Environmental Impacts—Terrestrial Ecosystems

11

Norbert Hölzel, Thomas Hickler, Lars Kutzbach, Hans Joosten, Jakobus van Huissteden and Roland Hiederer

Abstract

The chapter starts with a discussion of general patterns and processes in terrestrial ecosystems, including the impacts of climate change in relation to productivity, phenology, trophic matches and mismatches, range shifts and biodiversity. Climate impacts on specific ecosystem types—forests, grasslands, heathlands, and mires and peatlands—are then discussed in detail. The chapter concludes by discussing links between changes in inland ecosystems and the wider North Sea system. Future climate change is likely to increase net primary productivity in the North Sea region due to warmer conditions and longer growing seasons, at least if summer precipitation does not decrease as strongly as projected in some of the more extreme climate scenarios. The effects of total carbon storage in terrestrial ecosystems are highly uncertain, due to the inherent complexity of the processes involved. For moderate climate change, land use effects are often more important drivers of total ecosystem carbon accumulation than climate change. Across a wide range of organism groups, range expansions to higher latitudes and altitudes and changes in phenology have occurred in response to recent climate change. For the range expansions, some studies suggest substantial differences between organism groups. Habitat specialists with restricted ranges have generally responded very little or even shown range contractions. Many of already threatened species could be particularly vulnerable to climate change. Overall, effects of recent climate change on terrestrial ecosystems within the North Sea region are still limited.

N. Hölzel (✉)
Institute of Landscape Ecology, University of Münster,
Münster, Germany
e-mail: norbert.hoelzel@uni-muenster.de

T. Hickler (✉)
Senckenberg Biodiversity and Climate Research Centre (BiK-F),
and Department of Physical Geography, Goethe University,
Frankfurt, Germany
e-mail: thomas.hickler@senckenberg.de

L. Kutzbach (✉)
Institute of Soil Science, CEN, University of Hamburg, Hamburg,
Germany
e-mail: lars.kutzbach@uni-hamburg.de

H. Joosten
Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt
University of Greifswald, Greifswald, Germany
e-mail: joosten@uni-greifswald.de

J. van Huissteden
Department of Earth Sciences, University Amsterdam, Amsterdam,
The Netherlands
e-mail: j.van.huissteden@vu.nl

R. Hiederer
Institute for Environment and Sustainability,
European Commission Joint Research Centre, Ispra, Italy
e-mail: roland.hiederer@jrc.ec.europa.eu

11.1   Introduction

The chapter starts with a discussion of general patterns and processes (Sect. 11.2), such as impacts of climate change on productivity, phenology and biodiversity. Climate impacts on specific ecosystem types, such as forests, grasslands and mires are discussed in more detail in subsequent sections (Sects. 11.3–11.6). The chapter concludes by discussing links between changes in inland ecosystems and the wider North Sea system (Sect. 11.7) and then summarises the main findings of this assessment in the form of a table (Sect. 11.8). The chapter focuses on the direct impacts of climate change; the potential impacts of indirect drivers are beyond the scope of this chapter.

11.2   General Patterns and Processes

### 11.2.1   Vegetation Zone Shifts, Productivity and Carbon Cycling

The terrestrial part of the North Sea region lies mainly in the temperate forest zone, with some boreal elements and treeless tundra at higher altitudes in Scandinavia and Scotland (Fig. 11.1). Below the tree line, significant areas of treeless vegetation would naturally occur only in wetlands (marshes,

river floodplains and mires), where soil saturation precludes tree growth.

Deforestation and land degradation as a result of grazing and other anthropogenic activities have decreased the natural forest cover over thousands of years (e.g. Simmons 2003; Kaplan et al. 2009; Gaillard et al. 2010). Most of the lowland forests in England, for example, had already been cleared 1000 years ago (Ruddiman 2003). Forest cover over large parts of the UK, the Netherlands, north-western Germany and Denmark is currently less than 15 % (Eurostat 2015; Fig. 11.2).

The current distribution of zonal vegetation types in the North Sea region is influenced climatically mainly by temperature because terrestrial net primary productivity (NPP) is less limited by water supply, which is relatively high during the growing season because this is when most rainfall occurs (see Sect. 1.5). In terms of future changes in climate and weather (see Chap. 5), the warming expected by the end of the century can be expected to lead to a northward shift in zonal vegetation types or up in altitude (Hickler et al. 2012), and an increase in NPP where the warming is not accompanied by substantially drier conditions. Most climate change scenarios project an increase in annual precipitation across the North Sea region by the end of the century, although substantially drier conditions have been projected for summer and in particular for the southern part of the

Fig. 11.1 Potential natural zonal (determined by macro-climate) vegetation types in the North Sea region. *Grey areas* were not classified (Bohn et al. 2003; simplified by Hickler et al. 2012)
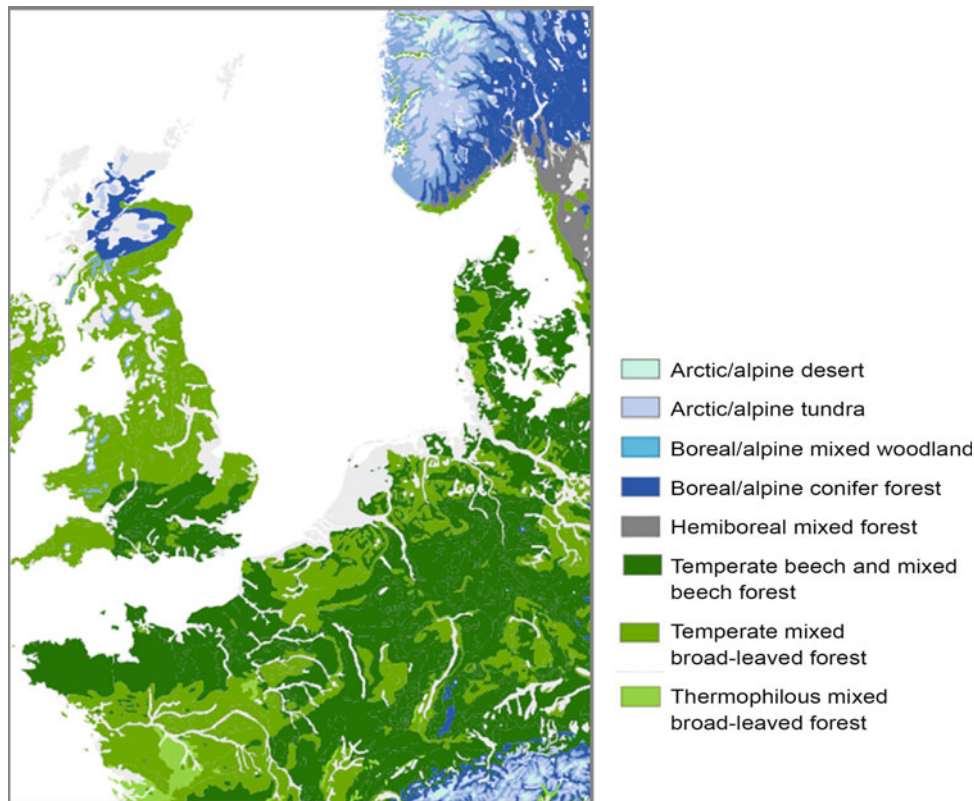
Fig. 11.2 Current land cover in the North Sea region according to CORINE Land Cover (EUROSTAT 2014)
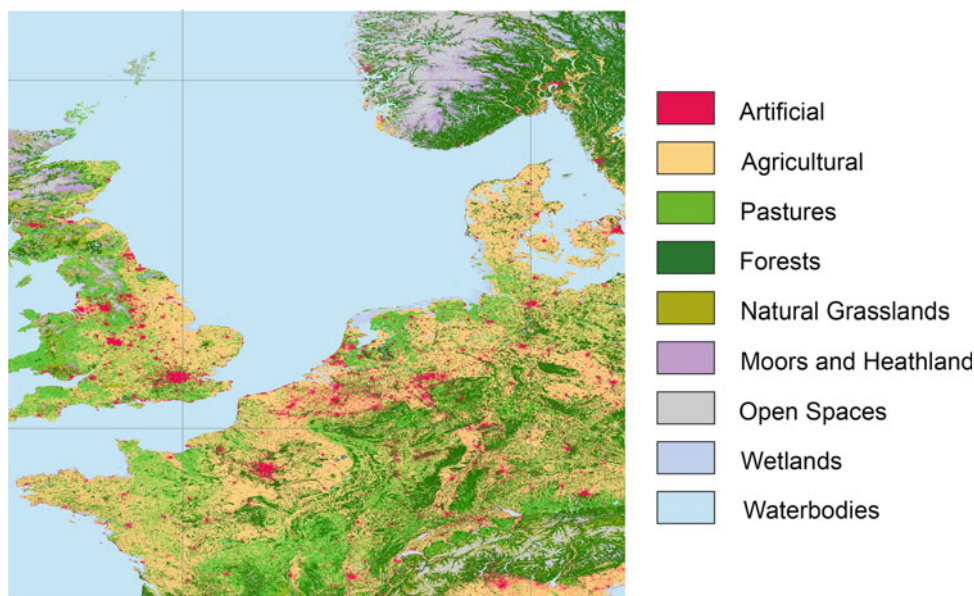
region, where water availability already constrains vegetation productivity (see Chap. 5). Together with the slight projected increase in dry spell length (see Chap. 5 and Jacob et al. 2014), vegetation productivity might, therefore, decrease in the southern North Sea region. However, these projections are based on average results from a number of regional and global climate models (RCMs and GCMs) and because not all models agree in terms of the sign of the change in summer precipitation for different parts of the North Sea region, these projections of future water availability during the main growing season contain uncertainties (see Chap. 5 and Jacob et al. 2014). Furthermore, water availability also controls forest productivity strongly in the south-eastern UK (Broadmeadow et al. 2005), not strictly the southern part of the study region. Here too, increasing drought stress in summer would probably negatively impact NPP. Nevertheless, it should be noted that unchanged precipitation implies less water availability because evapotranspiration will increase with rising temperature. According to the multi-model mean of the CMIP5 models (see Chap. 5), the net outcome of changes in precipitation and evapotranspiration is projected to be an increase in annual run-off in the northern part of the region and a decrease in the south (Collins et al. 2013). These changes in the water balance are particularly important for wetlands (see Sect. 11.6).

