy, located in the understorey. Tall herbs also responded to treatment, where *A. sylvestris* initially increased in cover, but was not sustained. Similarly, *O. lachenalii* also decreased in cover in the second year; both effects are probably owing to the renewed growth from graminoids, also observed in the subsequent year. Wetland pioneer species *L. salicaria* and target fen species *C.flacca* also increased; the latter species is usually present in high frequency (Rodwell 1992), which suggests some target fen species can persist.

Biomass reduction was only shown at one site (CG), although an overall treatment effect was observed. This is possibly associated to within and between site heterogeneity, which has driven change in productivity (Wheeler & Proctor 2000), imposing control on restoration outcomes. There is a clear environmental gradient, where high moisture, high litter cover, low bare ground and increased canopy height are collectively negatively associated with species richness.

Conversely, species that have increased in response to treatment are associated with low moisture, high bare ground cover, low litter cover and low canopy height. Therefore, secondary succession species are present in wetter conditions, support a taller canopy and higher litter cover. These species were evident in the species ordination plot and include *P.australis* and *S. nigricans.* These

robust graminoids inflict strong competitive vigour and impose change within the community's micro-climate and canopy height, typically imposed by fast growing rhizomatous species (Rosenthal 2010).

2.5.2.1 SN community site response

High spatial heterogeneity is evident across and within all sites and it is these inherent diverse conditions (Cusell *et al.* 2014; Lamers *et al.* 2014) which are likely to be contributing to the varied response to treatment. Species richness is negatively associated with increased moisture [EF] and reduced bare ground [B]. Therefore, those sites experiencing prolonged hydro-periods will have reduced bare peat, due to inundation. As discussed earlier, this can inhibit plant colonisation (Kennedy *et al.* 1992). Overall, CG appears to be on the best trajectory, as it is the only site which demonstrated increased species richness. This may be driven by the reduction in biomass, solely observed at this site, and an apparent ecological species shift from more aquatic to emergent species following increased light and bare ground, where more species are now able to colonise tussocks. CE demonstrated a strong species richness divergence, which did not appear to be associated with treatment, where a large number of samples were located in wetter conditions. Furthermore, this site did not show a reduction in biomass, which in addition to high moisture has impeded species recovery. CB did not respond well to treatment, which does not appear to be related to high moisture, rather this site has exhibited no change in biomass.

A higher mowing frequency is needed in the SN community to combat graminoid and sub-shrub cover. This should be undertaken on alternate years to sustain herb diversity (Wheeler 1980b; Bissels *et al.* 2006; Leng *et al.* 2011; Valko *et al.* 2012) and switch between autumn and summer to favour overall plant diversity (Valko *et al.* 2012; Kolos & Banaszuk 2013). Autumn mowing impedes shrub encroachment (Sundberg 2011) and inhibits internal eutrophication (Aerts & Chapin 2000; Hovd & Skogen 2005).

2.6 Conclusion

This short term study has demonstrated that both communities have exhibited varying degrees of restoration success, and that litter removal was more efficient via hand cutting and raking rather than machine mowing with has likely influenced the increased DOC/TON inputs to the pore water in the CM community. However, the CM community experienced rapid rehabilitation, which resulted in an increase in species richness, although the same progress was not achieved in the SN community. As Bradshaw (1996) and later others (Pfadenhauer & Grootjans 1999) have stated;

restoration is gradual and projecting target community composition is very difficult, given the contrasting influence of abiotic, biotic and historical management activities between sites (Lamers *et al.* 2014).

Principally, rehabilitation is driven by increased bare ground, reduced vegetation height, litter and graminoid cover, which was achieved in the CM community, primarily because mowing reduced cover of the dominant graminoid, *C.mariscus*. Conversely, the SN community's species richness remained constant, due to sustained graminoid cover, imposed by *S.nigricans,* which is also likely to have caused the sustained vegetation height. A finer control on the dominant sedge, *S.nigricans* is needed, so that runnels remain clear; however, light shade is important for target fen herbs and bryophytes to colonise.

In the CM community, winter mowing has also caused *P.australis* to expand. Summer mowing may be necessary to reduce *P.australis* cover as the removal of shoots during the growth season intercepts the carbohydrate translocation to rhizomes (Asaeda *et al.* 2006; Fogli *et al.* 2014).

Although success has been achieved in the short term, the trajectory for each plant community is not optimal. The SN community supports indicative species but falls below the mean number of species for a characteristic SN community (Rodwell 1992) and the CM community is increasing in species but early indications suggest these are not target fen species that are colonising. However, it is expected that with ongoing mowing, more target species will colonise through natural processes, although seed banks will need investigation at these sites prior to further investment and management intervention. If evidence suggests the species pool is in poor condition, species reintroduction would be needed to increase species richness along an alkaline fen trajectory. This is more likely to be a possible barrier to species recovery in the impoverished CM community, which is located further away from a seed source and most sites are inundated year round which may affect seed viability. Finally, optimum mowing frequency will facilitate sustained control over graminoid and sub-shrub cover, as succession towards these vegetation components, as shown here, is very strong (Shea *et al.* 2004).

2.7 Recommendations

Future restoration intervention should include extensive baseline surveys to record environmental variables such as water table depth, N and P inputs (groundwater, surface water) as well as biological surveys. Pre-determining hydro-chemical and/or biological barriers to restoration will provide an insight in to pre-restoration site conditions (Bakker & Berendse 1999; Holzel *et al.* 2012;

Lamers *et al.* 2014). Fen systems which are free from deleterious environmental issues should be targeted first and other sites may require additional management to ensure any environmental barriers are removed prior to mowing (Lamers *et al.* 2014). This will ensure restoration is efficient and a higher rate of success is secured.

Furthermore, seed/spore bank viability and availability of diaspores (Holzel *et al.* 2012) needs investigating for each plant community, as little work has been undertaken on abandoned rich fens and seed bank viability, which may be limiting target species establishment (Bakker & Berendse 1999; Bart *et al.* 2015). It is likely both communities will require further intervention by way of seed re-introduction and or hay transfers, in order to maintain a positive rich fen trajectory. Site and plant community specific interpretations to restoration must also be examined carefully so that individual management plans can be established (Schmitz 2012). Careful monitoring will also avoid further investment in sites which support inhibitory conditions.

Restoration success should not be based on species presence alone; improvements in ecological function and interaction must also be examined to ensure natural ecological processes initiate for the system to be considered restored (Mitsch & Gosselink 2007). Ecosystem function affects plant diversity and vice versa, so below-ground processes such as microbial interactions, soil condition and resource availability should also be examined in addition to phenotypic plasticity of plant traits (within and between sites) which collectively affect ecological function (Loreau & Hector 2001; Zak *et al.* 2003; Sutton-Grier *et al.* 2011).

Finally, the majority of restoration has been undertaken on degraded wetlands and so more research into the biogeochemical functioning of pristine systems is needed to better understand how to restore degraded systems back to a reference state (Zak *et al.* 2011). It is suggested future research should focus on rich fen trajectory to predict end point communities and set targets based on varying   starting   points.

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3.0 CHAPTER 3: HYDRO-CHEMICAL EFFECTS FOLLOWING RESTORATION MOWING IN TWO RICH FEN PLANT COMMUNITIES

3.1 Abstract

Mowing is a common management technique employed in Europe and North America to manage seral wetland plant communities by: (a) preventing development to late succession, (b) minimising internal eutrophication and (c) to conserve biodiversity. However, little is known about the effect mowing has on water quality, and the duration of any effects. Therefore, mowing treatments were applied in two abandoned fen plant communities: a *Schoenus nigricans-Juncus subnodulosus* (SN) community (hand-cutting) and a *Cladio-Molinietum* (CM) community (machine mowing). Mowing took place once in each community across three sites in North Wales, U.K. Effects on pore water chemistry were followed for two years post mowing.

Mowing led to a rise in water table towards the ground surface in the CM plant community, persisting throughout the duration of the study. Increases in electrical conductivity, pH, calcium and magnesium concentrations were observed in both plant communities following mowing. This represents a positive impact on fen hydro-chemistry, promoting base rich conditions favoured by calcicolous plants, however this may be a result of peat compaction and or disturbance. Contrary to expectations, mowing did not lead to a reduction in nutrient or dissolved organic carbon (DOC) concentration in either plant community. In contrast, the CM community exhibited an increase in DOC and dissolved organic nitrogen, which decreased by the second year. It is suggested that these changes were attributed to disturbance effects in this high productivity, relatively nutrient-rich plant community, following increased litter inputs. Overall, it appears that any disturbance to the carbon and nitrogen cycles may be short-lived following mowing, whereas the increased availability of base-rich cations and associated increase of pH and electrical conductivity may confer longer term ecological benefits.

3.2 Introduction

In the UK, rich fens are quite rare as a consequence of being restricted to deep peat deposits that are hydrologically connected to underlying or adjacent calcareous geology, and have a fragmented distribution (Rydin *et al.* 1999; Ilomets *et al.* 2010). Hydro-geological requirements include mineral rich, nutrient poor water, which maintains pH > 6.5 (Giller & Wheeler 1986; Wheeler & Proctor 2000; Toberman *et al.* 2010). Water and nutrient supply can occur via surface flow, precipitation and groundwater, with the latter providing the main source of base cations: calcium and magnesium (Aerts *et al.* 1999; Rydin *et al.* 1999). In a pristine system, low nutrient availability deters

competitive plant species, in favour of low stature uncompetitive species such as: sedges (e.g. *Carex spp.),* herbs (e.g. *Mentha aquatica* and *Cardamine pratensis*) and "brown mosses" in the families of *Amblystegiaceae* and *Calliergonaceae* (Rodwell 1992; Bedford & Godwin 2003; Hedenas 2003).

In spite of their relatively small surface area, fens are usually an important component of the wider landscape; in terms of biodiversity, flow regulation, nutrient retention, water supply and climate regulation; which is why ongoing restoration of these wetlands is important (Gorham 1991; Bedford & Godwin 2003; Zedler & Kercher 2005; Middleton *et al.* 2006a; Lamers *et al.* 2014; Mitsch *et al.* 2014). Failure to manage and protect these systems may inhibit or reduce their capacity to provide ecosystem services (Hassan *et al.* 2005). Abandonment leads to mono-functional systems which are low in biodiversity; restoration can reverse this situation and return degraded fens to multi-functional wetlands, which are rich in biodiversity (Lamers *et al.* 2002; Foley *et al.* 2005; Verhoeven & Setter 2010).

In the main, UK fens exhibit botanical degradation, as a result of abandonment, following cessation of traditional management activities (Garcia 1992). In addition, as rich fens are commonly located within depressions and surrounded by intensively managed farmland, they are also at risk of nutrient pollution from agricultural sources (Grootjans *et al.* 2006; Smolders *et al.* 2010). Eutrophication through diffuse and point source pollution from adjacent farmland, together with abandonment leads to displacement of low stature species by fast growing, nutrient demanding graminoids; this group of plants produce a closed canopy and large amounts of biomass (Berendse & Aerts 1984; Grime *et al.* 1988; Bergamini *et al.* 2001; White & Jentsch 2001; Hajkova & Hajek 2003; Middleton *et al.* 2006b). Another source of enrichment which is also detrimental to biodiversity, is atmospheric deposition of nitrogen (N) (De Kroon & Bobbink 1997; Verhoeven *et al.* 2011). The UK fens investigated in this study currently experience 16.1 kg N ha^{-1} year^{-1} which exceeds the minimum critical loads for rich fens by 1.1 kg N ha^{-1} year^{-1} (APIS 2014).

Given these pressures on water quality and biodiversity; oligotrophic wetlands can have a limited capacity to remove nutrients; particularly via phosphorus (P) adsorption to the soil; although plant and microbial uptake of inorganic and organic nitrogen, via biogeochemical pathways e.g., denitrification are vast; which highlights the importance of these freshwater wetlands as "nutrient sinks" (Nichols 1983; Richardson 1985; Fisher & Acreman 2004). Furthermore, marginal, (e.g. SN) plant communities, which are adjacent to nutrient inputs from farm land, often demonstrate a decline in species richness, as a result of acting as a nutrient buffer for the fen interior (Criodain & Doyle 1997; Middleton *et al.* 2006a; Smolders *et al.* 2010).

Nutrient uptake via plants combined with biomass removal is an important component of management, if vegetation is harvested routinely (Venterink *et al.* 2009; Bombonato *et al.* 2010). In the absence of management, plant biomass acts as a temporary nutrient store; this is because 50 - 60% of nitrate and 80 - 90 % of phosphate, contained within the biomass is recycled and is re-released to the nutrient pool during senescence (Aerts & Chapin 2000). Inhibiting the recycling of these macro-nutrients is an important consideration for oligotrophic rich fens, as they are usually N and P co-limited, which compliments high biodiversity and low productivity (Grime, 1979; Venterink *et al.* 2003). Therefore, routine management, in the form of biomass removal, particularly when undertaken prior to senescence at the end of the growth season is considered to reduce nutrient recycling and retain low N and P concentrations (Venterink *et al.* 2009).

Surface water DOC concentrations vary spatially, with the highest concentrations observed in waters draining peatlands (Hope *et al.* 1997). Long-term increases in DOC loss have been documented from numerous upland areas, including peatlands (Freeman *et al.* 2001a; Evans *et al.* 2005; Monteith *et al.* 2007; Oulehle & Hruska 2009; Parn *et al.* 2009; San Clements *et al.* 2012). There is little evidence for similar long-term DOC trends from lowland fens, although it appears that DOC losses from both bogs and fens can increase following drainage and related management disturbance in clear cut peatlands (Nieminen *et al.* 2015; Schwalm & Zeitz 2015). Spatial and temporal heterogeneity of DOC production from peatlands is complex, as DOC release is influenced by variations in: soil temperature, peat composition (e.g. proportion of vegetation components in the peat substrate), nutrient status, pore water acidity, hydrology and redox conditions (Kalbitz *et al.* 2000; Kalbitz *et al.* 2002; Evans *et al.* 2005; Fenner & Freeman 2011; Strack *et al.* 2011). Mowing objectives for restoration also aim to reduce DOC losses from fens to receiving waters and reservoirs, as fen catchments can be an important resource for drinking water supply. Low DOC concentrations are desirable for water utility companies, as high DOC concentration is problematic to pre-treatment processes of potable water. Disinfectant by-products are produced during chlorination, which are harmful to health and are costly to remove (Rook 1974; Singer & Iwa Programme 2002).

Whilst mowing is widely employed throughout Europe and North America for restoration and biological conservation of managed fens, there is currently little evidence regarding the impacts of mowing on water quality. In this study, paired plots were set up and replicated over three sites to examine this question. At each site, two botanically and edaphically contrasting plant communities were selected, chosen for their degraded condition and rarity in the UK. These are the SN community; a tussock forming botanically rich, soligenous mire located on the fen margin and the

CM community, a tall sedge, botanically poor, topogenous mire, located within the fen basin. Pore water chemistry changes were recorded over a two year period, before during and following mowing. It was hypothesised that mowing would lead to initial, disturbance-related pulses of DOC and nutrient leaching, but that this would be followed by a reduction in concentrations (compared to the control plots), due to depletion of active organic matter pools (i.e. removal of above ground biomass and litter), and increased nutrient demand by the re-growing vegetation. Similarly, it was also proposed that DOC quality (physical and chemical properties) or dissolved organic matter would have changed in mown plots.

3.3 Materials and Methods

3.3.1 Site descriptions

The study was conducted on the island of Anglesey, North Wales, U.K, within the Anglesey Fens Special Area of Conservation (SAC). The SAC comprises seven Sites of Special Scientific Interest (SSSI) covering 467 hectares, and forms part of the larger Anglesey and Llŷn fens Ramsar site (Jones 2013). The three study sites are shown in Figure 3.1 and comprise: (i)
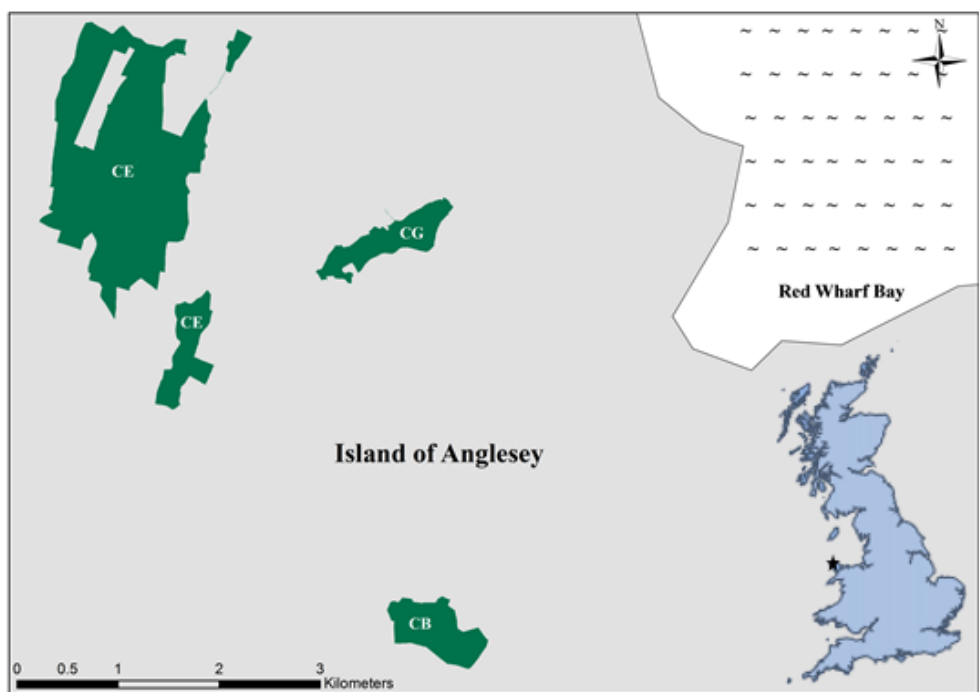
Figure 3.1 Sites' map shows in grey the outline of the Island of Anglesey and the sites which are located within it: Cors Erddreiniog (CE), Cors Goch (CG) and Cors Bodeilio (CB). Replicate paired plots are distributed across all sites for each plant community: CM (*n*=9) and SN community (*n*=8). The bottom left inset of the Great Britain boundary map derived from OS Strategi data (Digimap Ordanance Survey

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Collection) shows the location of the Island of Anglesey,   located off the North-west Wales, coastline in the U.K.

Cors Erddreiniog (CE) (53.3125 N, -4.29670 E), a valley head fen system, containing three peat basins, which is the largest of the three sites at 200 hectares (Prosser & Wallace 1995; Jones 2013), (ii) Cors Goch (CG) (53.3075 N, -4.2575 E), a basin fen comprising 67 hectares of which 25 hectares are wetland and (iii) Cors Bodeilio (CB) (53.2726 N, -4.2507 E), which is the smallest site, at 39 hectares, situated on shallow peat within a limestone valley (Jones 2013). Between 2007 and 2013, a mean annual temperature of 9.4 °C and mean annual rainfall of 625 mm were measured on an automated weather station located at Cors Erddreiniog (http://environmental-change.ccw.gov.uk/).

3.3.2 Treatments

Management intervention involved a single mowing event and biomass removal in both plant communities. Mowing was undertaken in the CM community plots using a Pistenbully 100 All Season soft tracked vehicle, modified with a 10 m^3 aluminium hopper and Mera Rabbeler forage harvester. Treatments were undertaken between 3 February 2012 and 28 March 2012. Vegetation was cut and collected in the hopper and removed from site immediately. The target mowing height varied between 5-10 cm, depending on local water table, peat structure and woody root density. In the SN community, hand cutting was undertaken between 7 February 2012 and 29 March 2012. Due to the sensitive nature of the tussock vegetation, this community was hand cut using strimmers (Stihl FS460C (Baden-Württemberg, Stuttgart, Germany), fitted with 3 mm nylon wire and hand raked the same day as cutting, so that biomass could be removed from the site immediately.