The uncertainties in projections of future summer moisture (see Chap. 5) make it difficult to predict the impacts of climate change on terrestrial ecosystems. Morales et al. (2007) simulated the combined effects of climate change and increasing atmospheric carbon dioxide (CO_2) levels on European ecosystems with a dynamic vegetation model, using projections from a variety of combinations of RCMs, bounding GCMs and emission scenarios (Christensen et al.

2007, not accounting for changes in land use). With the exception of north-western France, all simulations indicated increasing NPP in the North Sea region by the end of the century. According to these simulations, the northern part of the study region remains a carbon sink, and the southern part continues to be a small source. However, different climate impact models can yield different results even when driven by the same climate scenario data. Using the SRES high A1Fi scenario (Nakićenović and Swart 2000), a number of dynamic global vegetation models (DGVMs) simulated increasing NPP over most of the North Sea region by the end of the century (Sitch et al. 2008), whereas the Lund-Potsdam-Jena (LPJ) DGVM showed decreased vegetation carbon storage especially in the southern part (Sitch et al. 2008). Most of the models in this study, as well as the model used by Morales et al. (2007), included the potential beneficial plant-physiological effects of increasing atmospheric CO_2 concentrations, but not the constraints on this effect through nutrient limitation.

Increasing levels of atmospheric CO_2 will increase NPP (sometimes referred to as the CO_2 fertilisation effect), and most plants reduce stomatal opening in response to higher CO_2 concentrations (e.g. Ainsworth and Long 2005; Hickler et al. 2015). Reduced stomatal opening leads to lower plant transpiration rates, commonly increasing soil water content and thereby counterbalancing potentially increasing drought stress under climate warming (Arp et al. 1998; Morgan et al. 2004; Körner et al. 2007). Increasing leaf area as a result of higher NPP can counteract this water saving effect (e.g. Gerten et al. 2004), but mostly under conditions of ambient nutrient supply, which enables plants to take advantage of increasing CO_2 and to increase their leaf area (Arp et al. 1998; McCarthy et al. 2006; Norby et al. 2010). According

to future simulations with a GCM that includes dynamic vegetation changes, the net outcome of the two effects will be a substantial increase in global run-off (Betts et al. 2007). However, CO_2 enhancement experiments with conifer trees have shown hardly any reduction in stomatal conductance (Körner et al. 2007), implying that the vegetation models probably overestimate the reduction in stomatal conductance and transpiration in conifer forests (Leuzinger and Bader 2012). The magnitude of the CO_2 fertilisation effect on NPP and carbon storage is highly debated (e.g. Körner et al. 2007; Thornton et al. 2007). Although photosynthesis increases under elevated CO_2, this enhancement of carbon assimilation often does not lead to increased biomass as the extra carbon is mainly allocated to below-ground carbon pools with fast turnover (fine roots, root exudates, transfer to mycorrhiza) (Körner et al. 2005; Finzi et al. 2007; Norby et al. 2010; Walker et al. 2014). Nitrogen (N) deposition can also increase NPP, but in the southern North Sea region, N-deposition is already so high that nitrogen is not limiting terrestrial productivity directly (but may decrease productivity through negative side effects such as soil acidification; Bowman et al. 2008; Horswill et al. 2008). N-deposition across the study region is expected to remain at similar levels as today (2014) or to decrease slightly (Tørseth et al. 2012), but N-mineralisation in the soil will probably increase in the northern North Sea region due to warming (Lükewille and Wright 1997; Melillo et al. 2011), which would increase terrestrial productivity particularly in N-limited vegetation on acidic soils (see also Sects. 1.7 and 11.6).

Net primary productivity is an important driver of many ecosystem services, including total carbon storage, but in the North Sea region its dynamics are determined largely by land use, which has not been accounted for in the DGVM study mentioned previously (Sitch et al. 2008). Over most parts of Europe, including the North Sea region, forest carbon stocks, for example, are currently increasing as forests grow older and less timber is harvested than a few decades ago (Janssens et al. 2003; Nabuurs et al. 2003; Ciais et al. 2008).

Total ecosystem carbon storage is further influenced by soil carbon dynamics. Soil respiration, and thereby carbon losses from the soil, is expected to increase under global warming, but the sensitivity of the soil carbon pool remains uncertain (Davidson and Janssens 2006; Luyssaert et al. 2010), and combined effects of potentially increasing NPP (and carbon inputs into the soil) and increasing soil respiration rates (reducing carbon storage) on total ecosystem carbon storage are very difficult to estimate.

11.2.2   Changes in Phenology

Changes in the phenology of biota currently provide the most sensitive and compelling evidence of climate warming

impacts in the North Sea region and elsewhere in the middle and higher latitudes. At the same time these changes are particularly well documented due to a pan-European network of phenological data collections that has been run continuously since the mid-20th century (e.g. Menzel 2000) as well as long-term data from bird-ringing stations (e.g. Sparks et al. 2005) and butterfly monitoring programmes (Roy and Sparks 2000). Phenological changes that can be attributed to climate change include leaf unfolding, flowering and leaf colouring as well as the arrival dates of migrant birds, dates of egg laying of birds or the timing of the first appearance of butterflies (Parmesan and Yohe 2003; Parmesan 2006).

An analysis of observational data from the International Phenological Gardens in Europe for the 1959–1996 period (Menzel and Fabian 1999; Menzel 2000) revealed that spring events such as leaf unfolding have advanced on average by 6.3 days (−0.21 days year^{-1}), whereas autumn events such as leaf colouring have been delayed on average by 4.5 days (+0.15 days year^{-1}). This trend has resulted in an average extension of the annual growing season by 10.8 days since the early 1960s. This trend is of particular significance for regions bordering the North Sea Basin such as Denmark and northern Germany. Similar results were obtained in a more regional study analysing data from the phenological network of the German Weather Service for the period 1951–1996. In this study, Menzel et al. (2001) found the strongest phenological advances in key indicators of earliest and early spring (−0.18 to −0.23 days year^{-1}) whereas changes in autumn were less pronounced (delay of +0.03 to +0.10 days year^{-1}). Overall, the mean growing season for the period 1974–1996 was up to 5 days longer than for the period 1951–1973. Similar findings were made by van Vliet et al. (2014) in the Netherlands. Using data from the Dutch phenological observation network they found that significant changes in life cycle events started only in the early 1990s. In a large-scale meta-analysis using data from 21 European countries for the period 1971–2000 (Fig. 11.3), Menzel et al. (2006) showed that 78 % of all bud break, flowering and fruiting records advanced, and only 3 % were delayed.

This study clearly demonstrated that phenology is directly linked to the temperature of preceding months with a mean advance of spring/summer by 2.5 days per °C and a mean delay of leaf colouring and leaf fall by 1.0 days per °C. So far, phenological changes of this type are reversible and depend on weather conditions in the year of observation.