3.3.3 Experimental design

Three paired plots were installed at each site for the CM community (*n*=9) and 3 paired plots were installed at CE and CG and two paired plots at CB for the SN community (*n*=8). Each half of the paired plots (100 m^2) was randomly assigned to either treatment or control. Paired plots were oriented parallel to groundwater contours to ensure that hydrological and topographical conditions were as comparable as possible within each pair, Figure 3.2. Within each control and treatment plot, 2 piezometers were randomly assigned locations next to 4 m^2 quadrats (employed for botanical monitoring) (Menichino *et al., accepted*). In addition, dip wells were installed at control and treatment plots within the CM community for monitoring the water table, as it appeared that the water table had increased above the peat surface following mowing.
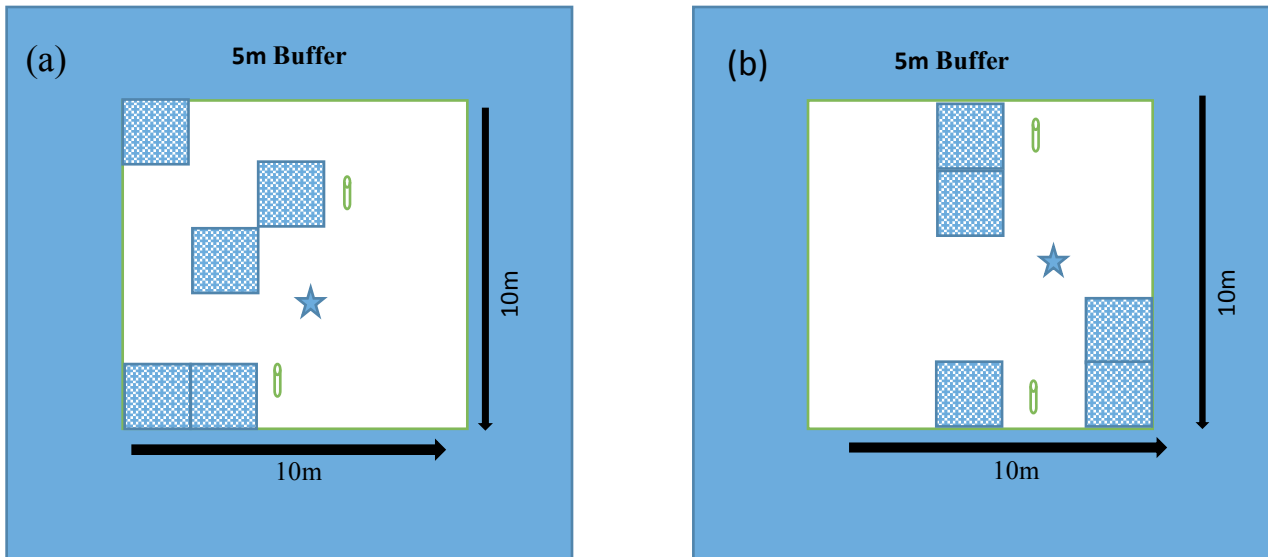
Figure 3.2 Schematic diagram of a typical 10 m^2 paired plot for (a) control and (b) treatment. 4m^2 quadrats, were randomly assigned within the control and treatment plot (employed for botanical monitoring, not reported here) and piezometers (cylinders) were randomly assigned location based on quadrat number. The star symbol shows that dip wells were located at equi-distant to the 2 piezometers in each plot (CM community only).

Co-ordinates for quadrats and piezometers were generated utilising an online random number generator (Random.org). The locations of the paired 100 m^2 plots were permanently marked by placing steel marker pegs in the peat at each corner of the plot, to allow for re-location with a metal detector after cutting. A Leica 1200 RTK digital global positioning system (dGPS) was used to permanently locate plots, quadrats and dip wells. Post data processing was undertaken using Leica Geo Office together with RINEX data and Holyhead reference station, downloaded from the ordinance survey GPS website (http://www.ordnancesurvey.co.uk/gps/os-net-rinex-data/). Bamboo canes were also used for ease of re-locating plots, but were temporarily removed or pushed into the peat during mowing. Treatment design included a 5 m buffer zone beyond the perimeter of each paired plot to allow for edge effects.

3.3.4   Plant   communities   and   site   characteristics

The *Cladio-Molinietum* (CM community) is a tall herb community found in base-rich (pH 6.5-8.0) calcareous fens, characterised as a swamp community owing to its location within the inundated interior of the fen (Wheeler 1980b; Saltmarsh *et al.* 2006). These calcareous fens which contain the dominant sedge, *Cladium mariscus* are rare in the UK, and are estimated to occupy just 5 km^2 in total as strict hydro-geological requirements restrict their geographic extent (Buczek & Buczek 1996; JNCC 2007).

The second fen plant community, is dominated by *Schoenus nigricans* and *Juncus subnodulosus* (SN community) which form tussocks and hollows, and is composed of a complex assemblage of rich fen species; some of which are rare (Wheeler 1980a; Rodwell 1992). The UK extent of this plant community is estimated at 16.3 km^2, although 18 – 48 % of these fens are considered to be managed ineffectively, in spite of statutory protection (JNCC 2007).

Table 3.1   Soil characteristics for the CM and SN communities. Sites are indicated as CB (Cors Bodeilio), CE (Cors Erddreiniog) and CG (Cors Goch) and values depict ±1 standard error.

	Carbon (%)	Nitrogen (%)	C:N Ratio	Moisture (%)
CM Community Sites:				
CB	40.85 ± 0.17	1.82 ± 0.01	22.67 ± 0.14	87.22 ± 0.12
CE	39.37 ± 0.11	2.19 ± 0.02	18.4 ± 0.20	88.43 ± 0.12
CG	34.0 ± 0.1	1.83 ± 0.01	18.68 ± 0.08	89.23 ± 0.25
Overall mean	38.24 ± 0.13	1.96 ± 0.009	19.92 ± 0.11	88.24 ± 0.103
SN Community Sites:				
CB	19.11 ± 1.33	0.80 ± 0.05	24.02 ± 0.52	68.08 ±1.30
CE	26.27 ± 0.51	1.50 ± 0.05	21.77 ± 0.57	74.27 ± 0.74
CG	29.92 ± 0.66	1.62 ± 0.04	20.53 ± 0.48	82.96 ± 0.99
Overall mean	26.3 ± 0.44	1.41 ± 0.03	21.73 ± 0.31	76.36 ± 0.58

Table 3.1 shows the contrasting edaphic conditions between each plant community and to a lesser extent between sites. The mean percentage of carbon, nitrogen, moisture and C:N ratio are all higher in the CM community (31 %, 28 %, 13 % and 9 % higher respectively than the SN community). This indicates that edaphic conditions differ considerably between plant communities, (particularly for carbon, nitrogen and moisture content and is consistent with the CM community's higher productivity and inundated conditions) as C:N ratios are comparable between plant communities, as calculated from the data shown.

3.3.5 Hydrological equipment and sampling

Piezometers were constructed using two plastic pipes. The base pipe was 10 cm in length with 1 mm slots cut transversely at 1 cm intervals, and had a 2.65 cm external diameter and 1.9 cm internal diameter and included a water tight stopper at one end. The open end of the base pipe was attached to a 40 cm length of solid pipe, employing a nitrile O-ring (13.1mm x 1.6mm). Once connected, a plastic, water tight bung was fitted to the top, pre-drilled with a 1 mm hole to exclude rainwater and

prevent hydro-tension. Aerobic water measurements were undertaken using a 60 ml syringe attached to a flexible pipe to draw up water from a 10 - 20 cm depth from existing pore water from the piezometer. After sampling, each piezometer was purged twice (120 ml) or evacuated if recharge was not instant. Water sampling was undertaken monthly across all control and treatment plots (2 samples per plot) on the same day, commencing on 19 December 2011 and ending on 12 December 2013. Piezometers were installed between 15 and 17 December 2011 to a 20 cm depth, to ensure samples were collected within the rhizosphere (Kalbitz 2001). Dip wells are DN35 (1.25") 1 m Geoscreen FT SL 1 GR150' wells with 42 mm MDPE push on caps and 42 mm DN35 PVC plugs (Marton Geotechnical Services Ltd) and were installed one year after treatment (25 April 2013) equi-distant from piezometers, to a 0.95m depth within each control and treatment plot in the *Cladio Molinietum*. Upstand (the height of the well top above the peat surface) and water level depth were measured monthly using a ruler and a 15 m Hydrokit dip meter respectively and recorded to the nearest 0.5 cm. Dip wells were sampled monthly to record water table level between 25 April 2013 and 11 March 2014.

3.3.6 Water chemistry analysis

Samples were collected in acid washed bottles; pH was recorded at the end of the sampling day and electrical conductivity was measured the following morning, using unfiltered samples using a pH SevenEasy pH probe (Mettler-Toledo AG Analytical, Switzerland) and 4320 Jenway electrical conductivity meter (Bibby Scientific Ltd, U.K) respectively. Within 24 hours, samples were vacuum filtered using Whatman sterile membrane filters (0.45μm pore size, 47mm diameter) and filtered samples were the stored in 20 ml sealed bottles and refrigerated in darkness at 4 °C to await further chemical analysis.

3.3.7 Ion chromatography

Dissolved inorganic anions (nitrate and phosphate) and cations (calcium and magnesium) were analysed using ion chromatography (Metrohm Ltd, UK). Detection limits for anions and cations were 0.005 mg L^{-1} with exception of nitrate (0.002 mg L^{-1}).

3.3.8 DOC/Dissolved organic nitrogen (DON)

Total dissolved carbon and total dissolved nitrogen were measured using a Thermalox 5001.03 analyser (Analytical Sciences Ltd, Cambridge, U.K). DOC concentrations were measured using the Non-Purgeable Organic Carbon (NPOC) method in which samples are acidified to below pH 3.0

and purged with oxygen to remove all inorganic carbon in advance of total carbon analysis. TON concentration was derived by measuring TN and subtracting TIN (ion chromatography).

3.3.9 Absorbance Analysis

Light absorbance in natural surface waters is associated with DOC concentration. Therefore, absorbance measurements can be used as a proxy metric for DOC concentration (Tipping *et al.* 2009). Specific ultraviolet absorbance (SUVA) is calculated as 254 nm wavelength multiplied by 100 and divided by DOC concentration. This is a proxy measurement for aromatic carbon content and E2:E3 ratio was calculated as the ratio of 250 nm and 365 nm wavelengths. This is indicative of photo-degradability and photo-reactivity of DOC. This metric also strongly correlates with total aromaticity and averaged molecular weights of humic solutes (Peuravuori & Pihlaja 1997; Chow *et al.* 2013). Pore water samples were prepared by pipetting 348 µl onto a microplate and wavelengths were scanned at 1 nm increments between 230 nm and 800 nm using a Molecular Devices M2e Spectramax plate-reader (Peacock *et al.* 2014; Jones *et al. in prep*).

3.3.10 Soil sampling

Two of the five vegetation quadrats from each side of the paired plots (control and treatment) were randomly selected for soil sampling using a random number generator (Random.org). Soil sampling was undertaken once on 15 November 2013 from 10-20 cm depth using a 2 cm diameter soil corer. Samples were collected in acid washed containers and refrigerated in the dark at 4° C in preparation for soil analysis.

3.3.11 Soil analyses

3.3.12 Carbon and nitrogen analysis

Soil samples were prepared for carbon (C) and nitrogen (N) analysis, by initial air drying for 3 weeks in an Astell Hearson (Catford, England) drying cabinet at 105 °C. Once dry, samples were then ground using a Glen Creston (Middlesex, UK) soil grinder and subsequently milled using a Retsch GmbH MM200 oscillating ball mill (Haan, Germany). Soil samples were weighed into tinfoil cups and placed in a sampling palette, and sample weights were between 0.1000g and 0.2000g and recorded to 4 decimal places.

Analyses of C and N were undertaken on a Leco TruSpec® Series CN instrument using a combustion technique. Infrared and thermal conductivity were employed for C and N analysis

respectively and Ethylenediaminetetraacetic acid EDTA standards for C (41 %) and N (0.18 %) were run every 10 samples as well as blanks at the start and end of each run to determine instrumental drift.

3.3.13 Moisture and organic matter content

The method follows the loss on ignition method developed by Ball (1964). Soil samples were weighed using a Reflex HP 220C Avery Weigh Tronix analytical balance (Smethwick, England), and placed in a Raven Z incubator oven (LTE Scientific Ltd, Oldham, England) at 105 °C for 16 hours. Samples were reweighed after cooling to determine soil moisture content. Dry weight samples were then placed in a Carbolite CWF1100 chamber furnace (Carbolite Ltd, Hope Valley, UK) at 450 °C for a further 16 hours to burn off organic matter. Samples were reweighed again after cooling to calculate organic matter content.

3.3.14 Statistical analysis

The statistical package 'R' (R-Core-Team 2014) was used to analyse all data. Each plant community was analysed separately, using a linear mixed effect model, employing the lmer function and lme4 package (Bates *et al.* 2014) and all analyses were performed on raw data (Kikvidze & Moya-Laraño 2008). To test the overall treatment effect over time model 1 was used: the null model comprised random effects only ("site", "plot" and "quadrat") and the full model tested the response variable as a function of treatment over time plus the random effects. Model 2 tested the overall treatment interaction effect over time; the null model comprised the response as a function of "month" plus random effects ("month", site", "plot" and "quadrat") and the full model tested response as a function of treatment and interaction over time "month" plus the random effects. Analysis of variance (ANOVA) was then used to compare differences between the variance in the null and full models to determine significance values. All treatment plots prior to treatment for December 2011 and January 2012 were assigned as control. Months 3-24 were assigned as control and treatment as per the experimental paired plot design. Nitrate, phosphate, DOC and DON analyses tested months 2-24 only as these variables demonstrated disturbance effects in month 1, which is a probable artefact of piezometer installation a week prior to sampling.

Months were aggregated as follows: baseline/pre-treatment (January 2012), post treatment summer 2012 (May-October 2012), post treatment winter 2013 (November 2012-April 2013) post treatment summer 2013 (May-October 2013) and winter 2013 (November-December 2013). To test for seasonal differences, seasons were selected and model 1 was applied. Seasonal treatment effects

were tested as the difference between control and treatment plots for each season selected and model 1 was applied.

Additionally, there was one anomalous control plot (both quadrats) in the SN community, probably due to the control half of the plot being located on a spring head, produced DOC, DON, calcium and magnesium concentrations which were: 75 %, 67 %, 9 % and 28 % higher respectively, compared to the mean concentrations for all other control plots. Therefore the Figures and analyses reported for all SN community results exclude this anomalous paired plot, reducing between site replication from $n = 8$ to $n = 7$.

3.4 Results

3.4.1 Electrical conductivity and pH

Overall, the SN community showed higher mean values for electrical conductivity (522 µs cm^{-1} ± 9) and pH (6.83 ± 0.01) compared with the CM community (197 µs cm^{-1} ± 6, pH 6.7 ± 0.0), calculated from the control plots, Figure 3.3 a-d.

A strong treatment effect was observed for electrical conductivity in the CM community, where conductivity increased 20 % overall in treatment plots compared to the control plots ($P<0.001$). A seasonal effect was also evident for electrical conductivity in summer 2012 following mowing ($P<0.01$), which demonstrates a 49 % increase in the summer following mowing. Indeed, electrical conductivity was persistently higher than control plots for 6 consecutive months from May to October 2012 and on one occasion in the following summer (2013), Figure 3.3a. pH also exhibited a strong treatment effect in the CM community ($P<0.01$), as well as a seasonal treatment effect for the summer (2012), when pH increased by 1.5% compared with control plots ($P<0.05$) , Figure 3.3 b.

The SN community also exhibited a treatment effect for electrical conductivity, which increased by 15 % in treatment plots, compared to control plots overall ($P<0.001$). No seasonal treatment effects were observed for electrical conductivity, although it was higher than the control on four occasions in 2012 and on one occasion in the following year, Figure 3.3c. The SN community also exhibited a weak significant treatment effect for pH, which increased in treatment plots by 0.5 % compared to the control plots ($P<0.06$) , Figure 3.3d.
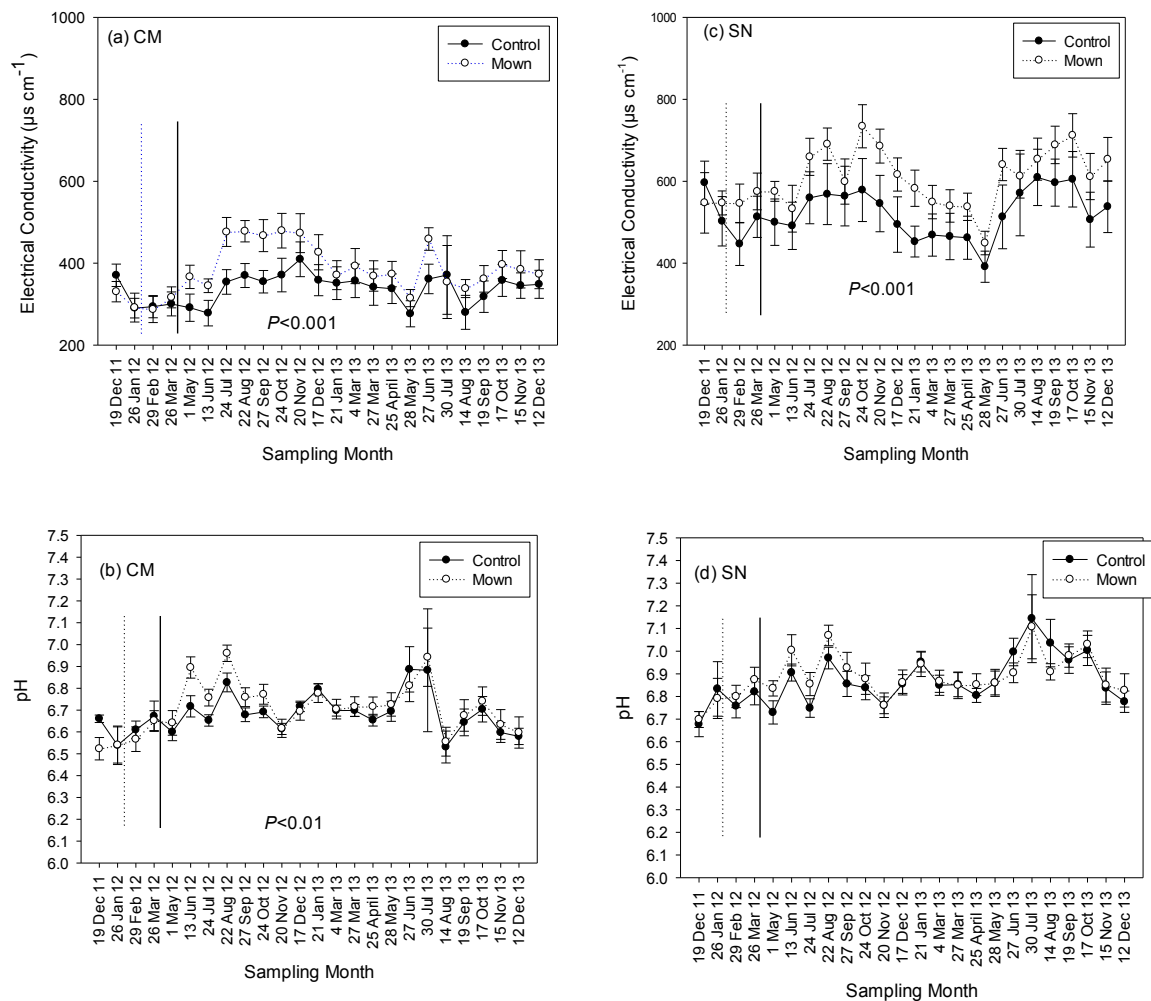
Figure 3.3 Water chemistry for the: CM community, (a) electrical conductivity, (b) pH and SN community (c) electrical conductivity (d) pH. All figures illustrate +/- 1 s.e. The dotted vertical line depicts when treatment commenced across sites as a single mowing event for each plot and the solid vertical line illustrates when treatment ceased.