In the UK, mean laying dates for the first clutches of 20 bird species advanced on average by 8.8 days between 1971 and 1992 (Crick et al. 1997). Similarly, spawning of two amphibian species (toads) in England advanced by two to three weeks between 1978 and 1994, and the arrival of three newt species in breeding pools advanced by as much as five
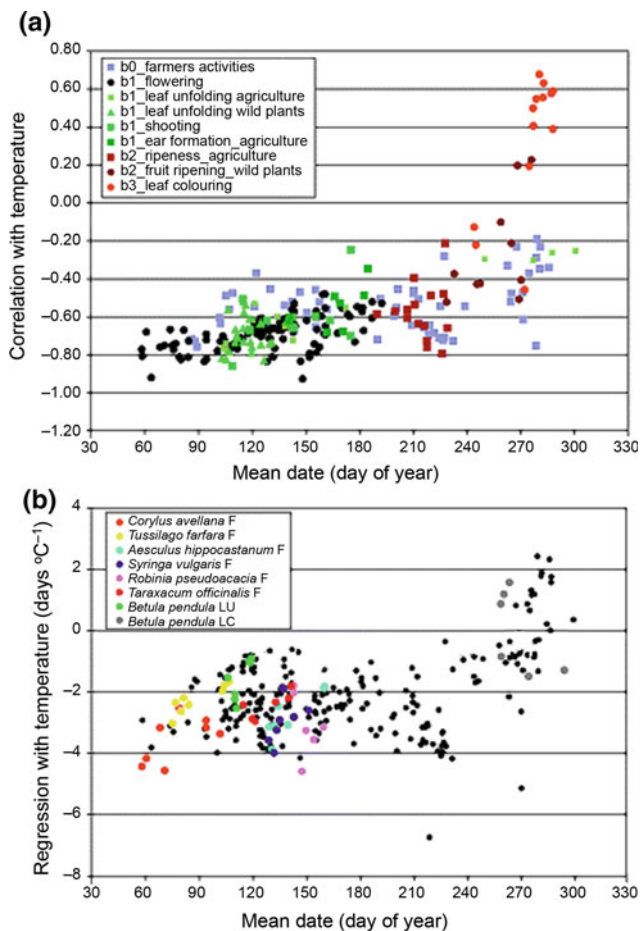
Fig. 11.3 Temperature sensitivity and response across the year. **a** Maximum correlation coefficients for 254 mean national time series of phenophases in nine European countries with mean temperatures of the previous months. **b** Regression coefficients against mean temperature of the previous month. *F* flowering; *LU* leaf unfolding; *LC* leaf colouring. The overall dependence of temperature sensitivity and response on mean date is high **a** $R^2 = 0.59$, $p < 0.001$; **b** $R^2 = 0.47$, $p < 0.001$) (Menzel et al. 2006)

to seven weeks (Beebee 1995). Based on a composite map of 70,000 records for 1998–2007 for the common frog *Rana temporaria*, Carroll et al. (2009) found an average advance of first spawning of about 10 days in the UK compared to map-based data 60 years before.

On the island of Heligoland in the south-eastern corner of the North Sea, mean spring passage times for 24 species of migratory birds advanced by 0.05–0.28 days year^{-1}, which in most species correlated strongly with warmer local temperature during the migration period as well as with the strength of the North Atlantic Oscillation (NAO; Hüppop and Hüppop 2003). Almost identical findings were made at a larger spatial scale from several ringing stations by Sparks et al. (2005). At the continental scale, Both et al. (2004) analysed 23 European populations of pied flycatcher *Ficedula hypoleuca* and found that nine showed an advanced

laying date, which were all from those areas with the strongest warming trend and mostly situated at the southern fringe of the North Sea basin. In an area of southern England (Oxfordshire), Cotton (2003) demonstrated that earlier arrival of 20 species of long-distance migratory birds was positively correlated with enhanced air temperatures at wintering grounds in Sub-Saharan Africa.

Climate change also has significant impacts on the winter distribution of migratory birds that fly south to avoid the northern winter. Based on ringing data from the Netherlands, Visser et al. (2009) found that 12 of 24 species studied showed a significant reduction in their migration distance to the south, and that this was strongly correlated with the Dutch winter temperature in the year of recovery. For three common waterfowl species, Lehikoinen et al. (2013) demonstrated that shifts in wintering areas to the northeast correlated with an increase of 3.8 °C in early winter temperature in the north-eastern part of the wintering areas, where bird abundance increased exponentially, corresponding with decreases in abundance at the south-western margin of the wintering ranges. In line with these findings, Maclean et al. (2008) showed that the centres of wintering distribution for five species of wading birds along the north-western European coast flyway shifted 95 km north-eastwards within the period 1981–2000.

For the UK, Roy and Sparks (2000) showed that 26 of 35 species of butterfly exhibited an earlier appearance over the relatively short period 1976–1998 (statistically significant for 13 species). The authors estimated that a warming of 1 °C might advance first and peak appearances of most butterfly species by 2–10 days.

11.2.3 Matches and Mismatches Across Trophic Levels

Shifts in phenology as a response to climate change differ among species and populations. This has been shown for a range of taxonomic groups (Parmesan and Yohe 2003; Parmesan 2006). If climate responses differ between strongly-interacting species, such differences can have immediate impact on key ecological interactions, such as plant–pollinator, herbivore–plant, host–parasite/parasitoid and predator–prey (Visser and Both 2005; Thackeray et al. 2010). This may lead to a phenological mismatch of evolutionary-synchronised species but also to a phenological match of formerly asynchronised species resulting in so far avoided competition, parasitism or predation (Parmesan 2006).
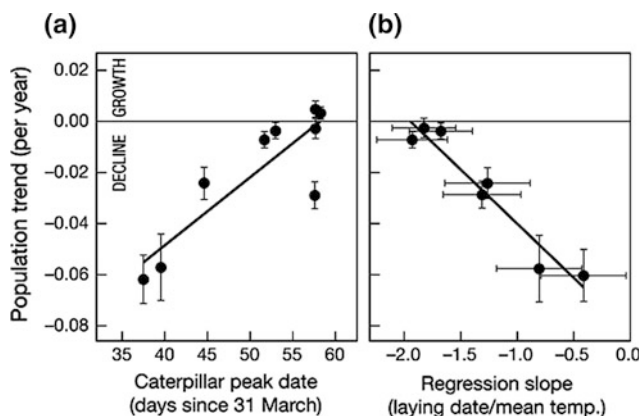
For the Netherlands (Fig. 11.4), it was demonstrated that earlier bud break in sessile oak *Quercus petraea* due to climate warming leads to an earlier appearance of caterpillars, thus disrupting food supply during the main hatching

period of the migratory pied flycatcher, which did not keep pace in its arrival at breeding grounds with the advance in peak food supply (Both and Visser 2001; Both et al. 2006). As a consequence of this mismatch in timing, pied flycatcher populations breeding in oak forest declined by 90 % between 1987 and 2003 (Both et al. 2006).

Such phenological mismatches may show effects across four trophic levels leading to deterioration in the timing of food demand and availability for passerines and their avian predators (Both et al. 2009). Biotic mismatches are also considered a major cause of the disproportionate decline in long-distance migratory bird species compared to short-distance migrants that are able to react more flexibly to phenological changes in their breeding areas (Møller et al. 2008; Both et al. 2010; Saino et al. 2011). Evidence for this phenomenon is, however, so far mostly correlative. The genetic basis of mechanisms of adaptation to phenological change is still poorly understood. Although the actual consequences of phenological changes on ecosystem functioning are not clear, several studies highlight the potential risk of desynchronising trophic linkages between primary and secondary consumers (Thackeray et al. 2010). This includes, for example, the distortion of entire food webs, in which top predators moving to cooler regions may trigger trophic cascades that lead to local extinctions and altered ecosystem processes (Montoya and Raffaelli 2010). To date, most of these assumptions are theoretical and more or less unsupported by experiments or empirical data.

Differences in response to climate change among species may also lead to a matching of originally asynchronous species, also with considerable ecological implications (Visser and Both 2005; Parmesan 2006). Case studies documenting this process are rare. Van Nouhuys and Lei (2004) showed that warmer, early spring-temperatures favoured the parasitoid wasp *Cotesia melitaearum* disproportionally, bringing it into closer synchrony with its host the butterfly *Melitaea cinxia*. Although the authors found no direct effect of the phenological matching on local host population size, the synchrony is likely to be important for overall host meta-population dynamics via variation in the rate of colonisation by the parasitoid.

In addition to phenological mismatches, trophic interactions can also become disrupted if host plants and species feeding on these host plants shift their ranges asynchronously. For the monophagous butterfly *Boloria titania* and its larval host plant *Polygonum bistorta*, Schweiger et al. (2008) showed that climate change may lead to a spatial mismatch of trophically interacting species due to asynchronous range shifts. Schweiger et al. (2012) analysed the potential for such mismatches in the future for 36 European butterfly species by simulating the potential range shifts for butterflies and host plants separately with bioclimatic envelope models, also taking into account land use. They found that those butterflies that are already limited in their distribution by their host plants could suffer most from global climate change, particularly if the host plants have restricted ranges.

## 11.2.4 Range Shifts and Biodiversity

Recent climate change has already influenced the distribution of species and their abundance (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006; Lenoir et al. 2008; Chen et al. 2011). According to a recent meta-analysis covering a range of taxonomic groups across the globe, species have on average shifted their ranges 16.9 km to higher latitudes and 11 m up in altitude per decade, more than estimates from earlier studies. The average shifts have been larger in those areas that have experienced the strongest warming and have, on average, been sufficient to track temperature changes, but with large variation between species, and most observations are from the temperate zone and tropical mountains (Chen et al. 2011). More than 20 % of species actually shifted in the opposite direction (in latitude and altitude) to the one expected based on temperature changes over the last few decades. Such changes can be explained by drivers other than temperature, such as habitat destruction and water availability, together with biotic interactions such as dependency on certain host plants and special physiological constraints (e.g. minimum or

Fig. 11.4 Trends in pied flycatcher populations in response to the local date of peak caterpillar abundance (Spearman rank correlation: $r_s = 0.80$, $n = 9$, $p = 0.013$) (**a**), and the slope of annual median egg laying date on spring (16 April–15 May) temperature ($r_s = -0.86$, $n = 7$, $p = 0.03$) (**b**). Populations of pied flycatchers with an early food peak and a weak response declined most strongly. Population trend is the slope of the regression of the log number of breeding pairs against year. In '**b**', the x axis shows the slope of a linear regression of median laying date against mean temperature from 16 April to 15 May. *Error bars* represent the standard errors of the slopes of the regression lines. All points in '**b**' are also in '**a**', except for one point, for which no data regarding the caterpillar peak were available (Both et al. 2006)

maximum temperatures during crucial phases of the life cycle) (Chen et al. 2011; Crimmins et al. 2011; Tingley et al. 2012). The differences between species reported here were only poorly related to broad taxonomic groups, such as birds and butterflies; rather the differences within such groups were larger than the differences between groups. In all taxonomic groups, habitat specialists and those with a low dispersal and colonisation capability show the lowest or even negative range shifts towards higher latitudes or altitudes (Warren et al. 2001; Chen et al. 2011). However, a recent global analysis of projected rates of temperature shift across landscapes compared to maximum projected speeds at which species can move across landscapes (from observations and modelling studies) showed that many species will probably be unable to track climate change, particularly for the warmer scenarios, which imply faster warming than in the recent past (Settele et al. 2014). Furthermore, this analysis also suggested large differences between organism groups in terms of their dispersal capacity. Herbaceous plants and trees seem to have particularly low dispersal capacity (Settele et al. 2014). An analysis for the British Isles (Fig. 11.5) also showed substantial differences in range expansion for different taxonomic groups (Hickling et al. 2006).

In the North Sea region, substantial average northward shifts have been well-documented for birds, butterflies, moths, dragonflies and damselflies, but mostly with large numbers of species also showing no shift or even retreating northern range boundaries (Parmesan 2006). Among the well-studied groups, plant ranges show the smallest responses to recent climate change, at least in lowland areas,

probably because of their limited capacity to disperse and colonise new habitats in highly-fragmented landscapes (Honnay et al. 2002; Bertrand et al. 2011; Doxford and Freckleton 2012). Analyses of community composition, however, show substantial increases in warm-adapted vascular plants and epiphytic lichens across the Netherlands, which have probably been partly driven by climate change (van Herk et al. 2002; Tamis et al. 2005). Also, as these changes have clearly been driven by other factors (such as changes in land use, eutrophication and, in the case of lichens, decreasing sulphur emissions) attributing them to climate change is challenging. Seventy-seven new epiphytic lichen species colonised the area between 1979 and 2001, nearly doubling the total number of species (van Herk et al. 2002) and overall vascular plant richness also increased (Tamis et al. 2005).

Average model projections for the migration rates that would be necessary to track climate change in Europe are substantially larger than those historically observed, but the magnitude of the mismatch depends heavily on the climate change scenario (Skov and Svenning 2004; Huntley et al. 2008; Doswald et al. 2009). Simulations with bioclimate envelope models suggest large local (per grid cell) species losses and turnover rates, assuming that species fully track climate change by migration (Thuiller et al. 2005; Pompe et al. 2008). For the SRES A1 scenario (Nakićenović and Swart 2000) and the HadCM3 climate model, for example, Thuiller et al. (2005) estimated an average turnover of 48 % per grid cell for the European plants considered (1350 for all of Europe) in the European Atlantic region by 2080. However, results from bioclimate envelope models should be
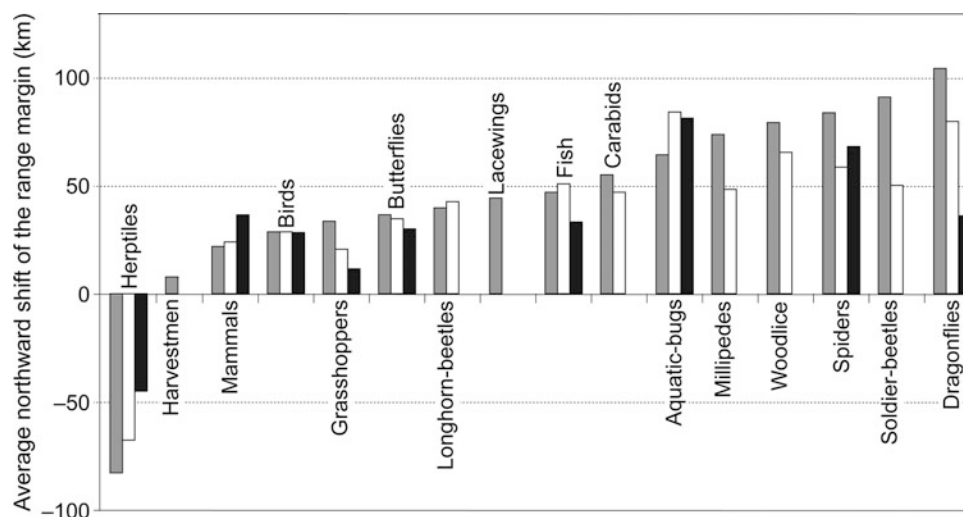
Fig. 11.5 Latitudinal shifts in northern range margins for 16 taxonomic groups in the British Isles during recent climate warming. Results are given for three levels of data subsampling (*grey* recorded; *white* well-recorded; *black* heavily recorded). Only species occupying more than twenty 10 km grid squares across two time periods (between 1960 and 2000, depending on organism group) are included in the analyses; for several of the species-poor groups, these criteria excluded all species from the analysis of 'heavily recorded' squares (Hickling et al. 2006)

interpreted more as potential shifts in the climatic window in which species can thrive rather than projections in range shifts. Furthermore, such models may overestimate change because they are developed based on correlations between species ranges and environmental factors. They do not capture the fundamental niche of species and so underestimate the climatic niche when species have not yet reached their distribution in equilibrium with the climate, which appears to be common, at least for trees (Svenning and Skov 2004; Normand et al. 2011). Furthermore, dispersal is rarely simulated explicitly, and dispersal projections are uncertain, for example, because of large uncertainties in projected wind speeds (Bullock et al. 2012). Nevertheless, it could be expected that many mobile, generalist species will continue to shift their distributions northward and up in altitude in response to climate change, although many habitat specialists (often those that are rare and already endangered) will not, and that many cold-adapted species will probably experience range losses at their southern distribution limit or at lower elevations (Hill et al. 2002; Chen et al. 2011; Sandel et al. 2011; Schweiger et al. 2012). As the area south of the North Sea region is generally more species-rich (e.g. Thuiller et al. 2005), biodiversity in the North Sea region could even increase. Negative impacts on cold-adapted species are expected to be most severe in mountain regions, where species have limited possibilities to migrate upwards or northwards, such as on mountains in the British Isles (Berry et al. 2002; Hill et al. 2002). Recent climate change has also affected the community compositions of birds and butterflies in Europe. Analyses of 9490 bird and 2130 butterfly communities in Europe show large changes, equivalent to a 37 and 114 km northward shift in bird and butterfly communities, respectively. However, these analyses suggest an even larger 'climatic debt', corresponding with a migration lag of 212 and 135 km for birds and butterflies (Devictor et al. 2012).

Intensification of agricultural activities and increasing anthropogenic nitrogen inputs since the 1950s and 1960s have been major drivers of biodiversity changes in the North Sea region (e.g. Ellenberg and Leuschner 2010). Wesche et al. (2012) found large changes in grassland community composition in five floodplain regions in northern Germany between the 1950s and 2008 and a decline in species richness at the plot level of 30–50 %. The decline was particularly strong among nectar-producing herbs, which is likely to have had negative effects on pollinators (Wesche et al. 2012). An analysis of Ellenberg indicator values for nutrient availability and a qualitative comparison with a protected area in the same region suggests that these changes were largely driven by increased nutrient inputs. Also, for a number of insect groups, a decline in species preferring low-productivity habitats and dry grassland specialists has

been recorded in northern Germany (Schuch et al. 2012a, b). Pollinators are generally declining in Europe, and this has been particularly well documented for the Netherlands and the UK (Biesmeijer et al. 2006; Potts et al. 2010). However, the reasons for the decline are unclear. Potential drivers include habitat loss and fragmentation, agrochemicals, pathogens, invasion of non-native species, climate change and the interactions between them (Potts et al. 2010). These changes show the significant role of land use practice for biodiversity in north-western Europe. Further intensification of agricultural practices, possibly driven by an increasing demand for biofuels, is likely to have negative effects on biodiversity even if atmospheric N-deposition does not increase.

11.3 Forests

Forests are currently considered the most important carbon sink in Europe (Janssens et al. 2003). Due to the relatively low proportion of forests in the present land cover for countries bordering the North Sea—except Norway—the regional significance of this area as a carbon sink is relatively small or even negative compared to other European regions with higher forest cover (Janssens et al. 2005).