3.4.2 Calcium and magnesium

The CM community exhibited strong treatment effects for calcium and magnesium which increased by 13 % ($P<0.001$) and 8 % ($P<0.001$) respectively with mowing, Figure 4a-b. A seasonal treatment effect was also evident in the summer (2012) following mowing, when calcium increased 19 % in concentration ($P<0.05$). The SN community also exhibited overall treatment effects for calcium and magnesium which both increased by 14% ($P<0.05$) and 10 % ($P<0.05$) respectively, Figure 4c-d. There was also a seasonal treatment effect for calcium in the SN community for the summer following mowing (2012), when calcium increased in concentration by 15 % compared to control plots ($P<0.05$).
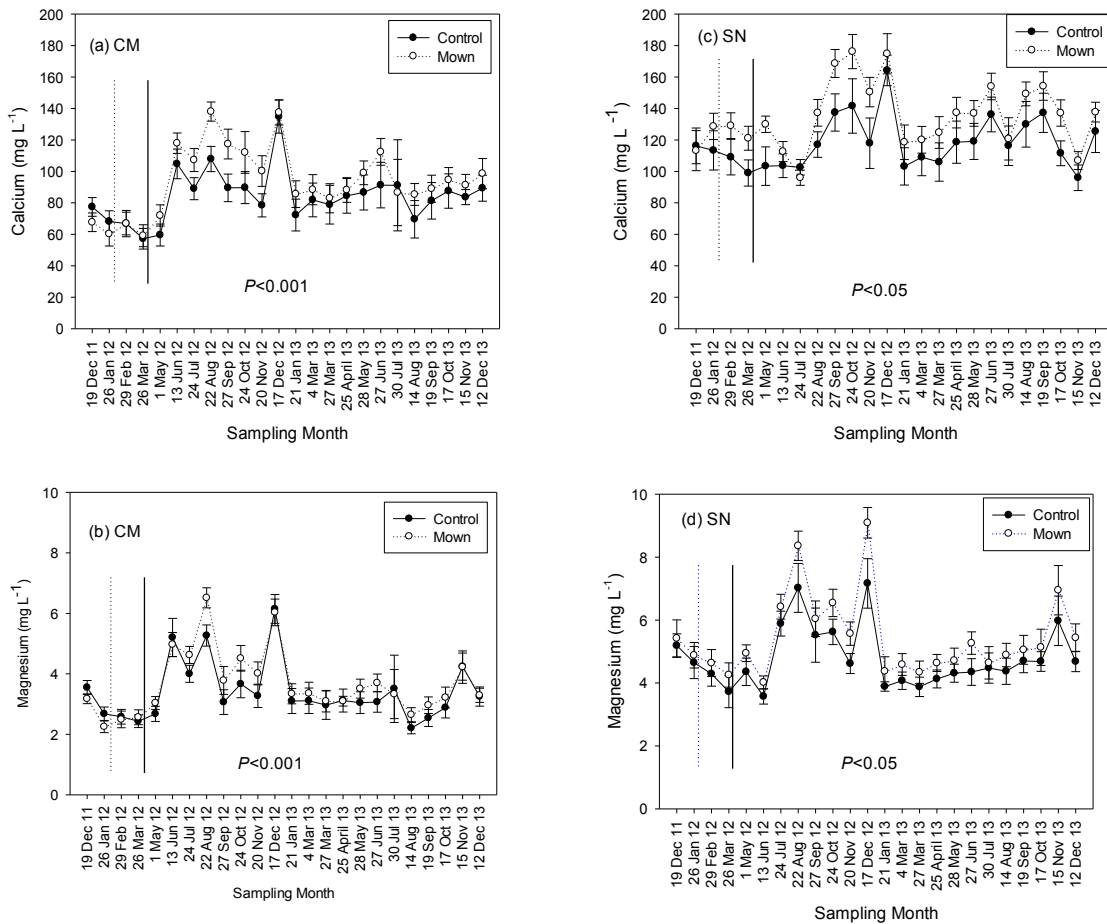
Figure 3.4 Water chemistry for the: CM community, (a) calcium, (b) magnesium and SN community, (c) calcium (d) magnesium. All Figures illustrate +/- 1 s.e. The dotted vertical line depicts when treatment commenced across sites as a single mowing event for each plot and the solid vertical line illustrates when treatment ceased

3.4.3 Water table depth

Measurements of water table depth were undertaken for the CM community only, to explore possible compaction effects from the harvester, Figure 3.5. A clear temporal seasonal pattern is followed by both control and treatment plots, with maximum water table drawdown in mid-summer. There was a significant treatment effect on water table depth ($P<0.05$), with higher water tables recorded (relative to the ground surface) in the mown plots. Most notably, the mean water table depth in the control plots was below the peat surface (-2.5 cm ± 0.5) whereas in the mown plots it was just above the surface (0.4 cm ± 0.4).
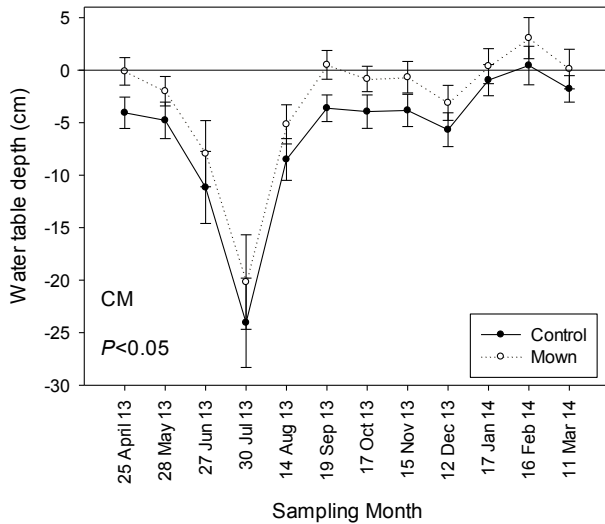
Figure 3.5 Water table depth for the CM community which show +/- 1 s.e. Water table depth measurements commenced in the second year following treatment.

Over the period of measurement, mean water table for mown plots was above the surface on four occasions, whereas this was only the case on one occasion in the control plots.

3.4.4 Dissolved organic carbon, E2:E3 ratio and dissolved organic nitrogen

Temporal patterns are evident in DOC concentration, demonstrated clearly by the control plots in the CM plant community. DOC concentrations are 23% higher in the summer/autumn periods of 2012 and 2013, compared to the winter periods of 2012 and 2013 ($P<0.01$), Figure 3.6a.

In the CM community a significant treatment effect was observed for DOC concentration, which increased by 16 % in the mown compared with control plots ($P=0.06$). In addition, a strong treatment interaction with time was also observed ($P<0.001$). DOC concentration did exhibit a 13 % decrease in concentration between the first and second summer, demonstrating a transitory reduction in the effect of mowing in the second year, compared with the first.

No overall treatment effect was observed for DOC concentration in the SN community. In addition, seasonal effects for DOC concentration were evident, but not as clearly defined (Figure 3.6c) as they were in the CM community; however, temporal patterns were observed in the SN community, where DOC concentrations in the control plots were 43 % higher in the summer/autumn period of 2012, compared to the winter 2012 and 2013 ($P<0.001$). The winters of 2012 and 2013 were comparable ($P = 0.82$); but there was a difference in DOC concentration between each of the summers 2012 and

2013 ($P<0.05$), with lower concentrations in 2013 than in 2012. This may be indicative of greater spatial heterogeneity in DOC concentration across sites, compared to the CM community.

Figure 3.6 Water chemistry for the: CM community (a) DOC, (b) E2:E3 ratio, (c) DON and for the SN community (d) DOC (e) E2:E3 ratio, (f) DON. All Figures illustrate +/- 1 s.e. The dotted vertical line denotes when treatment commenced across sites as a single mowing event for each plot and the solid vertical line illustrates when treatment ceased.

No treatment effect was observed for SUVA absorbance (Abs) in CM community control and treatment plots (4.20 Abs ± 0.04, 4.02 Abs ± 0.04, P=0.37) or in the SN community control and treatment plots (5.67 Abs ± 0.78, 6.73 Abs ± 0.08, P=0.45).

The CM community exhibited a 5 % increase in the E2:E3 ratio ($P<0.05$) in treatment plots, Figure 3.6b). Therefore, the E2:E3 ratio suggests there has been a change in DOC quality in mown plots. The E2:E3 treatment effect was only evident in the first summer following mowing ($P<0.05$), after which time the treatment effect was no longer evident. Conversely, the E2:E3 ratio measurements for the SN community did not exhibit a treatment effect ($P = 0.72$), Figure 3.6e.

In the CM community, dissolved organic nitrogen (DON) follows a similar temporal pattern to DOC, as the concentrations in control plots are comparable between summers 2012/2013 ($P = 0.2$) and winters 2012/2013 ($P = 0.07$). DON also exhibited a 25 % decrease in concentration between summer 2012 and winter 2012 / 2013 seasons ($P<0.01$). The CM community also exhibited a treatment effect for DON, demonstrated by a 22 % increase in concentration in treatment plots compared to control plots ($P<0.05$), Figure 3.6c. A seasonal treatment effect was also detected for the summer following mowing ($P<0.05$), which was not evident in subsequent seasons, suggesting the DON treatment effect was also transitory. There was no treatment effect observed for DON concentration in the SN community ($P = 0.33$), Figure 3.6f.

3.4.5 Nitrate and phosphate

Both the CM and SN communities showed no overall treatment effect for nitrate ($P = 0.22$, $P = 0.72$) or phosphate ($P = 0.46$, $P = 0.98$) respectively, Figure 3.7a-d.
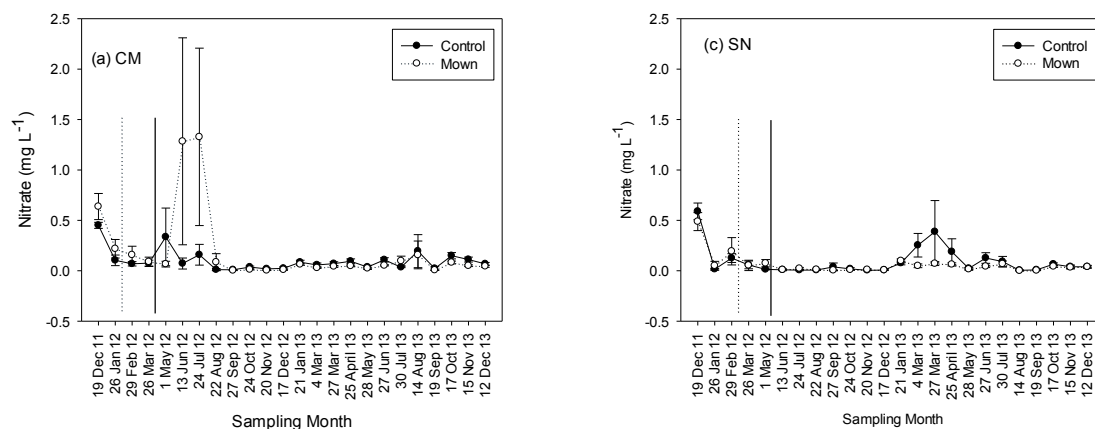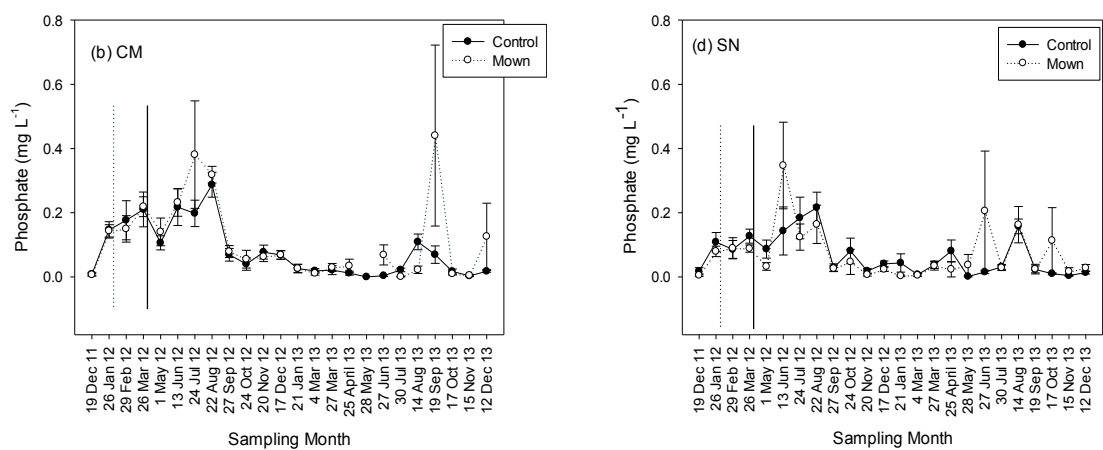
Figure 3.7. Water chemistry for the: CM community (a) nitrate, (b) phosphate and for the SN community (c) nitrate, (d) phosphate. All Figures illustrate +/- 1 s.e. The dotted vertical line denotes when treatment commenced across sites as a single mowing event for each plot and the solid vertical line illustrates when treatment ceased.

3.5 Discussion

In this study, the mowing intervention caused a strong but transitory hydro-chemical response in the CM community. Multiple treatment effects were observed and were strongest in the first summer following mowing in the CM community, but were reduced in magnitude or lost entirely by the second year.

3.5.1 Electrical conductivity, pH, base cations and water table depth

No previous studies have documented increasing water table (CM community) pH, electrical conductivity and subsequent increases of base cations (calcium and magnesium) following mowing in rich fen plant communities. The mechanism driving these increases is uncertain and the strength of treatment effects are higher in the CM community compared to the SN community.

In the CM community, prior to mowing, it appears that near-surface pore water may have been at least partially isolated from base-rich groundwater, and therefore influenced more by dilute rainfall inputs, particularly in the CM community which supports inundated conditions year round and is located within the interior of the fen, further away from lateral groundwater inputs, with lower levels of base cation supply and lower pH and electrical conductivity (Wheeler 1980b; Saltmarsh *et al.* 2006). In contrast, the SN community occurs at the fen margin, closely located to springs, which supply high concentrations of base cations, which support higher pH and electrical conductivity, compared to the CM community and therefore is likely to experience less rainfall dilution effects due to a lower water table and proximity to an undiluted constant supply of calcareous rich ground water (Wheeler 1980a). Therefore, contrasting edaphic conditions and differences in treatment

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methods are proposed to have contributed to the observed stronger treatment effects in the CM plant community, in comparison to the SN community, which also demonstrated significant treatment effects to a lesser extent.

In addition to plant community related effects as described above, results suggest mowing in both plant communities may have had the unintended consequence of enhancing groundwater connectivity with near-surface peat; particularly where disturbance was high in the machine mown CM plant community. In addition, water table measurements in the CM community, suggest that there has been a small but ecologically important increase in relative water level, leading to more frequent and sustained inundation of the peat surface, and enhanced concentrations of base cations. Although it is possible that a reduction in transpiration rates following mowing could have contributed to the change in water table, the consistent year-round offset between mown and control plots suggests that a more likely explanation is compaction of the peat surface by the machinery used for mowing in the CM community. Soil disturbance and compression (CM community) is consistent with other studies using large tracked harvesters, and it is thought that plant composition change as a result; shifting from a sedge dominated community to a semi-aquatic community (Gusewell & Le Nedic 2004; Kotowski *et al.* 2013).

Additionally, it is well documented that clear cutting in forests demonstrates prolonged nutrient release from the brash (litter), which is why it is common practice not to remove it following harvesting, as litter slowly releases nutrients through time (Titus & Malcolm 1992; Ashagrie & Zech 2010). Versini et al. (2014) also shows that litter is an important source of dissolved inorganic nutrients as well as DOC and DON. Therefore, it is possible that litter inputs are also affecting the observed increase in base cations and associated increase in pH and electrical conductivity; however the vast majority of litter was removed during or directly following biomass removal and associated increases in concentrations would have been expected for nitrate and phosphate, which were not evident.

The increase in pH combined with the increase in electrical conductivity and base cation supply is likely to lead to beneficial effects for both plant communities, in particular, the rich fen plant specialists. The higher water table through the growing season is also beneficial, which is likely to reduce the invasion by aggressive competitor species, as well as reduce acidification and the desiccation of bryophytes (van Belle *et al.* 2006; Cusell *et al.* 2014).

However, these benefits may be at the expense of increased DOC release, in that organic matter solubility is pH-dependent (Monteith *et al.* 2007; Toberman *et al.* 2010; Evans *et al.* 2012;

Schwalm & Zeitz 2015). However, as pH was already relatively high prior to intervention, it is likely that any such effect is minor.

3.5.2 DOC, DOC quality and DON

In spite of the heterogeneous complexity of DOC production, (Kalbitz *et al.* 2000; Kalbitz *et al.* 2002; Evans *et al.* 2005; Fenner & Freeman 2011; Strack *et al.* 2011) the CM community demonstrated an increase in DOC concentration that unexpectedly persisted beyond the initial intervention period. However, DOC concentration in mown plots was comparable to control plots by the following winter after mowing. Conversely, the SN community did not demonstrate a treatment effect in the hand cut plots.

The consequence of an increase in DOC concentration in a rich fen's pore water may have an impact on receiving surface waters, although there are no comparative studies to date that have investigated this. There is evidence of fluvial carbon losses in minerotrophic peatlands following forest harvesting, which are high compared to harvesting ombrotrophic peatlands (Nieminen 2004; Nieminen *et al.* 2015). These carbon losses have been shown to impact on receiving surface waters, although this is dependent on harvesting intensity (Schelker *et al.* 2014) and the longevity of these effects in deforested peatlands was up to three years (Nieminen 2004; Schelker *et al.* 2014; Nieminen *et al.* 2015).

Mowing in the CM community has been undertaken on a relatively small scale, given that only nine 100 m^2 plots were mown. However, the intensity of the disturbance was high; evident from the increase in DOC concentration observed in the pore water, which is probably emphasised at these wetlands which have remained undisturbed for the past five decades. Therefore the treatment effects observed at this plant community are probably due to a number of factors, the mechanisms of which are not clearly identified: although it is likely that peat compaction from the physical disturbance of the caterpillar tracked harvester has compressed the peat, which has inadvertently increased the water level above the peat surface and forced DOC from peat pores. In addition, increased litter inputs from inefficient litter removal has subsequently led to increased rates of decomposition. A combination of these factors are thought to have contributed to the increase in DOC production (Chow *et al.* 2003; Zak & Gelbrecht 2007; Fenner *et al.* 2011). Peat compaction was unexpected as machine mowing was undertaken by a low pressure harvester. In addition, winter mowing may have amplified the disturbance effects; sites were heavily inundated and therefore prone to more disturbance, due to seasonally soft water logged peat, and litter removal was less efficient due to

high winds. The latter led to some of the cut biomass being blown across the peat, instead of being deposited in to the hopper.

Therefore, if litter decomposition is the main source of DOC and DON, this may account for the lack of treatment effects for DOC and DON in the SN community. There was a much lower percentage cover of litter (22 %) following hand cutting and raking in the SN community, compared to machine mowing (54 %) in the CM community (Menichino et al., *accepted*). Therefore, reduced disturbance to the peat surface, due to hand cutting and a more efficient method of removing cut biomass and litter in the SN community may explain the different treatment responses for DOC and DON concentrations, compared to machine harvested biomass in the CM community.

The treatment plots in the CM community showed a change in DOC quality, demonstrated by an increase in the E2:E3 ratio in mown plots, which indicates a shift from large DOC molecules to hydrophilic fractions, controlled by oxidation and photo-degradation, possibly associated with water table and seasonal litter inputs (Chow *et al.* 2013). This suggests that machine mowing and the associated increase in litter inputs has caused DOC to become more resistant to microbiological degradation, e.g. recalcitrant polyphenols, which are largely derived from leaves, rather than other parts of a plant (Crawford *et al.* 1977; Hattenschwiler & Vitousek 2000; Adamczyk *et al.* 2009).

Therefore, the objective to reduce DOC concentration in mown plots in either plant community and potentially reduce downstream DOC concentrations in the longer term has not been achieved over the duration of this study. In contrast, DOC actually increased in the short term in the CM community. Based on measured concentration differences between mown and control plots, and mean runoff for the catchment, it is estimated that mechanical mowing of the CM community generated an additional 3 g C m^{-2} exported as DOC via drains leading to receiving waters. Although not trivial in terms of the annual carbon balance, as an infrequent event, it appears unlikely that mowing will lead to major additional carbon loss through DOC leaching. Fluvial carbon losses are also associated with nitrogen exports evident by low C:N ratios (Qualls & Richardson 2003).

3.5.3 Nitrate and phosphate

The hypothesised reduction in pore water concentrations of plant available nutrients was not observed during this study. Nitrate and phosphate concentrations were low at these sites and it is probable that this made it more difficult to detect a treatment effect in the short term. Nutrient concentrations were expected to be higher at these wetlands due to their location within an intensely managed landscape.

It is still possible that once a mowing regime is established within each plant community, subsequent reductions in nutrients will occur in the longer term (Grime *et al.* 1988; Bobbink *et al.* 1998; Venterink *et al.* 2003), although this will be difficult to achieve if atmospheric inputs of ammonia are greater than tissue N exports from the biomass (Venterink *et al.* 2002).

3.6 Conclusion

The increase in base cations, electrical conductivity and pH in both plant communities, and higher water level (CM community), although unintentional, are expected to support long term benefits to rich fen biodiversity by facilitating colonisation of rich fen target species. Therefore, this study has revealed the positive effects mowing has on fen hydrochemistry, although these benefits need to be considered alongside potential carbon and nitrogen losses.

The short term increase in DOC and DON concentrations in the CM community's pore water may lead to a large temporary export of carbon and nutrients to receiving surface waters if mowing is undertaken over large areas, but is unlikely to last more than two years. In the longer term, it is possible that this may be counteracted due to the associated compression and subsequent increased inundation of the peat in the CM community, leading to inhibited oxidative processes and therefore increased rates of peat accumulation.

Further research is needed to determine if there are other factors in addition to peat compaction and litter inputs that would cause base cations, pH and electrical conductivity to increase. It is also important to investigate the change in quality of carbon fractions as well as quantifying the carbon and nitrogen exports from the CM community's pore water to receiving surface waters, and whether these effects would be reduced if mowing was undertaken in the summer.