11.3.1 Climate Impacts on Productivity and Carbon Stocks

Although estimates of the mean long-term carbon forest sink (net biome production, NBP) are more reliable than those from grasslands (Janssens et al. 2003), the role of wood harvests, forest fires, losses to lakes and rivers and heterotrophic respiration remains uncertain and difficult to predict. Almost one third of the NBP is sequestered in the forest soil, but large uncertainty remains concerning the drivers and future of the soil organic carbon pool under climate change (Luyssaert et al. 2010). Nevertheless, increasing temperatures, longer growing seasons, higher atmospheric CO_2 concentrations, and in the north, increasing N-mineralisation, are likely to increase the potential forest productivity where summer precipitation does not decline (Lindner et al. 2010). Moreover, it is uncertain to what extent this potential can be realised as forests will increasingly face a climate to which the planted species or provenances are not adapted, which might increase their susceptibility to pests and pathogens, such as bark beetle (Scolytinae) outbreaks, which can lead to major forest die-back events particularly in Norway spruce *Picea abies* stands (Schlyter et al. 2006; Bolte et al. 2010). Furthermore, warmer and longer vegetation periods will accelerate the development of bark beetles, in some regions

allowing for additional generations within a growing season (Jönsson et al. 2009). Other insect herbivores will also benefit from warmer conditions (Lindner et al. 2010). In a climate manipulation experiment in a Norwegian boreal forest, raised temperature and CO_2-level stimulated the outbreak of heather beetle *Lochmaea suturalis* and led to a shift in the ground vegetation from common heather *Calluna vulgaris* to blueberry *Vaccinium myrtillus* and cowberry *Vaccinium vitis-idaea* (van Breemen et al. 1998).

The complex interplay between climatic stress, pests and pathogens, and further disturbance such as windfall is hardly captured in the forest models used to project potential future impacts of climate change (e.g. Kirilenko and Sedjo 2007). As a result, it is highly uncertain whether climate change will lead to higher standing biomass in forests.

11.3.2 Shifts in Communities and Species Distribution

Projections of potential climate-driven transient shifts in broadly-defined forest types suggest only moderate changes in the North Sea region by 2100 (Hickler et al. 2012). The most significant changes projected are the spread of broad-leaved and hemi-boreal mixed forests northward in southern Sweden and Norway as well as an upwards shift of the tree-line in the southern Scandes, which is already taking place (Kullman 2002).

Long-term equilibrium of shifts in forest type could be much more substantial, with thermophilous forests dominating in the south-western UK and temperate broadleaved forest along most of the Norwegian coast (Hickler et al. 2012). Recent range shifts northward (Fig. 11.6) have already been observed for cold-hardy, broadleaved, evergreen species such as holly *Ilex aquifolium* at their northern distributional limit in Europe (Walther et al. 2005; Berger et al. 2007).

Many European tree species have not yet filled their potential climatic niche in Europe because of dispersal limitations (Svenning and Skov 2004; Normand et al. 2011). Thus dispersal-limited species may be unable to track future climate change, unless foresters assist migration.

In contrast, there is almost no evidence of range shifts in herbaceous forest plants. Unlike mountain forest with short migration distances, there is some evidence that in lowland forests plant distribution changes will lag behind climate warming (Bertrand et al. 2011). Observational (Honnay et al. 2002) and modelling studies (Skov and Svenning 2004) suggest that this is probably due to dispersal limitation resulting from forest habitat fragmentation in lowlands. Where significant range shifts of forest herbs northward and eastward have been documented, such as for the oceanic annual woodland herb climbing corydalis *Ceratocapnos claviculata*, it is

questionable whether this is due to climate change or to other drivers such as eutrophication or assisted migration through the international timber trade (Voss et al. 2012).

Among the major forest tree species, beech *Fagus sylvatica* is expected to extend its range northward in Britain and southern Scandinavia (Kramer et al. 2010; Hickler et al. 2012), whereas environmental conditions for the commercially-important Norway spruce will become less favourable (Pretzsch and Dursky 2002; Schlyter et al. 2006; Hanewinkel et al. 2013). Although beech is often considered to be very sensitive to drought, several studies (Lebourgeois et al. 2005; Meier and Leuschner 2008; Mölder et al. 2011) showed considerable phenotypic plasticity in response to drought stress (e.g. Bolte et al. 2007). The same is true for sessile oak, which proved to be highly resilient even to extreme drought (Leuschner et al. 2001; Lebourgeois et al. 2004; Friedrichs et al. 2009; Merian et al. 2011; Härdtle et al. 2013). Given the generally damp climatic conditions of north-western Europe, major broadleaved forest trees such as beech and sessile oak are probably not constrained by the projected climate change, which is in line with predictions of vegetation models (Kramer et al. 2010; Hickler et al. 2012). However, using older climate projections with lower projected rainfall than the latest average projections (see Chap. 5), simulations with a forest tree suitability model based on climatic and edaphic factors suggested that the majority of native broadleaved species would become unsuitable for commercial timber production in southern England due to increasing drought severity (Broadmeadow et al. 2005).

Forest management includes a wide range of measures to mitigate climate change effects, such as the selection and planting of species and provenances adapted to future climate (Isaac-Renton et al. 2014); a reduction in rotation cycles to accelerate the evolution and establishment of better adapted genotypes (Alberto et al. 2013); and the use of mixtures of high genetic variation across an array of environmental conditions (Hemery 2008; Köhl et al. 2010). Scientifically-sound implementation of such adaptation measures requires a wide range of research and monitoring activities such as testing of the suitability of new tree species and provenances, a regional risk analysis based on retrospective performance as well as the analysis of climate envelope and climate matching under potential future climates (Hulme 2005; Bolte et al. 2009; Hemery et al. 2010).

11.4 Grasslands

After cropland, grasslands are the dominant land use type in the North Sea catchment area. In the UK, grasslands comprise more than 40 % of land cover (EUROSTAT 2015).

Fig. 11.6 Distribution of holly *Ilex aquifolium* and the 0 °C-January isoline at different times. **a** Former range of *I. aquifolium* based on Enquist (1924) and Meusel et al. (1965), isoline based on Walter and Straka (1970), symbols based on Iversen (1944); *circles*: *I. aquifolium* within or at the border of the station area; *circles*: *with cross I. aquifolium* strayed into woods from gardens; *stars*: *Ilex* area lies immediately outside the station area; *crosses*: *I. aquifolium* missing in the station area. **b** Modelled range of *I. aquifolium* in the recent past (1931–1960), isoline as in 'a'. **c** Former range of *I. aquifolium* as in 'a'; isoline updated for 1981–2000 based on Mitchell et al. (2004), symbols as for 'a'. **d** Former range of *I. aquifolium* complemented by the simulated species distribution under a moderate climate change based on 1981–2000 climate data, isoline as in 'c'; *triangles* represent locations with new observations of *I. aquifolium* (Walther et al. 2005)
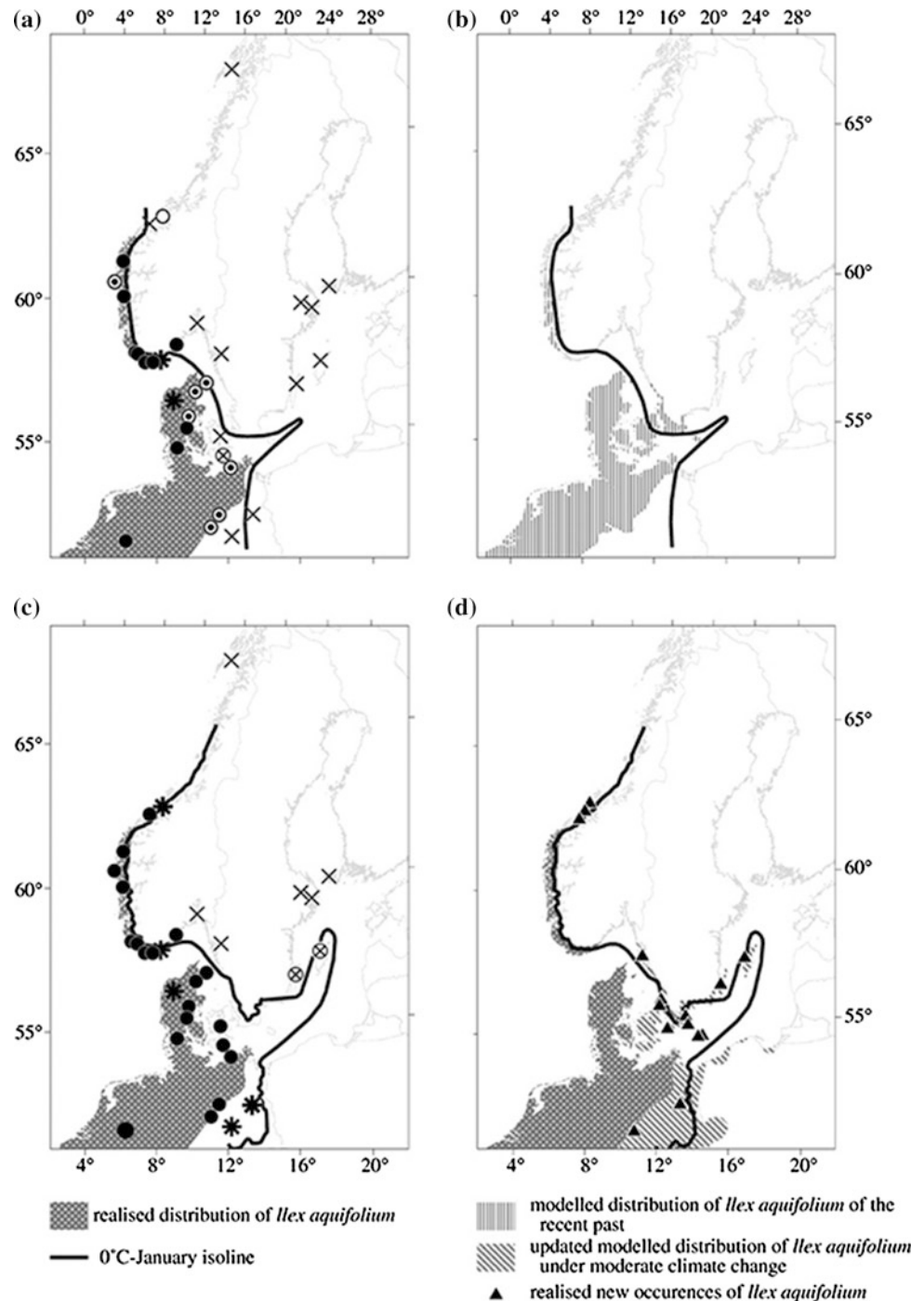
Due to conversion into cropland, and the cessation and intensification of agricultural practices, grasslands underwent fundamental change during the 20th century (Bullock et al. 2011). Changes in management practice and eutrophication are currently the major drivers of ecological change in grasslands. At the same time, grasslands are of major significance for biodiversity and nature conservation in north-western Europe.