3.7 References

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4.0 CHAPTER 4: INVESTIGATING SPATIAL HETEROGENEITY OF GREENHOUSE GASES BETWEEN A DEGRADED AND GOOD CONDITION TEMPERATE RICH FEN

4.1 Abstract

There are many studies that have investigated the temporal drivers of greenhouse gases, however, few studies have examined the plant mediated, spatially predictive relationships, associated with carbon sequestration and methane (CH_4) emissions. This study was undertaken at a botanically good condition, and a botanically degraded site, within a rich fen peatland in North Wales, U.K. Carbon dioxide (CO_2) and methane fluxes were measured using a chamber design, and net ecosystem exchange (NEE), respiration (Reco) and gross primary productivity (GPP) was calculated. Six plant communities (6 collars per community) were measured across two sites (botanically degraded and good condition) at monthly intervals over a year.

Reliable predictors were identified for greenhouse gas fluxes and results show that both species rich and species poor plant communities have a comparable net flux of gaseous carbon exchange. Within site heterogeneity demonstrated that 50 % of the plant communities were a net gaseous carbon source. The net ecosystem exchange (NEE) was highest for the *Sphagnum* ($-17,251$ mg CO_2 m^{-2} day^{-1} $\pm$ 3,203) and *Cladio-Molietum* ($-15,573$ mg CO_2 m^{-2} day^{-1} $\pm$ 1,257) plant communities, which also had the lowest CH_4 fluxes (102 ± 29 mg CH_4 m^{-2} day^{-1}), (86 ± 29 mg CH_4 m^{-2} day^{-1}) respectively. The highest methane fluxes were observed in the brown mosses (328 ± 90 mg CH_4 m^{-2} day^{-1}). It appeared that ecologically comparable communities (*Sphagnum* and brown mosses) demonstrate opposing fluxes and ecologically different communities (*Sphagnum* and *Cladium-Molinietum*) have similar fluxes. Furthermore plant mediated predictors were identified for CH_4, carbon sequestration and respiration.

4.2 Introduction

Rich fens are freshwater peat forming wetlands, which are globally significant due to their high conservation value and provision of ecosystem services, e.g. water purification, flood prevention biodiversity conservation, and many can mitigate for climate change (Whiting & Chanton 2001; Mitra *et al.* 2005; Mitsch & Gosselink 2007). Globally, fens comprise 26 % of all wetlands and 42 % of all peatlands, however in the U.K they comprise less than 10 % of all peatlands, making them quite rare (Joosten & Clarke 2002; JNCC 2011b; Ramsar Convention Secretariat 2013). Rich fens are spatially heterogeneous, due in part to their minerotrophic hydrology (Wheeler 1993). Water is sourced via precipitation, surface waters and groundwater. The latter is an important source of

nutrient poor, mineral rich water (Wheeler 1993; Joosten & Clarke 2002; Bedford & Godwin 2003; JNCC 2011b). The latter ensures pH values between 6.0 and 8.0(Wheeler 1980a).

In good condition, rich fens are amongst the most biodiverse wetlands in the world (Sjörs 1950; Wheeler 1980b; Wheeler & Proctor 2000; Ilomets *et al.* 2010). Intact, they can support a complex assemblage of bryophytes, herbs and small stature sedges (Wheeler 1980b; Rodwell 1992). However, these transition (seral) communities rely on management (mowing/grazing) and good water quality. Left unmanaged, there is an ecological shift in species composition; from a low production species rich community, to a high production species poor community (Rodwell 1992; Verhoeven & Bobbink 2001; Billeter *et al.* 2007; JNCC 2011b).

Wetlands contribute substantially to the global carbon store; in spite of covering 6-8 % of the earth's surface, they are estimated to store one third of the world's carbon (Roulet 2000; Mitra *et al.* 2005; Lal *et al.* 2007; Mitsch & Gosselink 2007). This is due to disproportionately slow decomposition of organic matter (OM), in relation to primary production, which can occur in the presence or absence of oxygen, and is controlled by an 'enzymic latch' (Freeman *et al.* 2001b). Where these conditions are combined with a low temperature, carbon sequestration is optimised (Gorham 1991; Freeman *et al.* 1998; Fenner *et al.* 2011). It is this process which leads to wetlands being significant 'carbon sinks' (Chmura *et al.* 2003; Mitra *et al.* 2005). However, when plants and animals in the soil respire and decompose, carbon is released in the form of carbon dioxide (CO_2) (Kucera & Kirkham 1971; Ryan 1991). The interface zone between the peat surface and the atmosphere is where greenhouse gas exchange occurs (Joabsson *et al.* 1999).

However, although wetlands are a net sink for CO_2, they are also a natural source for methane (CH_4) and nitrous oxide, both of which can offset the CO_2 sink capacity of a wetland, and switch it over to a source of GHGs (Bridgham *et al.* 2006; Liu & Greaver 2009). However, natural sources, such as wetlands, are a significant source of GHGs to the atmosphere (12 %), of which CH_4 contributes 25 % (Bubier & Moore 1994). Recent attention has been given to wetlands, as increases in GHG emissions are associated with degradation, severe disturbance or drainage (MEA 2005; Gao *et al.* 2014).

It is estimated that 3 % of CO_2 gains are recycled back to the atmosphere as CH_4 emissions (Whiting & Chanton 1993, 2001). In order to quantify the net carbon gas exchange; both CO_2 and CH_4 fluxes need to be quantified (Waddington & Roulet 2000; Bridgham *et al.* 2006). This will identify whether a wetland and the plant communities located within it, are acting as a carbon sink, or a carbon source. This carbon balance is fundamental to a wetlands regulatory control on the

global climate (Lal *et al.* 2007; Lal 2008). In the past two decades, scientists' attention have focused on how to manage increasing CO_2 and CH_4 concentration being released to the atmosphere, due to their positive relationship with global temperature (Petit *et al.* 1999; Crowley 2000; IPCC 2001; Thomas *et al.* 2004).

The anaerobic conditions found in wetlands promote optimum conditions for CH_4 production (Drösler *et al.* 2008). CH_4 is produced at lower concentrations to CO_2, however, it has a disproportionately higher radiative forcing, which, over a one hundred year time frame, is up to twenty five times stronger than CO_2 (Lelieveld *et al.* 1998; Whiting & Chanton 2001).

CH_4 is produced by bacteria (methanogens and methanotrophs), located in the peat water (Conrad 1996; Hanson & Hanson 1996). Methanogen bacteria produce CH_4 following CO_2 assimilation and respiration in oxygen depleted anoxic peat water, in a process known as methanogenesis (Conrad & Frenzel 2002). The rate of CH_4 being released from anoxic production sites is partly controlled by methanotrophy, undertaken by methanotroph bacteria, which assimilate CH_4 in the presence of oxygen (Hanson & Hanson 1996). This process acts as a temporary store for CH_4, before it is oxidised and released to the atmosphere during respiration (Hanson & Hanson 1996). CH_4 production and release is well documented as being associated with water table depth (Moore & Roulet 1993; Strack *et al.* 2004). However, this is not the only control on CH_4 production, which is highly complex.

CH_4 production and its spatial distribution, is also associated with land modification, plant succession, plant composition, botanical substrate, microtopography, soil temperature, pH and light intensity (Williams & Crawford 1984; King 1990; Svensson 1992; Bubier *et al.* 1993; Dise *et al.* 1993; Moore & Roulet 1993; Nilsson & Bohlin 1993; Bubier & Moore 1994; Bubier 1995; Bubier *et al.* 1995; Kettridge & Baird 2007; Waddington & Day 2007).

In spite of CH_4 being produced in the anoxic layer of the peat, it can be transported through the oxic peat layer to reach the atmosphere. The three main pathways are: (i) diffusion, (ii) transport via aerenchymatous tissue (large conduit compartments) in vascular plants and (iii) ebullition (episodic losses of CH_4 from bubbles in the peat water) (Whalen 2005).

The second pathway, via aerenchymatous tissue is one of two plant mediated mechanisms, and is not present in all species, due to physiological and morphological differences between species (Whalen 2005). However, where it is present, CH_4 enters the plant and is transported either by molecular diffusion, which is known to occur in *Carex spp.* or via pressurised ventilation, under

stomatal control (Dacey & Klug 1982; Sebacher *et al.* 1985; Chanton & Dacey 1991; Morrissey *et al.* 1993; Joabsson *et al.* 1999). Plants with pressurised flow demonstrate CH_4 fluxes which are two to four times higher, than plants with molecular diffusion. This is due to solar radiation, which heats up the leaves and drives thermal transpiration (Chanton *et al.* 1993). Furthermore, plant root exudates promote CH_4 production, and the oxygen that is supplied via the plant from the atmosphere permits rhizopheric CH_4 oxidation (Bubier & Moore 1994; Strom & Christensen 2007). However, it is not agreed how much plant mediated CH_4 losses compare to other environmental variables (Joabsson *et al.* 1999). Some suggest that in pristine fens, vascular transport has stronger explanatory power than water table and temperature (Turetsky *et al.* 2014).

Although temporal variation of GHGs in peatlands has been shown to be strongly associated with water table and temperature; these environmental parameters do not reliably explain spatial variability of GHGs (Hargreaves & Fowler 1998; Updegraff *et al.* 2001; Dinsmore *et al.* 2009). Therefore, the aim of this study was to gain insight on greenhouse gas emissions' spatial distribution, based on functional traits within rich fen plant communities. Unlike the temporal variability of water table data, plant species composition is less variable, providing more reliable data to ascertain spatial heterogeneity of GHG fluxes (Dias *et al.* 2010; Levy *et al.* 2012; Gray *et al.* 2013). Botanical data has the potential to provide inexpensive proxy data for GHG emissions, as the distribution of plant communities is likely to be associated with gas flux drivers, whereas environmentally derived data is expensive and difficult to measure (Couwenberg *et al.* 2011; Gray *et al.* 2013).

Therefore, this study will examine CO_2 and CH_4, emissions at a good condition (species rich) and degraded (species poor) plant communities, as well as quantify if there are differences between the plant communities that are located within each site. Predictors of CO_2 and CH_4 will be derived from vegetation components and known plant functional traits. Questions to be addressed: (i) whether a botanically degraded rich fen site has a lower carbon balance compared to a botanically good condition site, as it is suggested that higher carbon sequestration is positively correlated with plant diversity and associated plant traits and carbon losses are associated with litter accumulation (Steinbeiss *et al.* 2008; Orwin & Ostle 2012; Ward *et al.* 2015), (ii) what are the plant mediated spatial effects on CH_4 fluxes within each site (iii) identify plant functional traits that can reliably predict CO_2 and CH_4 to provide finer resolution spatial data.

4.3 Materials and methods

4.3.1 Site description

Figure 4.1   Aerial photograph for Cors Erddreiniog showing study sites: degraded (a) and good condition (b). Each site has 18 collars *n*= 6 for each plant community. (a) depicts the location of *Cladium* collars (rectangle), PM collars (diamond) and PPM collars (triangle) and (b) shows Bryophyte collars (rounded rectangle), *Juncus* collars (circle) and Sphagnum collars (oval). Refer to Table 5.1 for abbreviations.

The investigation was undertaken at a rich fen lowland peatland; Cors Erddreiniog, located on the island of Anglesey off the North-west coast of Wales, U.K (53.3098 N, -4.2908 E). The study site extends 200 hectares in area within a valley head fen system, including three peat basins (Prosser & Wallace 1995; Jones 2013) and was chosen as it is a large site which contains both degraded and good condition fen. Two locations within the study site were selected, which are a distance of approximately 700 metres apart and are botanically different, Figure 4.1. As outlined below the good condition site is composed of species rich communities and the degraded site is composed of species poor communities.

4.3.1.1 Plant communities and sub-communities

The good condition site has undrained semi-natural vegetation which covers a 4 hectare area and encompasses a mosaic of plant communities. It is dominated by a *Juncus subnodulosus-Cirsium palustre* fen meadow, which comprises rushes and sedges as the prominent vegetation components. The also comprises a smaller areal cover of *Molinia-caerulea-Potentilla erecta* community, characterised by the tussock forming graminoid *Molinia* caerulea as well as rushes (*Juncus spp.*) and sedges (*Carex spp.*).

The degraded compartment comprises an area of approximately 3 hectares and is botanically poor. Tall graminoid species dominate, such as *Cladium mariscus, Phragmites australis* and tussock forming *Molinia caerulea.*

4.3.2 Experimental design and equipment

4.3.2.1 Collar and static chambers

A total of thirty six collars were installed between 11 and 20 December 2012, following which they were left to settle for four months. There were six collars (*n*=6) in each plant community and three plant communities at each site. Location of collars were determined using Phase 2 habitat mapping prior to installation, to guide where to install collars and ground truthing was undertaken to ensure collars were botanically comparable.

Collars were constructed using grey PVC (60 cm x 60.6 cm x 30 cm x 0.45 cm) to provide a vegetation surface area of 363.6 cm ^{2} and corners were strengthened with aluminium angle along the height of each corner, Figure 4.2 (a). Collar sills were covered with white silicon foam (0.8 cm x 0.6 cm) and adhered with sealant around the perimeter to ensure there was an air tight seal between the collar and the chamber section. Collars were installed to a depth of 15 cm and holes were drilled along the vertical face of the collar below the peat surface to enable water movement.

Chambers sections were constructed with clear PVC for light measurements and modified for dark measurements by covering in thick black polythene, Figure 4.2. Middle chamber sections (50 cm x 60.6 cm x 60 cm x 0.45 cm) each had a small fan affixed to one interior wall and an additional fan was affixed to the underside of the chamber top facing down (30 cm x 60.6 cm x 30 cm x 0.45 cm) to ensure each sample was consistently mixed. The side wall of the chamber top also supported a valve which had a pressure equalisation balloon. A 5 cm diameter port was constructed on the chamber top, to support the bung which provided an air tight seal for the gas analyser's inlet/outlet sampling conduits.
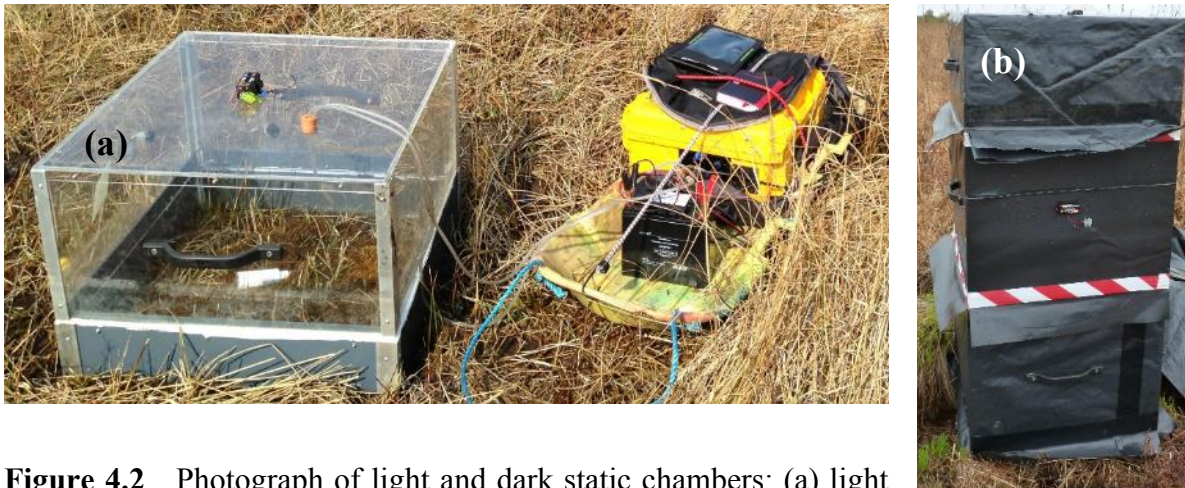
Figure 4.2 Photograph of light and dark static chambers: (a) light static chamber and collar located in *Sphagnum* (S) community (low height vegetation) shown with Los Gatos gas analyser to the right and (b) dark static chamber using two middle sections, located in the tall *Phragmites* (PM) community.

4.3.2.2 Dip well measurements

Dip wells were constructed using grey PVC tubes 27.4 mm internal diameter (32 mm external diameter) with one 32 mm end caps installed at the base and at the top to inhibit peat intrusion and rainwater inputs respectively. The dip well was 1.5 m in length and was installed to a 1 m depth. The length of intake was 10 cm using a 5 mm diameter drill bit with even spacing. Dipwells were installed to a 1.5m depth and located within 5 metres of each vegetation group of collars. Water table measurements were undertaken using an In-Situ Rugged Level TAPE 200 dip meter (In-situ Europe, Solihull, U.K.). Measurements were undertaken once a month, during a monthly gas sampling campaign below.

4.3.3.3 Gas measurements and meta data

Sampling was undertaken over one year, commencing on 8 April 2013 and concluding on 26 March 2014. Sampling frequency was monthly and consisted of eleven sampling events (excluding August). Gas measurements were undertaken over a 3-4 day period and where possible vegetation groups were measured on the same day.

Prior to measurement, a Traceable lollipop shock/waterproof thermometer (Fisher Scientific UK ltd) was inserted to a 5 cm soil depth externally, adjacent to each collar/chamber and was recorded for each collar. A HOBO V2.0 (Tempcon Instrumentation, UK) data logger was placed amongst the vegetation within each collar area, and was used to measure chamber air temperature and humidity every ten seconds. In addition, an Extech SD700 Barometric pressure humidity temperature probe

(Extech Instruments, USA), was also placed within the chamber during measurement, in order to record a single pressure value for each collar/chamber measurement.

Gas measurements were undertaken using a Los Gatos Ultra-portble gas analyser (Los Gatos Research, California, USA) which was calibrated to measure CO_2 (ppm) and CH_4 (ppm) simultaneously every 2 seconds. The number of middle chambers (0-2) was decided at each visit, dependent on vegetation height and was kept consistent within vegetation communities and recorded. Chambers were carefully placed on each collar, followed by the chamber hood, after which the inlet and outlet tubes carrying sampling gas to and from the analyser were quickly and securely placed within the chamber hood port. The measurement start and end time was recorded, for five minutes or until a linear relationship was evident. Following a light chamber measurement, clear chamber sections were carefully dismantled from the collar and replaced with the same number of dark chambers and the measurement was repeated. Each light and dark measurement was over a 5 minute duration for each chamber or until a linear relationship between CO_2 concentration (ppb) and time (seconds) was evident, displayed on a Nexus 370T tablet. In the event of ebullition episodes, due to disturbance or otherwise, measurements were repeated.

4.3.4 Flux chamber calculations

Flux calculations between peatland and atmosphere were undertaken using Denmead's (2008) formulae (a) for a closed static chamber and modified to (b) for a dynamic chamber which accounts for air flow rate:

(a)   (b)

$$F_g = \frac{V}{A}\frac{d\rho_g}{dt}$$ $$F_g = \frac{1}{A}\frac{dg_m}{dt}$$

where F_g, denotes the gas flux density at the peatland surface (mg m^{-2} day^{-1}), V is the total volume of the chamber and collar above the peat surface (m^3), A is the internal surface area of the collar (m^2), ρ_g is the mass concentration of the gas in the chamber (mg m^{-3}), and t is time (days).

The formulae was modified to transform units from moles to mass. For equation (b); g_m denotes the mass of gas in the chamber ($g_m = V$ x P_g units (mg) where volume was converted to an equivalent volume under standard temperature and pressure (STP).

Flux chamber processing and calculations were undertaken within the R statistics programme (R-Core-Team 2014). A linear regression was then fitted in R, using the mass and time data to provide the rate of decrease/increase gas concentration per chamber. Using the best line of fit, the mass flux density (F_g) of gas from the soil was calculated (mg CH_4 / CO_2 m^{-2} day^{-1}) and r^2 and P values were also calculated.

Each chamber measurement flux calculation for CO_2 and CH_4 was then validated by observing the r^2 values, which if lower than 0.7 were rejected, or if below this threshold, were only retained where gas concentration values were low, which would result in a poor line of fit.

4.3.4.1 Annual flux calculations

Annual mean CH_4 and CO_2 fluxes (mg m^{-2} day^{-1}) were calculated independently, by taking the annual mean for each collar for the twelve month campaign, for each plant community. The annual mean fluxes and standard errors were then derived from the six collars for each plant community. CO_2 light measurements provided values for net ecosystem exchange (NEE), which measures total respiration and photosynthesis (Campbell *et al.* 2000). Ecosystem respiration (Reco) was derived from dark measurements. Gross primary production (GPP) was calculated as NEE minus Reco, which provided the net carbon uptake minus respiration. CH_4 values were derived from the mean of light and dark measurements and to calculate the annual mean CO_2 equivalent. These values were multiplied by 25, to take account of the stronger radiative forcing of CH_4 compared to CO_2 and finally the CO_2 equivalent value was added to the NEE value to provide a CO_2 equivalent balance value (Lelieveld *et al.* 1998; Whiting & Chanton 2001).