11.4.1 Climate Impacts on Carbon Stocks and Cycling

Unlike forests, carbon accumulation in grassland ecosystems occurs mostly below ground. As fluxes of greenhouse gases in grasslands are intimately linked to management and site conditions, grasslands can be either a sink or a source of greenhouse gases. Although many studies consider

temperate grassland to be a carbon sink (Soussana et al. 2004), there is still high uncertainty about their current and future net global warming potential (in terms of CO_2 equivalents) at both a regional and continental scale (Janssens et al. 2003, 2005; Smith et al. 2005).

For Britain and Wales, both dominated by grasslands, Bellamy et al. (2005) suggested that significant losses of soil organic carbon (SOC) between 1978 and 2003 must be attributed to climate change because they occurred across all types of land use. However, as shown by Smith et al. (2007), this assumption was precarious and lacked clear empirical evidence. At a global scale (Guo and Giffort 2002), current SOC losses and gains in grasslands can be predominantly attributed to changes in land cover and management, whereas the role of climate change remains uncertain but is predicted to increase over the coming century (Smith et al. 2005). These considerable uncertainties are because grassland ecosystems are particularly complex and difficult to study owing to the wide range in management and environmental conditions to which they are exposed. As a result, studies on the effects of climate change on grasslands are often affected by this variability as well as by other confounding effects such as eutrophication and changes in

management practice, which cause difficulties for observational studies and modelling (Soussana et al. 2004).

11.4.2 Climate Impacts on Plant Communities

Few experimental studies attempt to isolate the effects of climate change from other confounding effects. A study simulating warming and extended summer drought in calcareous grasslands at Buxton and Wytham in northern England (Grime et al. 2000) covered two different types of grassland with contrasting effects: after five years of climate manipulation, the more fertile, early successional grassland at Wytham showed significant changes in species composition and aboveground productivity especially for the combination of winter warming and summer drought. In contrast, an oligotrophic and more traditional calcareous grassland at Buxton exhibited almost no response to warming and drought treatments. This was still true even after 13 years of climate modification (Fig. 11.7; Grime et al. 2008). One reason for the high resistance of this infertile grassland may be the small-scale spatial heterogeneity in soil depth allowing the coexistence of

Fig. 11.7 Mean dissimilarity of treatment and control species composition for each year of the Buxton climate change experiment conducted in a nutrient-poor calcareous grassland. Dissimilarity was measured by Sørensen distance estimated separately within each replicate (n = 5 per treatment year). *Dashed lines* indicate mean dissimilarity in year 1 of the experiment. *Error bars* indicate one standard error of the mean. Statistics indicate whether treatment dissimilarity progressively increased over time based on linear autoregressive models (Grime et al. 2008)
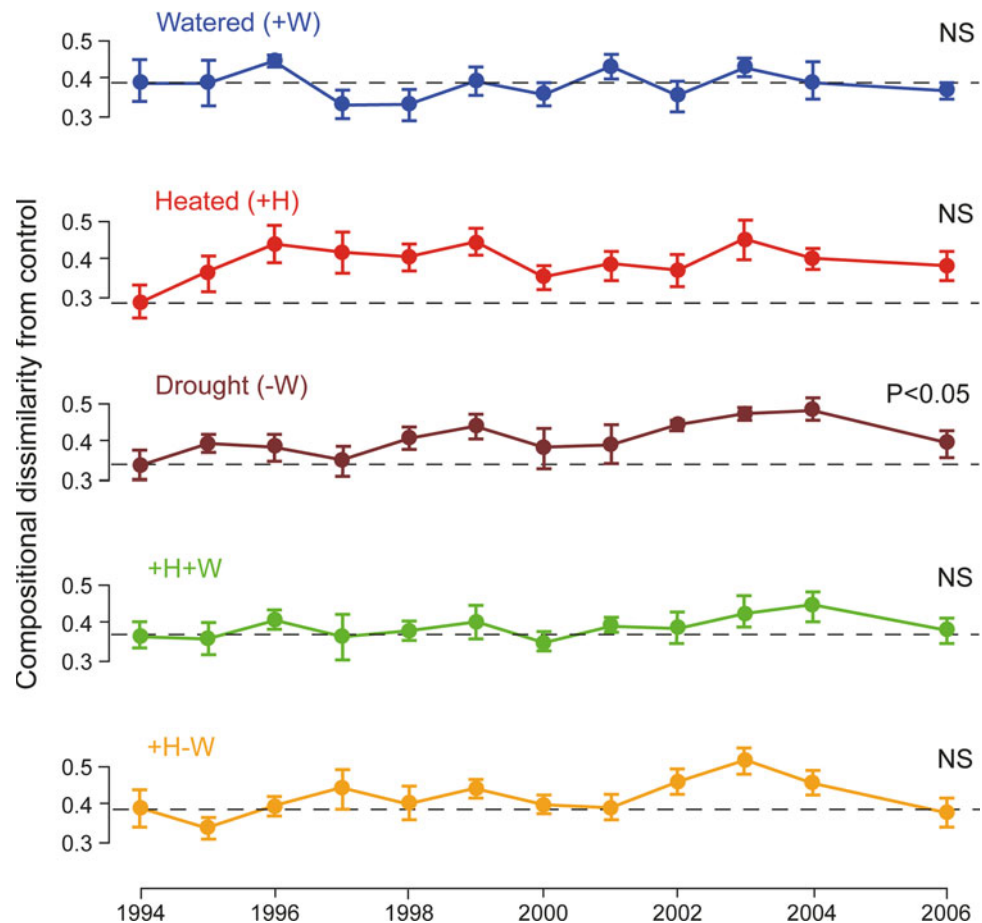
drought-tolerant and more mesic species at small spatial scales (Fridley et al. 2011). As indicated by seed addition experiments, the minor changes in species composition, even after long-term climate treatments, are significantly affected by dispersal limitation rather than just biotic resistance (Moser et al. 2011). The prominent role of dispersal limitation as a cause of delayed response to climate effects has also been highlighted in several other studies (Buckland et al. 2001; Stampfli and Zeiter 2004; Zeiter et al. 2006).

Overall, the results of the Wytham and Buxton experiments suggest that more productive grasslands, strongly altered by human activities, might respond more to effects of climate change than infertile and more traditionally managed grasslands with rich species pools that can buffer climate effects (Grime et al. 2000, 2008). However, infertile traditional grasslands show low resilience towards eutrophication and changes in land management, which are currently more important drivers of ecological change in grasslands than climate change. Conversely, future warming potentially in association with increased drought risk could supersede eutrophication as the main driver of change, and in so doing potentially favour the persistence or even spread of dry and infertile grassland types (Buckland et al. 1997).

Observational studies also suggest that changes in the grasslands of north-western Europe can be attributed to recent regional climate change (e.g. Gaudnik et al. 2011), but these are mostly of high uncertainty due to strong confounding effects (McGovern et al. 2011). However, flowering phenology of many typical grassland plants in the UK does reveal significant effects of climate warming. Of 385 plant species, 16 % flowered significantly earlier in the early 1990s compared to previous decades, and earlier onset of flowering was most significant in annual species (Fitter and Fitter 2002). Williams and Abberton (2004) confirmed a significant trend of earlier flowering within different agricultural varieties of the common grassland legume white clover *Trifolium repens*.

11.4.3 Climate Impacts on Animal Communities

More convincing evidence of climate change effects in grasslands comes from animal groups typical of grassland habitats such as butterflies and grasshoppers; several have extended their range northwards significantly over past decades (Parmesan et al. 1999; Hill et al. 2002; Hickling et al. 2006). Unlike most vascular plants, which are often chronically persistent and immobile, highly-mobile animal species can often quickly respond to changing climate by significant range extensions. In north-western Germany, for example, the Roesel's busch-cricket *Metrioptera roeselii*, a typical grassland species, has been rapidly extending its range northward since the early 1990s, which was probably helped by increased rates of macroptery in this normally short-winged species, as a sign of density stress at the range margin (Hochkirch and Damerau 2009; Poniatowski and Fartmann 2011; Poniatowski et al. 2012).

Significant northward range expansions have also been documented for many typical grassland butterflies in the UK (Hill et al. 1999, 2002). However, only particularly mobile habitat generalists can fully exploit the emerging potential offered by climate warming (Fig. 11.8), whereas less mobile species and habitat specialists still suffer from habitat fragmentation and deterioration of habitat quality (Hill et al. 1999; Warren et al. 2001). Thus, range expansion is in many cases significantly lagging behind the current climate and can be reduced or even reversed by non-climatic drivers (Hulme 2005; Oliver et al. 2012).
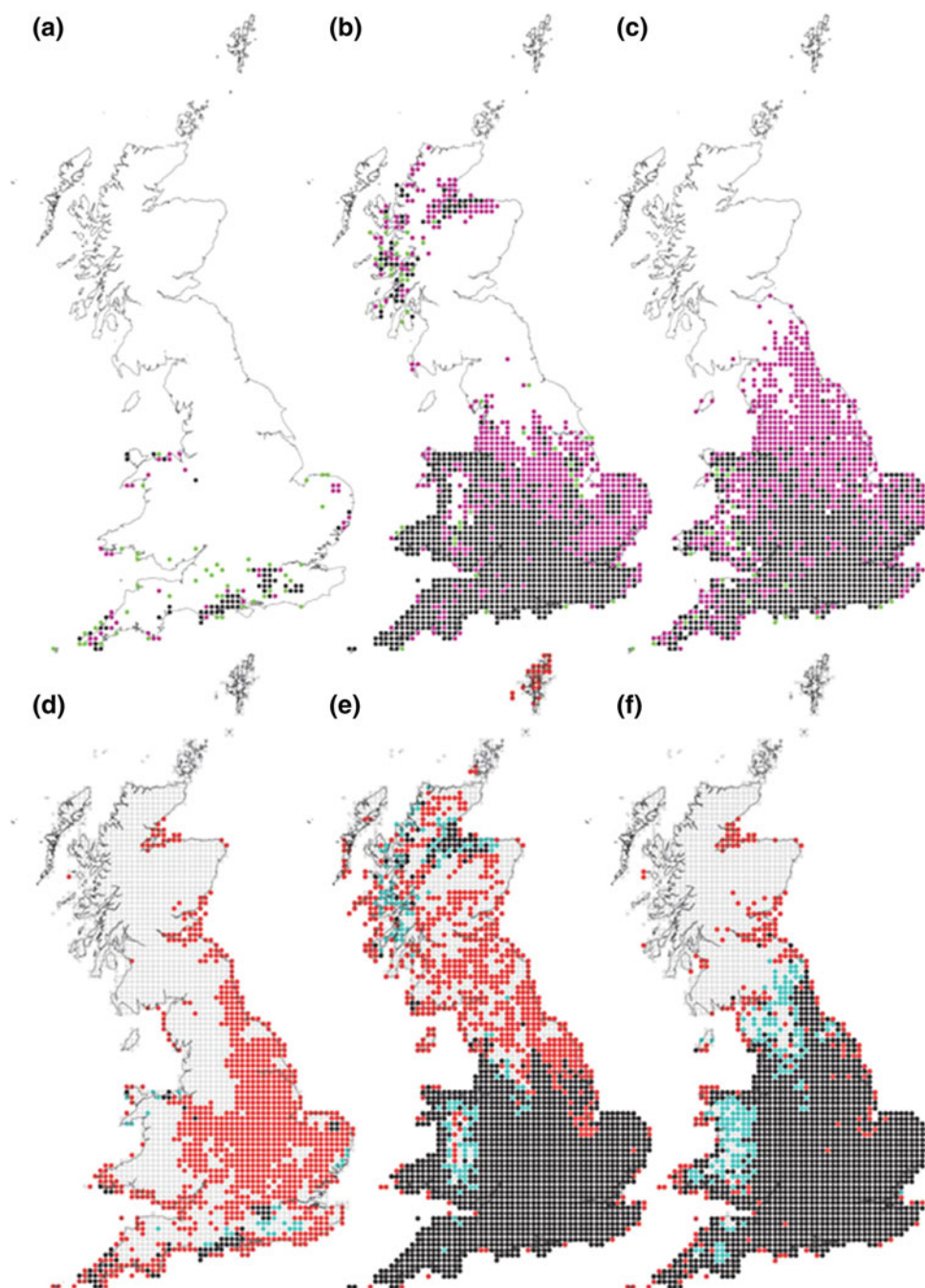
11.5 Heathlands

In countries bordering the North Sea basin, heathlands dominated by shrubs of the ericaceous family still cover extensive areas especially in highlands of the UK and the southern Scandes (Webb 1998; van der Wal et al. 2011). Due to conversion into cropland and afforestation, heathlands have declined dramatically in the UK-lowlands and in the southern part of the North Sea region (Denmark, Germany, Netherlands). In these regions, they are at the edge of extinction in many sites and have become a major object of biodiversity and nature conservation efforts. Eutrophication and acidification through atmospheric inputs and changes in land management are currently the major drivers of change in these ecosystems (Härdtle et al. 2006), which makes the identification of climate change impacts difficult.

11.5.1 Climate Impacts on Ecosystem Processes

Effects of climate change on ecosystem processes in European heathlands were specifically addressed within the framework of two EU-projects simulating raised temperatures and drought (Wessel et al. 2004). These studies included sites in the UK, Denmark and the Netherlands. Experimental warming of 1 °C induced a significant increase in total above-ground plant biomass growth of 15 % in the most temperature-limited site in the UK, whereas drought treatments led only to a slight decline (Peñuelas et al. 2004). Drought decreased flowering (by up to 24 % in the UK). Warming and drought decreased litterfall in the Netherlands (by 33 and 37 %, respectively). Tissue concentrations of phosphorus (P) generally decreased and the N:P ratio increased with warming and drought except at the UK site,

Fig. 11.8 The degree to which three butterfly species have changed their ranges (**a–c**, without subsampling) and are lagging behind current climate in Britain (**d–f**; 10-km grid resolution). **a+d**, silver-studded blue *Plebejus argus*; **b+e**, speckled wood *Pararge aegeria*; **c+f**, comma *Polygonia c-album*. For maps **a–c**, *black circles* show butterfly records for both 1970–1982 and 1995–1999; *green circles* show apparent extinction (recorded 1970–1982; not 1995–1999); *pink circles* show apparent colonisation (no record 1970–1982; record 1995–1999). For maps **d–f**, *black circles* (climate suitable, butterfly recorded) and *grey circles* (climate unsuitable, butterfly not recorded) show where observed 1995–1999 and simulated distributions agree; *red circles* (climate predicted suitable, butterfly not recorded) and *blue circles* (climate deemed unsuitable, butterfly recorded) show mismatches (Warren et al. 2001)

indicating the progressive importance of P-limitation as a consequence of warming and drought.

Owing to their richness in soil organic matter, mature heathlands may become important sources of C and N-release triggered by increasing temperatures and more frequent periods of drought. For the same experiments as above, Schmidt et al. (2004) found mostly weak and insignificant effects of warming and drought treatments on nitrogen and carbon budgets in the soil solution. Only at a strongly N-saturated site with high atmospheric N-deposition in the Netherlands, did warming trigger a significant increase

in N-leaching. Similarly, in the same warming and drought experiments, Jensen et al. (2003) and Emmett et al. (2004) found largely weak or inconsistent responses in major soil processes such as decomposition, respiration and N-mineralisation. The latter turned out to be predominantly controlled by soil moisture. The response of soil-related processes to warming and drought treatments was generally found to be strongly dependent on local site conditions (Emmett et al. 2004). At mesic sites in the Netherlands and Denmark, soil respiration decreased in response to drought but recovered quickly to pre-drought levels after re-wetting in

the following winter. In contrast, repeated drought treatments at a particularly damp site in the UK, which was particularly rich in organic matter, caused a disturbance in soil structure and a persistent reduction in soil moisture, which induced increased and continuing carbon losses through soil respiration (Sowerby et al. 2008).