4.3.5 Botanical survey and plant community characteristics

All 36 collars were botanically surveyed over a 3 day period during 8 - 10 July 2013. Areal percentage cover was recorded for all species present, including bryophytes. In addition, percentage cover of litter and bare ground were measured and a mean vegetation height was recorded, derived from 5 measurements taken within each collar using a measuring cane.

The mean water table depth for each site and plant community provides some explanation to the plant community assemblage and distribution, Table 4.1. However there was no difference between sites (*P,*0.81).

Table 4.1 Naming convention for vegetation communities and the dominant species present. Site denotes where each site is located: good condition (GC) or degraded (D). Mean annual water table depth denotes on average whether the water is above (positive

number) or below (negative number) the peat surface. Mean water table for each site is in bold.

Collar Name	Vegetation Type	Site	Constant species	Mean Annual Water Table Depth (WTD) (cm)
B	Brown mosses	GC	*Calliergonella cuspidata* and *Campylium stellatum*	2.55 ± 0.34
J	*Juncus*	GC	*Juncus subnodulosus* and *Molinia caerulea*	-2.35 ± 0.33
S	*Sphagnum*	GC	*Sphagnum subnitens*	-3.47 ± 0.42
			GC Mean (WTD)	**-1.09 ± 0.25**
CM	Tall sedge	D	*Cladium mariscus*	-2.19 ± 0.36
PM	*Phragmites*	D	*Phragmites australis (low density), Molinia caerulea*	3.30 ± 0.36
PPM	*Phragmites* and bryophytes	D	*Phragmites australis (high density), Molinia caerulea* and bryophytes	-2.15 ± 0.23
			D Mean (WTD)	**-0.09 ± 0.23**

4.3.6 Trait selection

A total of 12 traits were tested; CH_4 traits were derived from Gray *et al.* (2013) and calculated by reporting the total percentage cover from all species containing CH_4 traits per collar. Plant functional traits were as follows: Trait A characterises species with aerenchymatous tissue in their roots (CH_4 emission pathway), trait B characterises species with actinorhizal N fixing capability (CH_4 emission pathway/root exudation) and Trait C, species with aerenchymatous tissue (CH_4 emission pathway and or pressurised flow). In addition, species richness, mean vegetation height and percentage cover of vegetation components (shrubs, graminoids, *Carex species,* herbs, bryophytes, litter and bare ground) were also incorporated in to the regression analyses, to determine whether they were an important component in controlling CO_2/CH_4 emissions.

4.3.7 Statistical analysis

Statistical package 'R' (R-Core-Team 2014) was employed to undertake all statistical analyses. Gas fluxes were tested to identify annual fluxes, growth season (May-October) and spring/winter (November-April). The spring and winter seasons were grouped as it was evident from the temporal gas flux series that there was no photosynthetic associated growth occurring prior to May. A linear mixed effects model was designed using the lmer function and lme4 package (Bates *et al.* 2014). This was designed to test differences between site and between plant communities. The null model comprised of the response variable (CH_4, NEE, Reco, GPP) and random effects ("site", "plant community", "collar" and "month") and the full model tested response variable as a function of fixed effects "plant community" or "site" and the balance of random effects ("site" or "plant community", "collar" and "month"), dependent on whether testing site differences and within site differences (between plant communities). Analysis of variance (ANOVA) was then employed to compare differences between the variance in the null and full models to determine significance values. Furthermore, to test which plant community significantly differed from others, TUKEY pairwise comparisons were undertaken, based on the full model's ANOVA analysis. The following transformations were undertaken for the response and explanatory variables to obtain linear relationships and normal distributions. CH_4 and Reco were log transformed and GPP and NEE were square root transformed. All explanatory variables were arcsine transformed.

Linear regression was undertaken on the calculated annual gas flux median for each collar, providing 6 data points for each plant community for the total sampling campaign. For the median regression plots, CH_4, Reco and GPP were log transformed and NEE was square root transformed. All explanatory variables were arcsine transformed, with exception of vegetation height which was log transformed.

4.4 Results

4.4.1 Botanical survey

The good condition site was the most species rich site, with 7.83 ± 0.1 species per collar, which was 61 % more species overall than the degraded site, which had 4.17 ± 0.06 species per collar. The most species rich community was the *Juncus* and the most species poor community was the PM, Table 4.2.

Shrub cover was low across all plant communities. The highest graminoid cover (excluding *Carex spp.*) was found in the *Juncus,* PM and PPM communities. The *Cladium* community had a lower

than expected cover of graminoids due to the high amount of litter, which is also prevalent in the *Juncus*, PM and PPM communities. Herb cover was less than 5 % in all plant communities, but is highest in the *Juncus* community. *Carex spp.* were only found in the brown mosses and *Juncus* communities. The highest percentage cover of bryophytes was found in the brown mosses and *Sphagnum* communities. The slightly lower cover of bryophytes shown in the brown mosses compared to the *Sphagnum* community is due to a higher cover of bare ground.

Litter cover was very high for all plant communities at the degraded site, however the good condition site only supported high litter cover in the *Juncus* community. Litter composition was not measured, however, collars were photographed monthly (appendix 1) which allowed identification of the contributing species. In the *Juncus* collars; litter was largely composed of *Juncus subnodulosus.* In the PM and PPM collars, litter was dominated by *Molinia caerulea* and standing litter from *Phragmites australis,* the former appears to reduce from season to season although the latter persists. In contrast, the litter from *Cladium mariscus* appears to decompose slowly, as it appears to accumulate year on year. Vegetation height was highest at the degraded site in the graminoid communities, and lowest in the brown mosses community.

Table 4.2   Percentage cover of vegetation components and traits (refer back to table 5.1 of the methods section) for each plant community: B, (Bryophytes), J (*Juncus*), S (*Sphagnum*), C (*Cladium*), PM (*Phragmites*), PPM (*Phragmites* with bryophytes).

Plant Community	Mean % cover of vegetation components						
	Shrubs	Graminoids	Herbs	Bryo.	Litter	Bare Ground	*Carex spp.*
B	0.8	7.3	2.5	81	5	7.5	6.2
J	6.7	61.2	3.9	0.3	78	3.8	2.7
S	3.5	38	2.4	93	12.5	2.2	0
C	5.8	36	2.7	0.03	97	0.8	0
PM	4.5	67	0.02	0.9	98	2.8	0
PPM	2.2	51	1	13	95	5	0

Plant Community	Mean Species Richness (per collar)	Vegetation Height (cm)	Mean % cover of species containing traits			
			A	B	C	D
B	8	24.3	4	0.8	4.7	34
J	9.2	57.7	32	6.3	1.4	0.8^{-3}
S	6.3	55	22	3.3	0	3.1
C	4.8	69.7	11.2	2.5	3	0
PM	3.2	60.3	46	3.7	11.7	0
PPM	4.5	77.5	26	1.7	23	0

Trait A was found in all plant communities and is highest in the PM community and lowest in the brown mosses community and is present in *Myrica gale, Juncus acutiflorus* and *Molinia caerulea,* Table 5.3. Trait B is also found in all plant communities and is only known to be present in *Myrica gale.* Trait C is found in all plant communities with exception to *Sphagnum* community and is present in *Carex echinata, Carex panicea* and *Phragmites australis.*

Table 4.3 Species list for each plant community and associated vegetation components and traits.

Species	Veg. Comp.	Trait	Plant Comm.	Species	Veg Comp.	Trait	Plant Comm.
Betula pubescens	Shrub	-	S, C	*Hypericum pulchrum*	Herb	-	S
Erica tetralix	Shrub	-	PPM	*Lysimachia vulgaris*	Herb	-	C
Myrica gale	Shrub	A, B	All	*Potentilla palustre*	Herb	-	B,C
Carex echinata	Carex spp.	C	B	*Polygala serpyllifolia*	Herb	-	S
Carex elata	Carex spp.	-	J	*Potentilla erecta*	Herb	-	J,S,PM,PPM
Carex flacca	Carex spp.	-	B	*Rubus fruticosus*	Herb	-	J
Carex panicea	Carex spp.	C	B, J	*Succisa pratensis*	Herb	-	B,J,S

Carex pulicaris	*Carex spp.*	-	J	*Triglochin palustre*	Herb	-	B
Carex viridula ssp.brachyrrhyncha/viridula	*Carex spp.*	-	B	*Aulacomnium palustre*	Bryophyte	-	S
Cladium mariscus	Graminoid	-	C	*Brachythecium rutabulum*	Bryophyte	-	J,PM
Festuca rubra	Graminoid	-	B, J	*Calliergonella cuspidata*	Bryophyte	-	B,J
Juncus acutiflorus	Graminoid,	A	B,J,C	*Campylium stellatum*	Bryophyte,	-	B,J,C,PM,PPM
Juncus subnodulosus	Graminoid	-	B,J,S,C	*Ctenidium mulluscum*	Bryophyte	-	J
Molinia caerulea	Graminoid,	A	All	*Fissidens adianthoides*	Bryophyte	-	J
Phragmites australis	Graminoid,	C	J,C,PM, PPM	*Hypnum jutlandicum*	Bryophyte	-	PM,PPM
Angelica sylvestrus	Herb	-	J	*Hymenophyllum wilsonii*	Bryophyte	-	PPM
Dactilorhiza spp.	Graminoid	-	PPM	*Kindbergia praelonga*	Bryophyte	-	J
Drosera rotundifolia	Herb	-	S	*Calypogeia fissa*	Bryophyte	-	S
Epilobium hirsutum	Herb	-	S	*Jungermania spp.*	Bryophyte	-	S
Epilobium palustre	Herb	-	S	*Sphagnum palustre*	Bryophyte	-	S
Eupatorium cannabinum	Herb	-	B,J,C	*Sphagnum subnitens*	Bryophyte	-	S

4.4.2 Temporal gas fluxes

4.4.2.1 CH_4 fluxes

There was no overall difference in the annual CH_4 fluxes between the degraded and good condition sites, Table 4.4. CH_4 fluxes during the growth season (May to October) were also comparable. However, during the growth season, all communities exhibited increased CH_4 losses during this time, Figure 4.3 a-b). However, differences between sites were observed during the winter/spring (November − April), when the degraded site (161 mg CH_4 m^{-2} day^{-1} ± 29) emitted 70 % more CH_4 than the good condition site (49 mg CH_4 m^{-2} day^{-1}± 17) ($P<0.05$).

Overall within site differences were also observed at the degraded site, between the PPM community (539 mg CH_4 m^{-2} day^{-1} ± 124) and the *Cladium* community (86 mg CH_4 m^{-2} day^{-1} ± 29), which exhibit the highest and lowest CH_4 fluxes across both sites respectively ($P<0.05$).

CH_4 losses between communities were comparable within each site during the winter. However, during the growth season, differences in CH_4 losses were evident at the good condition site, between the *Sphagnum* (94 mg CH_4 m^{-2} day^{-1} ± 10) and brown mosses (657 mg CH_4 m^{-2} day^{-1} ± 108) communities ($P<0.01$). The degraded site also exhibited differences during the growth season, between the *Cladium* (106 mg CH_4 m^{-2} day^{-1} ± 17) and PPM (860 mg CH_4 m^{-2} day^{-1} ± 179) communities ($P<0.01$).

4.4.2.2 Net ecosystem exchange (NEE)

There was no difference in the annual NEE flux, between the good condition (9,602 CO_2 m^{-2} day^{-1} ± 1,739) and degraded site (10,818 CO_2 m^{-2} day^{-1} ± 1,040), Figure 4.3 c-d, Table 4.4. The NEE flux for the growth season was also comparable between the good condition (-17,375 CO_2 m^{-2} day^{-1} ± 2053) and degraded (-17,236 CO_2 m^{-2} day^{-1} ± 2377) sites. In addition, no differences were observed for NEE during the winter/spring for the good condition (-4,594 CO_2 m^{-2} day^{-1} ± 702) and degraded (-1,674 CO_2 m^{-2} day^{-1} ± 220) sites, Figure 4.3 b-c, Table 4.4. However, differences were observed within each site, at the good condition site between the *Sphagnum* (-17, 251 CO_2 m^{-2} day^{-1} ± 3,203) and brown mosses (-3,436 CO_2 m^{-2} day^{-1} ± 321 mg) communities (*P*<0.001) and the *Sphagnum* and *Juncus*   (-8,119 CO_2 m^{-2} day^{-1} ± 864) communities (*P*<0.05).

In the degraded site, annual fluxes for NEE were observed between the CM (-15,573 CO_2 m^{-2} day^{-1} ± 1,257) and the PM (-7659 CO_2 m^{-2} day^{-1} ± 1,026) communities (*P*<0.01). During the growth season, good condition site communities differed from one another as follows: *Sphagnum* (-33,303 CO_2 m^{-2} day^{-1} ± 5278) and brown mosses (-4900 CO_2 m^{-2} day^{-1} ± 1330) (*P*<0.001), *Sphagnum* and *Juncus*   (-15,037 CO_2 m^{-2} day^{-1} ± 3138 mg (*P*<0.001) and *Juncus* and brown mosses (*P*<0.05). The degraded community also exhibited a weak difference during the growth season between the PM (-14,443 CO_2 m^{-2} day^{-1} ± 3809) and CM community (-23,473 CO_2 m^{-2} day^{-1} ± 3045) (*P*, 0.06).
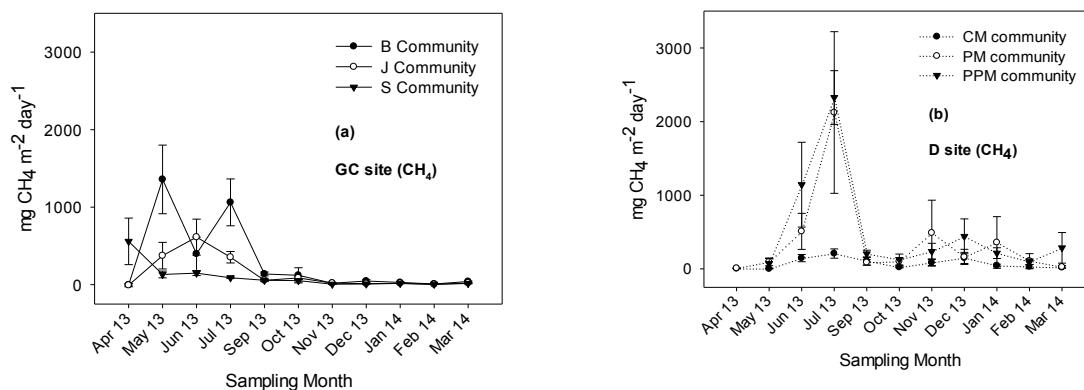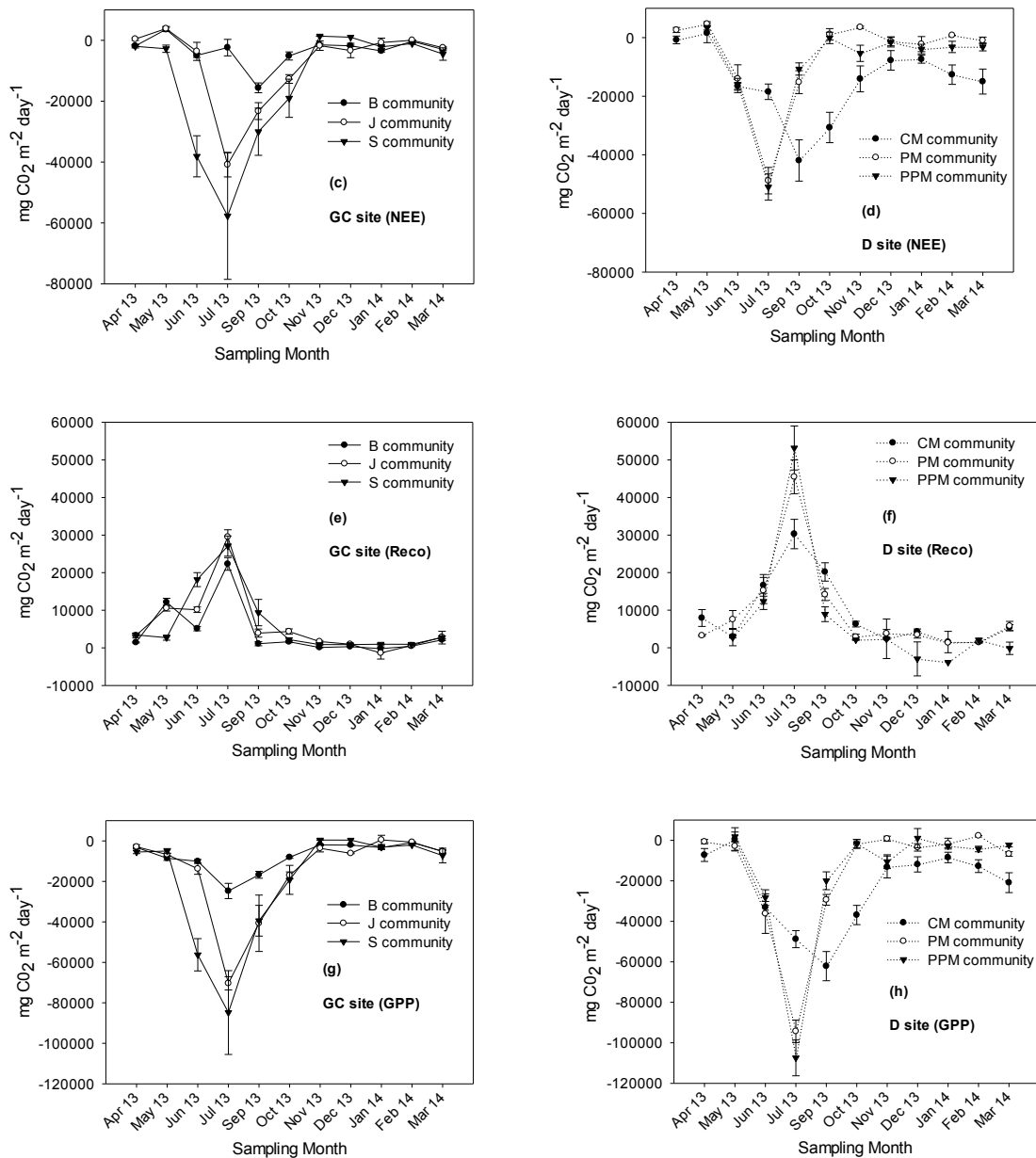
Figure 4.3 Temporal CO_2 and CH_4 fluxes between good condition (GC) and degraded (D) site (a) CH_4 GC site, (b) CH_4 D site, (c) NEE GC site, (d) NEE D site, (e) Reco GC site, (f) Reco D site, (g) GPP GC site, (h) GPP D site. Error bars indicate 1 standard error $\pm$ mean.

Differences were also evident in the winter/spring at the degraded site. Differences were also evident between the PM and CM (-9352 CO_2 m^{-2} day^{-1} $\pm$ 1392) communities ($P<0.001$); the latter had the highest CO_2 uptake during the winter/spring period and notably has a lag in CO_2 uptake, and demonstrates CO_2 uptake beyond the growth season compared to all other communities. However, the *Sphagnum* community is the earliest community to respond to the season as it started increasing NEE in May, whereas all other communities started in June, with the exception to the CM, which commenced in June but exhibited a lag in peak NEE values compared to all other communities.

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4.4.2.3 Ecosystem respiration (Reco)

The annual respiration at the good condition site (6,062 CO_2 m^{-2} day^{-1} ± 406) was 58 % lower than the degraded site (11,018 CO_2 m^{-2} day^{-1} ± 617) (*P<0.05*), Figure 4e-f. In the growth season, the good condition site also demonstrated 40 % lower respiration (11,254 CO_2 m^{-2} day^{-1} ± 1,039), compared to the degraded site (16,800 CO_2 m^{-2} day^{-1} ± 1755) (*P<0.05*). The largest differences were observed during the winter/spring seasons, when respiration was 75 % lower in the good condition site (1,381 CO_2 m^{-2} day^{-1} ± 168) compared to the degraded site (3,027 CO_2 m^{-2} day^{-1} ± 439) (*P<0.05*).

Annual within site differences for respiration were also evident. In the good condition site, the brown mosses community (4,544 CO_2 m^{-2} day^{-1} ± 870) showed the lowest respiration amongst all plant communities, which was 41 % lower than the *Juncus* community (6,876 CO_2 m^{-2} day^{-1} ± 1,084) (*P<0.001*) and 38 % lower than the *Sphagnum* community (6,680 CO_2 m^{-2} day^{-1} ± 1142) (*P<0.001*). At the degraded site, annual within site differences were also observed for respiration, between the *Cladium* (9,879 CO_2 m^{-2} day^{-1} ± 1,286) and PPM communities (11,349 CO_2 m^{-2} day^{-1} ± 2,402) *P<0.01*). The highest overall respiration loss was observed in the PM community (11,735 CO_2 m^{-2} day^{-1} ± 1,773) at the degraded site.

During the growth season, within site differences were only observed at the good condition site. A 40 % difference was observed between the brown mosses community (8,698 CO_2 m^{-2} day^{-1} ± 1,541), which had the lowest loss to respiration overall for both sites and the *Juncus* (12,964 CO_2 m^{-2} day^{-1} ± 2001) community (*P<0.05*). During the growth season the highest losses to respiration were demonstrated by the PPM community (17,676 CO_2 m^{-2} day^{-1} ± 3,921).

During the winter/spring seasons, within site differences were observed at the good condition site between the brown mosses (778 CO_2 m^{-2} day^{-1} ± 206), which had the lowest respiration loss across both sites and was 74 % lower than the *Sphagnum* community (1689 CO_2 m^{-2} day^{-1} ± 328) (*P<0.001*). During winter/spring at the degraded site, differences were observed between the *Cladium* (4,070 CO_2 m^{-2} day^{-1} ± 782) and PPM community (-401 CO_2 m^{-2} day^{-1} ± 865) (*P<0.05*); the latter community showed a carbon gain.

4.4.2.4 Gross primary productivity (GPP)

There was no difference in annual GPP fluxes between the good condition (-16,404 CO_2 m^{-2} day^{-1} ± 2,065) and degraded (-20,924 CO_2 m^{-2} day^{-1} ± 1,392) sites, Figure 4.3 g-h, Table 4.4. Seasonal net CO_2 uptake was also comparable between sites. However, overall within site differences were

observed at both sites. The good condition site demonstrated that GPP was lowest in the brown mosses community (-8,674 CO_2 m^{-2} day^{-1} ± 585) which demonstrated a 94 % lower net GPP flux, compared to the *Sphagnum* community (-23, 985 CO_2 m^{-2} day^{-1} ± 4,209) (*P*<0.001); the latter community showed the second highest net GPP across all plant communities. At the degraded site, overall within site differences were evident between the *Cladium* (-25, 408 CO_2 m^{-2} day^{-1} ± 1,759) community, which exhibited the highest annual GPP which was 30 % higher than the PPM community (-18, 745 CO_2 m^{-2} day^{-1} ± 3,079) (*P*<0.01).

During the growth season, within site differences were only observed at the good condition site, between the brown mosses (-13,813 CO_2 m^{-2} day^{-1} ± 1,023), which showed the lowest GPP flux; this was 72 % lower than the *Juncus* community (-29, 331 CO_2 m^{-2} day^{-1} ± 3,510) (*P*<0.05) and 105 % lower than the *Sphagnum* community (44,400 CO_2 m^{-2} day^{-1} ± 4915) (*P*<0.001). The latter community exhibited the highest GPP flux across all plant communities during the summer months.

During the winter/spring season, within site differences were observed at both sites. At the good condition site, differences were observed between the *Sphagnum* community (-3,704 CO_2 m^{-2} day^{-1} ± 565) which was 34 % higher than the *Juncus* community (-2, 616 CO_2 m^{-2} day^{-1} ± 413) (*P*<0.001) and 28 % higher than the brown mosses (-2,799 CO_2 m^{-2} day^{-1} ± 214) (*P*<0.001). At the degraded site, winter/spring season differences were also shown between the *Cladium* (-12, 044 CO_2 m^{-2} day^{-1} ± 1,063) community, which also demonstrated the highest GPP flux and the PPM community (-3,439 CO_2 m^{-2} day^{-1} ± 686 mg) (*P*<0.001).

4.4.3 Gas flux predictors
4.4.3.1 CH_4 predictors

The strongest positive predictor for CH_4 fluxes at both sites was trait C, Table 4.4. This trait was present in the following species: (and associated communities) *C.echinata, C.panicea* at the good condition site, and *P.australis* at the degraded site, which is having the strongest influence on increasing CH_4 emissions.

Table 4.4   Gas flux vegetation predictors for the good condition site, degraded site and both sites. Dashed lines indicate poor predictors and all other poor predictors not listed have been excluded from the Table. Bold text indicates the strongest overall positive and negative predictors for each group, which are illustrated in Figure 5.3 a-h.

Traits	Good Condition site			Degraded site			Both sites		
	r^2	slope	*P* value	r^2	slope	*P* value	r^2	slope	*P* value
	CH_4			**CH_4**			**CH_4**		

Predictor									
Trait B	-	-	-	-	-	-	**0.13**	**- 3.02**	**P<0.05**
Trait C	0.38	+ 3.3	P<0.01	0.18	+ 2.9	P,0.07	**0.29**	**+ 2.9**	**P<0.001**
Graminoids	0.15	- 0.8	P, 0.06	-	-	-	-	-	-
Carex spp.	0.28	+ 2.5	P<0.05	-	-	-	-	-	-
Bryophytes	-	-	-	0.18	+ 3.2	P,0.08	-	-	-
Bare ground	-	-	-	0.2	+ 5.5	P,0.06	-	-	-
NEE				**NEE**			**NEE**		
Trait A	-	-	-	0.5	- 109	P<0.01	**0.1**	**- 41**	**P<0.05**
Sp. richness	0.2	- 251	P, 0.06	0.44	+ 842	P<0.01	-	-	-
Bryophytes	0.17	+ 13.2	P, 0.09	-	-	-	-	-	-
Bare ground	-	-	-	-	-	-	**0.13**	**- 111**	**P<0.05**
Herbs	-	-	-	0.22	+ 196.4	P<0.05	-	-	-
Reco				**Reco**			**Reco**		
Trait A	0.59	+ 1.48	P<0.001	-	-	-	0.11	+ 0.75	P<0.05
Trait B	0.52	+ 2.8	P<0.001	-	-	-	-	-	-
Sp. richness	-	-	-	-	-	-	0.11	- 4.14	P<0.05
Graminoids	0.46	+ 0.9	P<0.01	-	-	-	**0.26**	**+ 0.97**	**P<0.01**
Carex spp.	-	-	-	-	-	-	0.22	- 2.5	P<0.01
Shrubs	0.53	+ 2.79	P<0.001	0.29	+ 1.39	P<0.05	0.18	+ 1.8	P<0.01
Bryophytes	0.37	- 0.47	P<0.01	-	-	-	**0.5**	**- 0.72**	**P<0.001**
Bare ground	-	-	-	-	-	-	0.21	- 2.4	P<0.01
Veg. Height	0.21	+ 1.21	P<0.05	-	-	-	0.3	+ 1.6	P<0.001
Litter	0.38	+ 0.62	P<0.01	0.27	+ 1.67	P<0.05	**0.59**	**+ 0.78**	**P<0.001**
GPP				**GPP**			**GPP**		
Trait A	0.23	+ 0.74	P<0.05	0.2	- 1.2	P<0.05	-	-	-
Trait B	0.26	+ 1.58	P<0.05	0.32	-1.3	P<0.05	-	-	-
Sp. richness	-	-	-	0.26	+ 10.7	P<0.05	-	-	-
Bare ground	-	-	-	0.2	+ 3.1	P<0.05	**0.13**	**- 1.86**	**P<0.05**
Herbs	-	-	-	0.2	+ 3.05	P,0.06	-	-	-

The only predictor to demonstrate a decrease in CH_4 concentration overall was Trait B, present in the shrub *M.gale*, present in all communities although associated most with the *Juncus* community, Figure 4.3b. In addition, at the good condition site only, graminoids (excluding *Carex spp.*) were negatively associated with CH_4 concentration, Table 4.4.

The degraded site also reflected a weak positive relationship to trait C, however this was not due to the presence of *Carex spp,* but to the presence of *Phragmites australis*. Increased cover of bryophytes and bare ground also showed a weak positive relationship to CH_4 production at the degraded site.
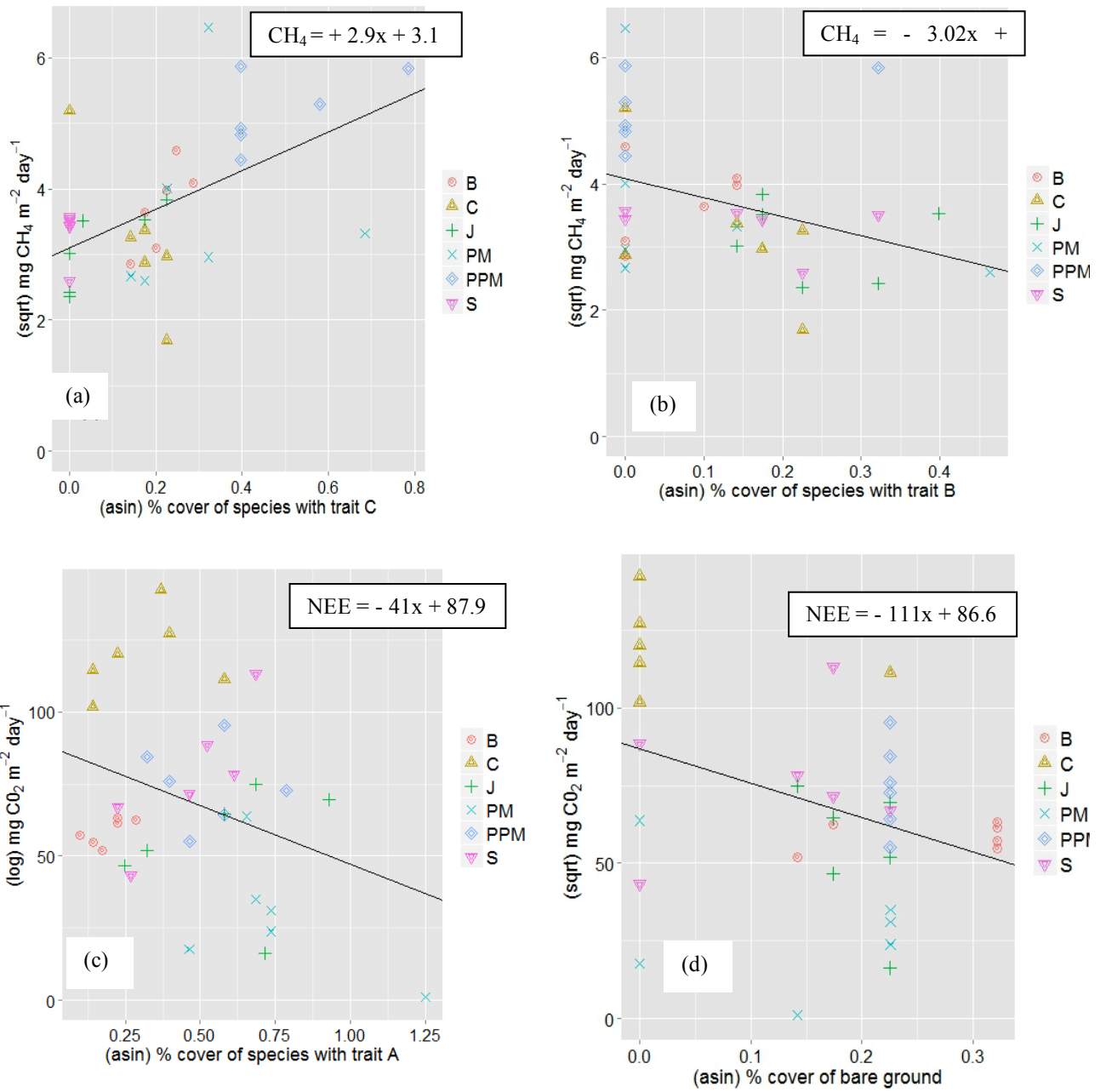
Figure 4.4 Regression analyses and strongest overall traits for CH_4 and CO_2 fluxes: (a) CH_4 production (b) CH_4 reduction, (c) negative NEE, (d) negative NEE.
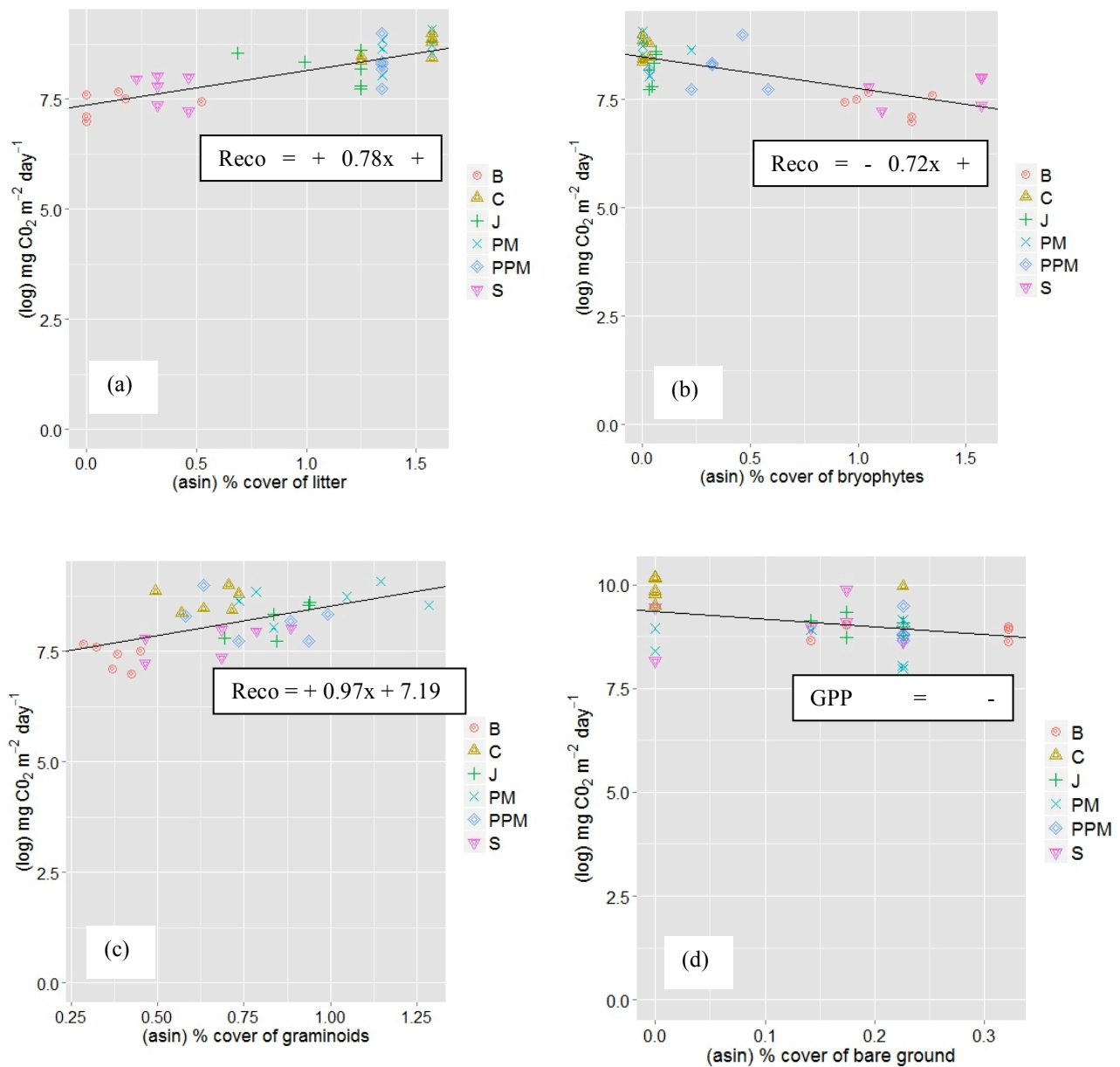
Figure 4.5 Regression analyses and strongest overall traits for CH_4 and CO_2 fluxes: (a) positive Reco, (b) negative Reco, (c) positive Reco, (d) negative GPP.

4.4.4 CO₂ predictors

4.4.4 CO$_2$ predictors

4.4.4.1 Net ecosystem exchange (NEE)

Overall, for both sites, two negative predictors for NEE were identified; percentage cover of species with trait A and percentage cover of bare ground, Table 4.4, Figure 4.4 c-d). The highest rates of carbon sequestration, as evident by high negative values, were most apparent in the *Sphagnum* community, seconded by the *Cladium* community, and the lowest carbon sequestration rates were most evident in the brown mosses. Furthermore, decreasing CO_2 losses were best predicted with

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bare ground, which again was associated with the brown mosses community, and low bare ground and higher CO_2 uptake was associated with the *Cladium* community.

Species richness was not a good predictor across sites as it exhibited opposing relationships on NEE. CO_2 flux is negatively associated with species richness at the good condition site and strongly, positively associated with CO_2 flux at the degraded site. In addition, herbs were weakly positively associated with increased NEE at the degraded site. The only predictor evident at the good condition site was bryophytes, which are weakly associated with increased NEE.

4.4.4.2 Ecosystem respiration (Reco) predictors

Respiration for both sites was most positively associated with litter, graminoid and shrub cover, and to a lesser extent species richness and vegetation height, Table 4.4, Figure 4.5 e- g). Lower Reco is strongly associated with bryophyte cover, Figure 4.5 f, bare ground, *Carex spp.* and Trait A, found in shrub, *Myrica gale,* and graminoids, *Juncus acutiflorus* and *Molinia caerulea.* The negative association between bryophytes was only evident at the good condition site where this vegetation group is most prevalent. The positive association with trait A was only evident at the good condition site only, as is the positive association with vegetation height.

4.4.4.3 Gross primary productivity (GPP) predictors

The only overall predictor for GPP is bare ground, which is negatively associated with CO_2 flux, and is most prevalent in the brown mosses community, Table 5.3. Traits A and B support opposing control on GPP, which also appears to be site dependent. The degraded site also showed that species richness and herb cover were positive predictors for GPP.

4.4.5 Net gaseous carbon flux

There is no significant difference in the net carbon balance between the good condition and degraded site; both are net atmospheric carbon sinks, Table 4.5. However, not all plant communities are net gaseous carbon sinks. The brown mosses in the good condition site and the PM and PPM communities in the degraded site are all a net source of carbon. This is due to the high CH_4 emissions at these three sites. The *Sphagnum* and the *Cladium* communities have the lowest methane losses and the highest net carbon uptake, which has suggests these communities are the most efficient net carbon sinks.

Table 4.5 Annual fluxes for CH_4, CO_2 equivalent (CO_2e), NEE and net CO_2e.

Plant Community	Annual Mean CH_4 (mg CH_4 m^{-2} day^{-1})	Annual Mean CO_2 Equivalent of CH_4 (mg CO_2e m^{-2} day^{-1})	Annual Mean NEE (mg CO_2 m^{-2} day^{-1})	Net Gaseous Carbon flux (mg CO_2e m^{-2} day^{-1})
Brown mosses	328 ± 90	8,198 ± 2,238	- 3,436 ± 321	+ 4,762 ± 2,400
Juncus	142 ± 32	3,559 ± 802	- 8,119 ± 864	- 4,560 ± 1,587
Sphagnum	102 ± 29	2,559 ± 730	- 17,251 ± 3,203	- 14,692 ± 3,549
GC Site	**191 ± 39**	**4,772 ± 980**	**- 9,602 ± 1,739**	**- 4,830 ± 2,340**
Cladium	86 ± 29	2,154 ± 729	- 15,573 ± 1,257	- 13,419 ± 1,688
PM	397 ± 228	9,922 ± 5,691	- 7,659 ± 1,026	+ 2,264 ± 5,569
PPM	539 ± 124	13,470 ± 3,110	- 9,221 ± 1,170	+ 4,249 ± 2,689
D Site	**340 ± 94**	**8,515 ± 2,343**	**-10,818 ± 1,040**	**- 2,302 ± 2,775**

4.5 Discussion

This investigation has demonstrated that both botanically degraded and good condition rich fens support equal gaseous carbon flux; providing an important climate mitigation ecosystem service. In spite of this, carbon source plant communities were identified at both sites. This was on account of these plant communities' emitting disproportionately high concentrations of CH_4, compared to their rate of carbon sequestration, and was particularly evident in the brown mosses. Therefore, the assumption that species rich plant communities in a rich fen are more efficient sinks, compared to impoverished plant communities, has not been met. In spite of the apparent contrast between these low and high production sites, differences in rates of decomposition are thought to contribute to comparable rates of carbon sequestration (Lamers *et al.* 2014). However, there does appear to be a consensus that higher productivity equates to increased carbon sequestration (Mitsch *et al.* 2014).

Indeed, Mo *et al.* (2015) also hypothesised that GHG emissions are driven by plant species richness, but concluded that differences are more likely to be driven by functional diversity, between emergent, floating and submerged species. Conversely, this study opposes that view, as large differences between emergent species, *C.marsicus* and *P.australis* as well as bryophyte groups (brown mosses and *Sphagnum*) were observed. Therefore, it is proposed that the spatial heterogeneity is due to physiological and morphological differences, between plant species and associated carbon traits (Andrews *et al.* 2013).

In addition, plant mediated gas flux predictors were identified for CH$_4$, NEE, GPP and Reco, which has provided further evidence to explain the cause of spatial heterogeneity, determined by the ecological setting in which these plant communities are located.

4.5.1 CH$_4$ fluxes

Although no overall between site differences were observed for CH$_4$ fluxes; differences between sites were observed in the winter. There have been many studies that have shown that CH$_4$ emissions outside the growing season are negligible (Alm *et al.* 1999; Hendriks *et al.* 2007). This was not evident in the degraded site, which emitted 70 % more CH$_4$ than the good condition site, however CH$_4$ fluxes were comparably high in the summer. This infers that this is a plant mediated response rather than environmental; given the high frequency of *P.australus* found in the PM/PPM communities at the degraded site, where *P.australis* contains trait C (aerenchymatous tissue present) which provides a direct CH$_4$ pathway from the CH$_4$ production site to the atmosphere, which appears to be accelerated in the winter, due to the broken grass stems. The CH$_4$ flux at the degraded site was almost four times higher than the CM community, and orders of magnitude greater than those at the good condition site. The dominant species in the PM and PPM communities is *P. australis,* which contains trait C, associated with transporting methane directly to the atmosphere without prior oxidation, which is the probable explanation for higher CH$_4$ concentration; however, clipping the stems to below the water's surface has been known to reduce CH$_4$ emissions, which will inhibit this by-pass mechanism to the atmosphere (Frenzel & Rudolph 1998). *P.australis* is a perennial emergent plant that dies back in the winter (Saltmarsh *et al.* 2006). Trait C was evident as the season progressed from autumn to winter, and the above ground standing litter became brittle and broken; this revealed hollow shoots and the apparent CH$_4$ pathway, Appendix 2. Additionally, respiration was also highest in the PM and PPM communities, which has contributed to these communities being a net carbon source. Indeed, this is consistent with a restoration program that experienced an increase in cover of *P.australis,* and subsequent increase in CH$_4$ emissions (Sheng *et al.* 2014). It is probable that this species is also driving the positive relationship observed between respiration and graminoid cover. It questions the use of this species in constructed wetlands to remediate eutrophic water, given their strong carbon source attributes.

Strong spatial heterogeneity of CH$_4$ fluxes was also evident at the good condition site, as the *Juncus* and *Sphagnum* communities' emissions were low, in contrast to brown mosses, which were two to three times higher, and appeared to fluctuate throughout the summer, probably associated with changes in water table (Bubier *et al.* 1995; Weltzin *et al.* 2001). However, high CH$_4$ emissions in brown mosses is not consistent with other studies in tundra and boreal peatlands, which act as net

carbon sinks (Liebner *et al.* 2011; Street *et al.* 2013). Bubier *et al.* (1995) reports that bryophytes cannot be compared over climatic regions, as even similar species will act differently, due to water table variability. Brown mosses are known to be reliably linked to water table, so it is possible, given the strong fluctuations observed for CH_4 emissions during the growth season, and oscillations in the water table, and subsequent periods of peat oxidation and reduction are associated with the production and release of CH_4 (Moore & Roulet 1993; Strack *et al.* 2004). *Carex spp.* had the highest cover in the brown mosses and were identified in the good condition site as a positive predictor for CH_4 fluxes. However there is conflicting evidence in the literature, as this group have been shown to attenuate and increase CH_4 emissions, based on the water table and nutrient inputs, and are not considered a reliable CH_4 predictor (Bubier 1995; Strack *et al.* 2006; Dinsmore *et al.* 2009; Koelbener *et al.* 2010). Finally, there are an increasing number of studies that associate plant composition with methanotropic functional groups, which may reveal the exact cause of high CH_4 production in this community with further examination of the soil (Conrad 1996; Segers 1998; Bridgham *et al.* 2013).

The two lower plant communities, brown mosses and *Sphagnum,* behaved very differently in terms of their capacity to sequester carbon and release CH_4. *Sphagnum* are indicative of late succession fen species which form hummocks, and are known to have low CH_4 fluxes (Bubier & Moore 1994; Laine *et al.* 2011), Appendix 1. Therefore, one explanation for the contrast in emission values is microtopography, as brown mosses are associated with hollows, which have been found to support higher CH_4 emissions (Bubier *et al.* 1993; Rochefort 2000; Laine *et al.* 2011). In contrast, *Sphagna* can modify the immediate environment, to include hummock formation, water acidification and lower rates of decomposition, and the sphagnum hummocks can exclude light to the peat surface, which indirectly adjusts temperature (Daulat and Clymo, 1998; Rochefort, 2000). These effects broadly suggest that the observed reduction in CH_4 emissions, as suggested by Daulat and Clymo (1998) may be light mediated, which reduces photosynthesis and causes low rates of CH_4 oxidation, where *Sphagnum* hummocks are more than 15 cm above the peat surface.

The CM community exhibited the lowest CH_4 fluxes across all plant communities, in spite of being in close proximity to the highest source communities (PM/PPM). It is suggested that this may be due to *C.mariscus*'s litter chemistry, which may support a higher lignin content, as does its *subsp. C.mariscus.jamaience* (Saunders *et al.* 2006). High lignin content has been shown to correlate with a reduction methanogenesis as the carbon source is impeded (Nilsson & Bohlin 1993). This is consistent with apparent slow rates of decomposition, as litter and standing biomass appeared high for this community, which was observed from season to season, Appendix 2.

Conversely, CH_4 gain is negatively associated with shrubs, such as *Myrica gale,* which opposes the CH_4 pathways assigned to trait A and B for this species; associated with CH4 pathways such as aerenchymatous tissue in roots and actinorhizal N fixing capability and root exudates respectively. However, this is consistent with Bubier's (1995) finding, which associates shrub cover is negatively associated CH_4 which is aligned to a lower water table.

4.5.2 NEE fluxes

It was expected that there would be higher sequestration rates with increased species richness, due to increased plant trait diversity (Steinbeiss *et al.* 2008). This assumption was not met, as one of the most species rich groups (brown mosses) had the lowest rate of carbon sequestration. Moreover, the degraded and good condition sites demonstrated comparable NEE. There is very little in the literature on NEE values for rich fens, although Carroll and Crill (1997) report values from a temperate poor fen within a range of -4,608 mg CO_2 m^2 day^{-1} to -11,808 mg CO_2 m^2 day^{-1}. Results from this study are at the highest poor fen range for the degraded and good condition fen respectively (-10, 818 mg CO_2 m^2 day^{-1} and -9,602 mg CO_2 m^2 day^{-1}). This suggests rich fens sequester more carbon than poor fens, which is likely to be due to differences in plant composition, temperature and pH between these two peatlands (Wheeler & Proctor 2000; Ward *et al.* 2015).

Differences were observed between plant communities within each site. The brown mosses showed the lowest NEE, which was at least two thirds lower than all other plant communities during the growth season. *Sphagnum* and CM communities showed the highest NEE, which demonstrates that rates of carbon sequestration can be driven by high production (CM) and low production communities. The CM community also appears to demonstrate a lag in reaching peak NEE values and proceeded to continue photosynthesising, at a lower rate throughout the year, which is consistent with its evergreen properties (Saltmarsh *et al.* 2006).

To be expected, all plant communities exhibited a net CO_2 gain, although the PM community, was a net source of CO_2 in the winter when it ceases to photosynthesise (Saltmarsh *et al.* 2006), when losses are likely to be associated with the plant's vascular transport path way, which is also mediating CH_4 losses, as described earlier.

4.5.3 Reco fluxes

Species richness was negatively associated with respiration, as demonstrated by the brown mosses which had the lowest rates of respiration. This is probably due to edaphic conditions associated with this plant community, such as higher water table. Bryophytes, were also identified as a negative

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predictors for respiration, which is consistent with these findings. Low respiration rates, and subsequently low CO_2 emissions occur where the water table is higher (Chimner & Cooper 2003).

Litter was also a significant positive predictor for respiration and was consistent with our findings (Orwin & Ostle 2012; Ward *et al.* 2015). Litter was higher in the graminoid communities at the degraded site, where respiration rates were also high, versus low litter cover and lower respiration at the good condition site.

4.6 Conclusion

This study has demonstrated that ecologically comparable plant communities exhibit high spatial variability, in spite of their close proximity, due to plant mediated mechanisms that demonstrate large differences in GHG fluxes (Bartlett & Harriss 1993; Bubier & Moore 1994; Bubier *et al.* 1995). Similarly ecologically different plant communities have proven to have equal carbon sequestration and CH_4 attributes (*Sphagnum/*CM), which is why the net gaseous carbon flux for each site was comparable.

Therefore, it is important that rich fens are managed sensitively, to increase plant communities which are a net carbon sink and reduce those which are net a carbon source. Brown mosses demonstrated they were a net carbon source, yet this group supports high conservation value, and also supports other important ecosystem functions, such as water retention and nutrient cycling, due to supporting nitrogen fixing bacteria and controlling oxidation/reduction processes, which can support phosphorus acquisition (Longton 1984; Kooijman 1992; Vitt *et al.* 1995; Crowley & Bedford 2011). Conversely, the brown mosses exhibited the lowest respiration rates, so if the CH_4 emissions, which appear to be controlled by water table are managed, this community has the potential to switch over to a carbon sink.

The species poor communities (PM and PPM) which were also a net carbon source may need management, in the form of mowing, so that standing litter, supporting brittle open stems, which are aerenchymatous are submerged, to prevent CH_4 and CO_2 pathways from below ground (Steinbeiss *et al.* 2008). Alternatively, the degraded site could be managed with the aim to increase the cover of the CM community, which has low CH_4 emissions and high NEE, as well as higher potential conservation value, than the PM/PPM communities, given its alliance with the *Caricion-davallianae* vegetation (Wheeler 1980b). It is also perturbing to consider that *P.australis* is commonly used in constructed wetlands, given its carbon source attributes, and should be harvested regularly, so that stems are submerged in the winter, and the carbon pathway is prevented.

This research provisions reliable predictors have been identified and will be useful to the growing number of studies of this kind in order to better understand the spatial complexity of GHG heterogeneity at lowland peatlands, which are botanically and hydro-chemically complex (Roulet *et al.* 1994; Bubier *et al.* 1995; Wheeler & Proctor 2000; Dias *et al.* 2010; Gray *et al.* 2013). There is a dearth of spatial GHG data available in the literature. This data will provision the finer resolution to more readily available temporal data, which can be modelled regionally with projected climate data to better understand the source and sink capacities of these wetlands (Moore *et al.* 1998; Yu *et al.* 2003).

It is important to note, this was a short term study and that inter annual variation may change the net gaseous carbon flux between plant communities and so longer term campaigns are favoured, to take account of temporal variability (Bubier *et al.* 2005; Whalen 2005; Roulet *et al.* 2007; Waddington & Day 2007).

4.7 Future research

The high net gaseous carbon uptake observed in the CM and *Sphagnum* communities may provide a potential application for constructed wetlands, as these are increasingly being used to remediate problems associated with eutrophication at this oligotrophic sites. However, research would also need to address the tolerance of these species to higher concentrations of nutrients.

Furthermore, research to date has focused on CH_4 attributes, and so more trait research is needed, and it is proposed that more NEE and Reco traits would also be useful to understand the overall effects on the net gaseous carbon flux regionally and in time with more data across biomes. This is particularly important for vascular wetland plants, as they are a key component for production, consumption and transport of carbon (Joabsson *et al.* 1999).

Further examination of edaphic and hydrological differences between the CM and PM/PPM communities may reveal how to increase cover from the sink community and reduce cover from the source communities respectively.

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5.0 CHAPTER 5: GENERAL DISCUSSION

5.1 Discussion

The following discussion outlines the overall impact, as well as limitations of this research, and provides recommendations for further investigations. This research encompasses three areas of wetland science to include: wetland plant ecology, wetland biogeochemistry (carbon and nutrient cycling) and greenhouse gas chemistry, all of which are ecologically linked, Figure 5.1. Therefore, findings from these three chapters are discussed together, to provide an overarching synthesis of these investigations.
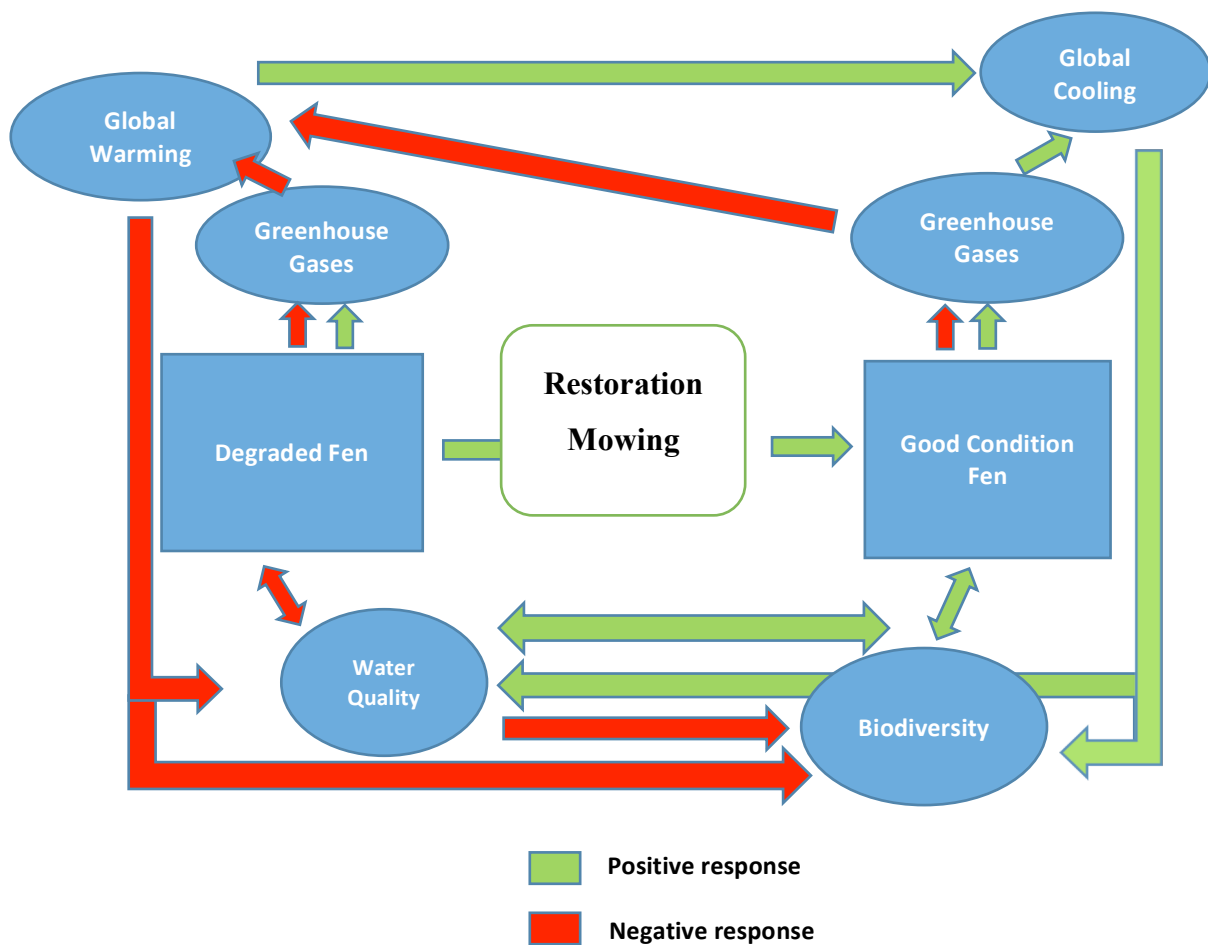
Figure 5.1 Schematic diagram illustrating environmental and ecological drivers that are the focus of this research and their effects at a good condition and a degraded fen. Arrows indicate the negative (red) and positive (green) response relationships between water quality, biodiversity and greenhouse gases.

It was hypothesised that mowing would reduce graminoid cover, litter cover and vegetation height; and that this would lead to an increase in bare ground and subsequent increase in species richness. It was also hypothesised that following biomass removal, and expected repressed internal

eutrophication and reduction in organic inputs; nitrate, phosphate and DOC concentrations would reduce. Additionally, the GHG investigation aimed to determine if a botanically degraded rich fen has a lower net gaseous carbon flux compared to a botanically good condition site and identify carbon source and sink plant communities within each site. On a finer scale, gas sampling also aimed to examine plant mediated carbon loss. It was expected that reliable CH_4 and CO_2 predictors would be identified comparing plant functional traits and vegetation components,' to determine their contribution to the spatial heterogeneity of GHG fluxes.

5.1.1 Summary of research outcomes

Overall, this research has revealed that:

(i)   Following a mowing treatment, species richness increased rapidly at the CM community.

(ii)   species richness remained constant at the SN community.

(iii)   the trajectory of each plant community is unclear due to differing starting conditions at each site. In order to determine trajectories for the long term; modelling botanical data with water chemistry may provide better projections.

(iv)   botanical and hydro-chemical response was site and plant community specific.

(v)   the assumption that biomass removal would reduce nitrate, phosphate and DOC concentrations was not met.

(vi)   there was an unexpected increase in base cations, pH and electrical conductivity, and a persistent increase in DOC concentration.

(vii)   mowing caused an increase in the water table (CM community).

(viii) there was no difference in the net gaseous carbon flux between the good condition and degraded sites.

(ix)   each plant community has a unique spatial contribution to the rate of carbon sequestration and CO_2/CH_4 emissions.

(x)   carbon sink and carbon source plant communities were identified.

(xi)   plants can predict the spatial distribution of CH_4, GPP, NEE and Reco fluxes.

5.2 Discussion of investigations

Ecological restoration is a multi-faceted applied science that relies on theory and applied research to provide underpinning, scientific, baseline and post restoration data. In view of the experience

gained during this research, the following questions should be prequalified prior to restoration, to determine whether objectives are achievable and can sustain important ecosystem services:

1. What biological, physio-chemical barriers exist to prevent restoration objectives?
2. Does a degraded rich fen have the capacity to be restored to a reference site?
3. What are the quantifiable ecological objectives?
4. What is the consequence of biodiversity focused ecological restoration on pre-existing ecological services?
5. How can restoration research facilitate management of biodiversity and ecosystem services in a changing climate?

These questions are now specifically addressed in the context of the research findings.

5.2.1 What ecological barriers exist at these rich fens and do they have the capacity to be restored?

Baseline monitoring was short, and the sites considered for restoration were chosen by the collaborator, Natural Resources Wales' (NRW). Therefore, prequalification of the suitability of these sites for restoration was not possible. However, this was an extraordinary opportunity to undertake large-scale wetland restoration research at rich fens in the U.K. To the author's knowledge, this type of restoration has not previous been researched in the U.K.

Initial surveys revealed that sites and plant communities contrasted in their edaphic and ecological characteristics. Hydrology, botanical composition, and physical structure also appeared to vary within and between sites. Spatial variance was verified by examining differences in species richness, biomass content, pH, electrical conductivity and moisture (Chapter 2, 3). The variation in starting conditions are commonly overlooked in restoration research, as they unavoidably were in this study (Lamers *et al.* 2014), and are likely to have been a contributory factor to the null treatment response in the SN community. Furthermore Brulisauer and Klotzli (1998) suggest that as long as the water table is appropriate, nutrients are low and species are present, then natural succession will take its course. In addition, Stroh *et al.* (2012) states that a better understanding of site specific, hydrology and edaphic starting conditions will help to predict the viability of success (Stroh *et al.* 2013). Listed below, are some of the ecological barriers encountered in this study, which have limited ecosystem recovery, in spite of restoration intervention (Prober *et al.* 2002).

5.2.2 Physical barriers

Physical barriers to restoration include hydrology, which is spatially complex in lowland minerotrophic peatlands (Giller & Wheeler 1986; Fojt & Harding 1995; Wheeler & Proctor 2000; Toberman *et al.* 2010). Indeed, this research showed that species richness was negatively associated with high moisture (Chapter 2). Water table increased following mowing in the CM community (Chapter 3), however, this significant treatment effect is not expected to hinder restoration objectives, although it may change the outcomes following creation of pools and subsequently different plant communities (Kotowski *et al.* 2013). Conversely, heavily inundated conditions affects germination, which suggests target species may be precluded, and is particularly problematic for bryophytes that are prevented to access the peat substrate (Kennedy *et al.* 1992; Ilomets *et al.* 2010). Therefore, if the water table remains high following restoration, it is likely that this may act as a barrier for target fen species to colonise, as their ecological niche relies upon a water level that remains close to the peat surface (Wheeler 1980a; Rodwell 1992). Therefore, as this study has shown (chapter 2), where sites are too wet, reversing succession is unlikely, and restoration objectives are unfulfilled.

In addition, this research has demonstrated that organic physical barriers such as litter cover and vegetation height, can also negatively affect species richness; the former leads to competitive exclusion and reduced light to the peat surface, and the latter prevents seedling establishment (Schaffers 2002; Billeter *et al.* 2007; Ruprecht *et al.* 2010).

5.2.3 Biological barriers

Following abandonment, many studies have reported on the deleterious effects of late succession species invading rich fen systems (Bergamini *et al.* 2001; White & Jentsch 2001; Hajkova & Hajek 2003; Middleton *et al.* 2006b; Rosenthal 2010). Principally, an ecological mechanism was identified, which caused the contrasting response to mowing at each plant community. This was due to re-invasion of the dominant graminoid, *S.nigricans* in the SN community, which also sustained canopy height. In contrast, the dominant graminoid in the CM community, *C.mariscus,* sustained a reduced cover, two years following mowing (Chapter 2). Therefore, *S.nigricans* has acted as both a physical (canopy height, reduction in light) and biological (competitive exclusion) barrier to increasing species richness in the SN community.

An alternative biological barrier for consideration (although not measured here); is seed bank depletion, which can occur over the course of succession, and long term abandonment, which is a

possibility for the CM community, as species that colonised following mowing were not, in the main, target fen species. This may pose a threat to species richness and could prevent a rich fen trajectory (Jensen 1998; Bakker & Berendse 1999; Hald & Vinther 2000; Donath *et al.* 2007).

5.2.4 Hydro-chemical barriers

There were no hydro-chemical barriers to restoration at the sites studied, as nitrate and phosphate starting concentrations were very low. High electrical conductivity, pH and base cations also provided evidence that all the sites were connected to mineral rich groundwater.

5.2.5 Proposed trajectory

The main purpose of this study was to remove ecological barriers in order to increase species richness. Investment of this scale requires measurable outcomes, which should be predicted in advance, to forecast whether the proposed trajectory has been met. However, it was established that inherent between site heterogeneity was high for both plant communities, and within site variance was also evident in the SN community (Chapter 2). The within site heterogeneity in the SN community is considered to have contributed to the prevention of increased species richness and achievement of a rich fen trajectory overall. Site specific trajectories and management is likely to lead to restoration success. Some sites were on a rich fen trajectory, and some were not, and due to the duration of this study it was difficult to make further predictions. Modelling the botanical data, with environmental data, combined with projected climate data, is more likely to provide a finer resolution and more accurate predictions.

5.2.6 Were the objectives of this study met?

All objectives were achieved in the CM community and species richness increased. However, graminoid cover and vegetation height was not reduced in the SN community, which has led to species richness remaining constant (Chapter 2). Both plant communities demonstrated an increase in: base cations, electrical conductivity, pH, and, in the CM community, increased water table. These results were not anticipated, as no other study has documented this occurrence. The cause, as described in Chapter 3 is likely to be physical rather than ecological, following disturbance to the peat surface, in these previously abandoned fens. However, these are beneficial responses to mowing, which are likely to promote target fen species colonisation, as long as there are no other ecological barriers present. In contrast, the persistent increase in DOC concentration (Chapter 3) observed only in the CM community, may counteract these beneficial effects, as water quality may

reduce to interconnecting ecosystems, such as rivers and reservoirs (Oulehle & Hruska 2009; Nieminen *et al.* 2015).

The expectation that DOC concentration would reduce in the longer term due to depletion of active organic matter pools (removal of live above ground biomass and litter) was not met during this study, however the expected pulse in DOC was observed. It was the persistence of increased DOC concentration which was unexpected and had not previously been documented in other studies. A mechanistic approach is needed to identify the exact source of DOC, although it is assumed that increased organic inputs (TON, DOC) associated with increased litter inputs following mowing, is main driver of this treatment response (Versini *et al.* 2014). This was evident from the higher litter cover in the CM community (54 %), compared to the SN community (22 %) (Chapter 2). More efficient litter removal is expected to lead to a depletion of active organic pools of carbon and nitrogen and reduce DOC in the longer term (Armstrong *et al.* 2012).

Due to the longevity of abandonment and knowledge that sorption rates following senescence is high, it was also expected that a reduction in nitrate and phosphate would be observed (Aerts 1996; Aerts & Chapin 2000; Venterink *et al.* 2003; Bombonato *et al.* 2010). However, there was no prior knowledge that nutrient concentrations were already so low. Therefore, it is not expected that this null treatment effect would have had a negative bearing on the restoration outcome, however winter mowing may have added to the lack of treatment effect for macro-nutrient reduction.

The GHG investigation demonstrated some interesting results, although the assumption that the degraded site would have a lower net gaseous carbon exchange compared to the good condition site was not met. The strong spatial heterogeneity within each site has contributed to this assumption not being met. Indeed, 50 % of all plant communities observed were a source of carbon across both sites. The brown mosses at the good condition site were a very strong source of CH_4, and a poor carbon sink. Conversely the *Sphagnum* also at the good condition site, produced low CH_4 emissions and could sequester as much carbon per day as the CM community. The degraded site would have been an overall source of carbon, had it not been for the substantial amount of carbon being sequestered by the CM community, which also supported the lowest CH_4 emissions. High rates of photosynthesis year round are thought to have contributed to this community's status as a climate mitigating sink (Saltmarsh *et al.* 2006). It is proposed that *C.mariscus* employs diffusive gas exchange, rather than pressurized bulk flow, which supports less carbon losses (Chanton *et al.* 1993). Another mechanism which is a possibility in the CM community, given the large amount of biomass accumulation is recalcitrant lignin chemistry of plant litter. This is thought to affect CH_4

production and CO_2 emissions, due to a reduction in methanogenesis and slower decomposition (Nilsson & Bohlin 1993; Steinbeiss *et al.* 2008; Orwin & Ostle 2012; Ward *et al.* 2015).

Furthermore, similar net gaseous carbon flux capacities were observed for contrasting ecological groups (*Sphagnum* and CM). Conversely, contrasting net gaseous carbon flux capacities were also observed for comparable ecological groups (*Sphagnum* and brown mosses). These results were in opposition to other studies to date, that suggest productivity is associated or that higher carbon sequestration, and that similar ecological groups, e.g. emergent species would react comparably (e.g. PM/CM) (Mitsch *et al.* 2014; Mo *et al.* 2015). This reinforces the issue of spatial heterogeneity in rich fens, and that predictions must be made on multiple site data as these wetlands are environmentally and ecologically complex.

Furthermore, the strong source communities (PM/PPM) were dominated by *P.australis*. This species is commonly employed in constructed wetlands to sequester nutrients. However, it is concerning that if its use is continued, it should be harvested regularly so that stems are submerged in the winter to reduce carbon losses. This is also a management approach that could be adopted at the degraded site, or alternately restoration objectives may consider reducing the cover of this species, with a view to increasing the CM community.

Plant mediated predictors for carbon fluxes were also identified for all flux determinants, although not all of them proved to be reliable; e.g. vegetation height predicted increased carbon sequestration, however, the *Sphagnum* community supports a low canopy, and has a high rate of carbon sequestration. As the gradient of the slope was shallow and r^2 value fairly low, it may prove useful to set guidelines for predictor validation. As stated previously, the spatial heterogeneity is also causing some skew in the data, which is why multi-site data is so important.

Reliable predictors were trait C, present in *P.australis* which indicate increased CH_4, and so where this species is unmanaged (not mown), it is likely to be a hotspot for CH_4 emissions. Similarly, it reinforces that bare ground indicates that have no capacity to sequester carbon. Graminoids were shown to be positively related to high respiration and brown mosses related to low respiration, which was consistent with these results. In particular, plant litter was a strong predictor for higher rates of decomposition and respiration, however this may not be the case for the CM community, if it shown to support recalcitrant litter and slow rates of decomposition (Nilsson & Bohlin 1993; Steinbeiss *et al.* 2008; Orwin & Ostle 2012; Ward *et al.* 2015).

5.2.7 What is the consequence of biodiversity focused ecological restoration on pre-existing ecological services, and ecosystem functioning?

Biodiversity and ecosystem services should be considered together, particularly at multi-functional wetlands, such as these (Foley *et al.* 2005; Lamers *et al.* 2014). This research has revealed that there are measurable effects on biodiversity, carbon and nutrient cycling, hydro-chemistry and hydrology. Additionally, although mowing is likely to mitigate for climate change in the long term, although it is unclear what effect it has on GHG fluxes, during and following intervention, as no previous work to the author's knowledge has been undertaken (Lu *et al.* 2015). However, given that bare ground, following biomass removal, has been observed to be a strong negative predictor for carbon sequestration, it is likely that rates of carbon sequestration are effected, and if litter inputs increase, higher respiration rates will also follow mowing events. However, it is unclear what effect this will have on CH_4 emissions.

5.2.8 How can restoration research facilitate biodiversity and ecosystem services so that are sustained with climate change?

Restoration research should not be undertaken in isolation for any single goal, as wetlands offer multiple benefits, including climate mitigation. Wetland restoration should consider all encompassing objectives as there is a global responsibility to ensure all services associated with an ecosystem remain intact (MEA 2005). Each of the investigations have revealed that rich fens are spatially heterogeneous, botanically, hydro-chemically and the way in which they cycle carbon. Rich fens are biodiverse and support many other ecosystem services that may conflict in the future with their increasing importance to mitigate for climate change. Therefore, more guidance is needed from policymakers, as scientists reveal how these systems function and how they recommend they should be managed.

5.3 Research Limitations

Due to the collaboration with NRW, the research had to be aligned with the objectives and schedule of the EU LIFE project. This meant that mowing was undertaken in the winter, as oppose to the end of the growth season, which unavoidably favoured *P.australis* expansion and had less force on inhibiting internal eutrophication (Aerts & Chapin 2000; Hovd & Skogen 2005; Sundberg 2011).

The choice of sites were also determined by NRW; although there were alternatives available, there was not enough time to make evidence based decisions. Baseline water chemistry data would have

allowed restoration to be undertaken on sites that were more affected by eutrophication and would have excluded sites that were too wet.

It would have also been insightful to have installed dip wells in both plant communities and across all sites to better understand site heterogeneity. This data may have helped to tease apart treatment effects on species richness in the SN community. Also the GHG investigation, would have benefited from dip well installation per collar, rather than per plant community to help tease apart environmental drivers, which appeared evident in the brown mosses.

The GHG experimental design and sampling campaign was labour intensive and permission to install collars was required, which is why only one site was studied. Therefore, a higher between site replication would have allowed more robust inferences about the data, as would a longer sampling period. It would also have been useful to have examined the predictive power of more carbon associated plant functional traits, to provide stronger explanatory power driving within plant community gas fluxes. This was due to the limited data available.

5.4 Synthesis and Conclusion

Wetlands require a holistic approach to restoration, to sustain their unique conservation value and provision of globally significant ecosystem services.

This research has demonstrated that increased biodiversity may counteract climate mitigation and water quality provision. Mowing, as intended, reduced *C.mariscus* cover, increased bare ground and unintendedly increased *P.australis* cover. Species richness has increased, but this may be at the detriment of reducing the capacity *C. mariscus* to sequester carbon. In addition, CH_4 emissions are also likely to be higher following mowing, due to the observed expansion of *P.australis* (dominant species in the net carbon source communities). The beneficial increase in bare ground, which allowed small stature species to colonise, is also associated with low rates of carbon sequestration. Furthermore, restoration, aimed to reduce shrub cover, was successfully achieved, although this is likely to be to the detriment of higher CH_4 emissions (Trait B species). These are a few examples of the conflict of interests when manging a wetland for multiple purposes. However, in this instance, as shrubs are also associated with dryer conditions, biodiversity outweighs is likely to be the priority, as without management the species will encroach and eventually terrestrialise the wetland. In addition, better rates of litter removal are required, as increased litter cover is associated with higher rates of respiration.

Mowing has also influenced water quality with beneficial and possibly deleterious consequences. Beneficial changes include a possible temporary reconnection to calcium rich ground water, which is likely to enhance biodiversity. Although, this may be counteracted by the deleterious increase in DOC concentration and change in DOC quality, which can influence CH_4 production rates (Bianchi *et al.* 1996). An increase in DOC exports from the fen catchment could have an ecological and economical consequence on receiving waters. Furthermore, changes in the biogeochemical gradient, as observed with an increase in pH, may affect microbial population distribution and their associated function on carbon and nutrient cycling as well as control DOC production (Evans *et al.* 2012; Lin *et al.* 2012; Liu *et al.* 2012).

Furthermore, in the two degraded carbon source communities, mowing is needed to submerge *P.australis* stems below the water surface and inhibit the CH_4 pathway from production site to atmosphere. Indeed, it would be favourable to increase the CM community, where possible at the expense of the PM and PPM plant communities (Frenzel & Rudolph 1998).

It is difficult to forecast accurately which trajectory each site and plant community will follow, and it is even harder to determine how these future (site specific) plant communities will influence biodiversity and ecosystem services. A shift in plant composition, is likely to change the suite of plant functional traits present in the new community, and these will in turn affect associated microbial communities and greenhouse gas emissions (Gray *et al.* 2013; Robroek *et al.* 2015; Song *et al.* 2015). Predictions are further complicated, as each site has demonstrated contrasting trajectories; and it is difficult to ascertain whether sites were on a rich fen trajectory. Further investigative research may reveal the outcome of changes in plant and functional trait composition, to better understand the effects on ecosystem services and ecosystem functioning.

Therefore, there are some conflicts of interest, particularly where sites are managed for biodiversity and climate mitigation. Some examples to consider are the positive relationship between increased species richness (vascular plants) and increased respiration, and the intention to increase brown mosses; an important botanical characteristic of rich fens, which demonstrate they are a net carbon source. In addition sedges (*Carex spp*) are also an important of the fen restoration objectives, however, other studies show that this group support high rates of decomposition and this correlates well with the predictors in this study, which is also correlated with high respiration and at the good condition site, high CH_4 emissions (Armstrong *et al.* 2012).However, there is conflicting evidence that *Carex spp.* are a reliable spatial source of information for GHG fluxes.

There are many questions that remain unanswered in this area of the research, as well as interesting results that require further investigation. However, the unpredictable nature of wetland restoration is well known, as others have stated how restoration is a gradual process, that may or may not result in the end point community that was predicted, as there is an element of "self design" (Bradshaw 1996; Mitsch & Wilson 1996; Pfadenhauer & Klotzli 1996).

5.5 Research Impact

- 50 % success rate to increase species richness, and rich fen trajectory is unclear as it is site specific.
- Large inherent site differences and need site specific restoration objectives.
- Large scale mowing increases groundwater connection and water level which will enhance conservation objectives.
- Large scale mowing may impact on stream biota and drinking water treatment.
- Reliable spatial data has been collected to feed in to climate models and allow efficient management at sites for climate mitigation.

5.6 Recommended Further Research

1. It would be useful to model the botanical response data with predicted climate change data and environmental variables for each site, to better forecast the trajectory of each plant community. In addition, functional trait data from the projected plant community will provide a better understanding of how these species will affect ecosystem functioning, as well as GHG emissions.

2. A mesocosm study to examine CH_4 production and losses, using peat cores from the *Cladium,* PM and brown mosses to test differences in gas emissions and uptake, under varying water level and temperature treatments, to tease apart the contribution to GHG emissions between vegetation, water table and temperature.

3. Given that *C.mariscus* demonstrated a highly effective carbon sink ability, it is proposed this species may perform well in a constructed wetland. It is suggested that *P.australis* and *C.mariscus* are studied, to compare nutrient uptake, as the latter species may have a dual capacity to manage eutrophication and sequester carbon; *P.australis* is commonly used in constructed wetlands, yet it is a strong net carbon source. In addition, it would also be useful to determine what is controlling spatial distribution, as Saltmarsh *et al.* (2006) suggest it is

due to water table and nutrient gradients to determine whether management could promote the expansion of *C.mariscus* to the demise of *P.australis.*

4. It would also be interesting to test differences in lignin content between the good condition and degraded plant communities, particularly to examine whether the low CH_4 emissions in the *Cladium* community is correlated with small CH_4 production sites (low methanogens). A functional microbial study of the peat would also provide further insight to the differences in CH_4 emissions between plant communities.

5. It is not clear whether a depleted seed bank is a biological barrier to restoration in the CM community; seed bank testing would determine whether future restoration is worth further investment at these sites, or whether hay transfer is required.

6. An investigation to examine where DOC inputs originate from following mowing, as well as looking at DOC quality, to observe DOC exports during mowing intervention in receiving waters and determine whether DOC quality is more recalcitrant and possibly more persistant, which may be problematic for drinking water treatment.

7. A laboratory analysis to investigate whether there is a redox and/or other bio-geo-chemical process which, following peat disturbance, has increased base cations and subsequently raised EC and pH, through oxygenating and compressing the peat.

8. Finally, a systematic review and meta analysis to establish whether restoration is working and whether there are common underlying barriers preventing success, such as if the wetland is too wet.

9. Mesocosm study to understand the ecology and management of *S.nigricans* to better manage this dominant graminoid.

10. Lignin chemistry testing of *C.mariscus* and *S.subnitens* to test its association with low CH_4 and possibly slower decomposition rates.

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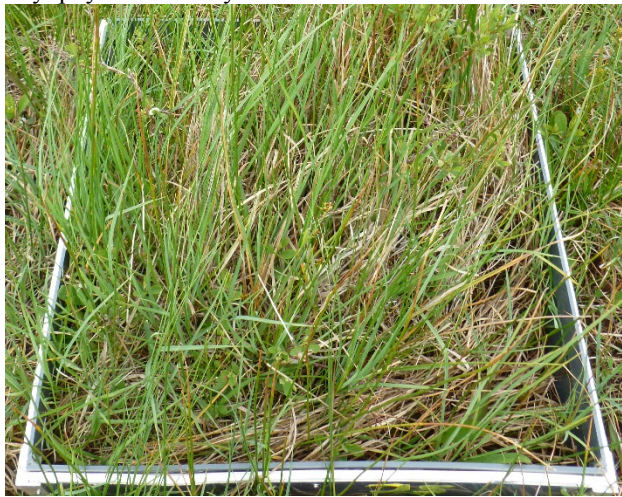
Bryophyte collar January 2014

Bryophyte collar July 2013

Juncus collar January 2014

Juncus collar July 2013

Sphagnum collar January 2014

Sphagnum collar July 2013

APPENDIX 2 GHG COLLAR PHOTOGRAPHS – DEGRADED SITE
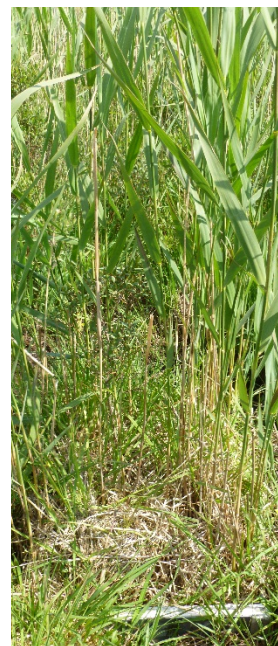

Cladium collar January 2014

Cladium collar July 2013

PM collar January 2014

PM collar July 2013

PPM Collar January 2014

PPM collar July 2013

APPENDIX 3 ABSTRACTS AND PUBLICATIONS

Papers accepted

Menichino, N.M., Fenner, N., Evans, C., Jones, P.S., Guest, J., Pullin, A.S., Jones, L. Contrasting response to mowing in two abandoned rich fen plant communities (Ecological Engineering). September 2015

Papers in preparation

Menichino, N., Jones, L., Evans, C., Jones, Peter, Guest, J, Pullin, A., Freeman, C., Fenner, N. Hydro-chemical response to restoration in two rich fen plant communities (to be submitted to Ecological Engineering).

Menichino, N.M., Fenner, N., Jones, L., Pullin, A., Evans, C. Greenhouse gas emissions from a degraded and good condition rich fen; source or sink? (in prep.)

Oral presentations

Menichino, N.M., Pullin, A.S., Fenner, N., Jones, L., Jones, P.S., Guest, J. Plant Species Response to the Restoration of Degraded Fens in north-west Wales. Proceedings of the INTECOL International Wetlands Conference, June 3-8 (2012), Orlando, Florida, U.S.A.

Menichino, N.M., Pullin, A.S., Fenner, N., Jones, L., Jones, P.S., Guest, J. Plant Species and DOC Response to the Restoration of Degraded Fens in North-West Wales. Joint Symposium - British Ecological Society & IUCN 'Investing in Peatlands, Demonstrating Success', June26-28 (2012), Bangor University, U.K.

Menichino, N.M., Jones, L., Evans, C., Pullin, A., Guest, J., Freeman, C., Fenner, N. Botanical and hydro-chemical response of alkaline and calcareous fen to restoration. Proceedings of the EU LIFE Conference, 'Breathing New LIFE into Anglesey and Lleyn's Wetlands,' October 9-11 (2013), Caernarfon, U.K.

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