The heathland studies conducted within the framework of the CLIMOOR and VULCAN projects (Peñuelas et al. 2007) show that the magnitude of the response to warming and drought was dependent on differences between sites, years, and plant species. Thus there are complex interactions between other environmental factors that condition plant and ecosystem performance, which makes it extremely difficult to predict net responses.

## 11.5.2 Climate Impacts on Plant Communities

Observational and experimental evidence for floristic changes in heathlands that can be clearly attributed to climate change is weak; for example, Werkman et al. (1996) found some indications that climate warming in combination with N-deposition might enhance the spread of the noxious weed bracken *Pteridium aquilinum* into heathlands in the UK. However, declines in arctic-alpine and boreal-montane lichen species in the heathlands of north-western Europe can be attributed to changes in traditional management practices and acidification, and are probably not directly connected to climate change (Hauck 2009).

11.5.3 Climate Impacts on Animal Communities

A significant decline has been observed over recent decades in arctic-alpine bird species inhabiting mountain heathlands in the north of the UK such as ptarmigan *Lagopus mutus*, dotterel *Charadrius morinellus* and snow bunting *Plectrophenax nivalis*. In contrast the thermophilous, submediterranean Dartford warbler *Sylvia undata* has increased its population and spread into southern England, probably due to warmer winters (van der Wal et al. 2011). There is currently almost no empirical evidence of climate change impacts in other heathland-specific animal groups. However, modelling approaches suggest (Thomas et al. 1999; Berry et al. 2002) that eco-thermic animal species in heathlands may benefit from climate warming at their northern range margin.

11.6 Mires and Peatlands

Peatlands store significant quantities of carbon, nitrogen and other elements in their soils (e.g. Limpens et al. 2008; Yu et al. 2010) and are widespread in the North Sea region (Montanarella et al. 2006, Fig. 11.9). According to Joosten and Clarke (2002), peatlands are areas with a naturally accumulated peat layer at the surface, whereas mires are peatlands where peat is currently being formed. While about 80 % of the peatlands in Sweden and Norway are still mires,
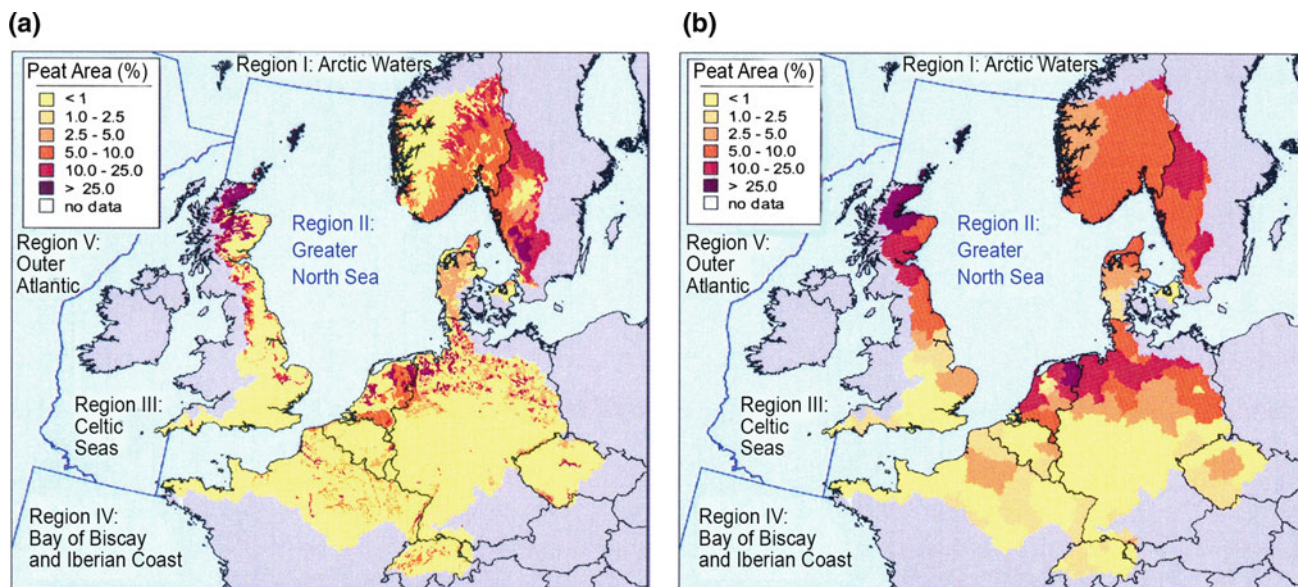
Fig. 11.9 Relative cover of peatlands and peat-topped soils in the North Sea catchment area. Maps based on **a** the soil mapping units of the European Soil Database (King et al. 1994, 1995) and **b** the NUTS (Nomenclature of Territorial Units for Statistics) level 2 administrative regions (R. Hiederer non-published data)

the contribution of mires to the total peatland area in the other, more southern North Sea-bordering states is only 1–7 % due to widespread drainage and intensive land use (Joosten and Clarke 2002).

Peatlands exchange C- and N-containing gases with the atmosphere, particularly the greenhouse gases CO_2, methane (CH_4) and nitrous oxide (N_2O) and thus influence climate (Blodau 2002; Frolking and Roulet 2007; Limpens et al. 2008; Finkelstein and Cowling 2011). Peatlands also exert strong influences on aquatic ecosystems by lateral water-borne export fluxes of elements, especially as particulate and dissolved organic matter (Urban et al. 1989; Freeman et al. 2001; Worrall et al. 2002; Billett et al. 2004; Dinsmore et al. 2010). Importantly, carbon accumulation, and vertical land-atmosphere and lateral waterborne bio-geochemical fluxes of peatlands are affected by climate change, and at the same time by changes in atmospheric chemistry and land use (e.g. Bragg 2002; Belyea and Malmer 2004; Dise 2009; Billett et al. 2010; Charman et al. 2013).

11.6.1 Climatic Impacts on Abiotic Conditions

Climatic change will have direct effects on the energy and water budgets of peatlands. Changing quantities and temporal patterns of precipitation will affect the water table in peatlands; with drought lowering and increased precipitation raising peatland water levels (e.g. Sottocornola and Kiely 2010). Higher temperatures, which are projected for the North Sea region in the future (Chap. 5) will increase evapotranspiration through a larger atmospheric water demand (Kellner 2001; Wu et al. 2010; Peichl et al. 2013). Other important variables influencing the energy and water budget of peatlands are net radiation and incoming short-wave radiation (Moore et al. 2013; Runkle et al. 2014). A continuation of the 'brightening period' through reduced aerosol loading (Wild et al. 2005) in Europe could increase evapotranspiration (Oliveira et al. 2011) leading to lower peatland water tables. However, most atmospheric models simulate a future decrease in shortwave radiation in the northern North Sea region and an increase in short-wave radiation in the south (Chap. 5). A long-term lowering of the water table due to increased evapotranspiration is expected to be modulated by changes in leaf area and the distribution of plant functional groups leading to increased surface resistance, reduced evapotranspiration and an attenuated fall in water tables (Bridgham et al. 1999; Moore et al. 2013). Desiccation of the moss layer during summer droughts can also lead to reduced evapotranspiration (Sottocornola and Kiely 2010). Higher winter precipitation as projected for the North Sea region (Chap. 5) would lead to larger winter discharge from

peatlands and probably to a larger lateral export of dissolved organic matter and nutrients (e.g. Tranvik and Jansson 2002; Worrall et al. 2002, 2003; Pastor et al. 2003; Holden 2005). Increasing summer drought and winter rainfall would enhance peatland erosion and export of dissolved organic carbon (DOC) and particulate organic carbon (POC) in susceptible areas, particularly in the upland blanket bogs of the UK and Norway (e.g. Bower 1960, 1961; Francis 1990; Evans et al. 2006b; Evans and Warburton 2010). Drier mire surfaces in summer would enhance the risk of peatland fires, which lead to strong local emissions of CO_2 (Davies et al. 2013) and waterborne DOC (Holden et al. 2007; Clutterbuck and Yallop 2010). At bare peat sites (under peat extraction or crop cultivation), higher wind speeds and rainfall intensities can lead to strong aeolian or water erosion of peat (Warburton 2003).

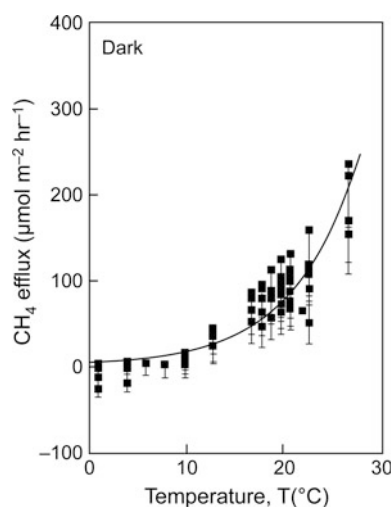## 11.6.2 Climatic Impacts on Biotic Interactions

Climate change is expected to have large impacts on biotic processes in peatlands (e.g. Heijmans et al. 2008; Charman et al. 2013). Higher temperatures will generally increase microbial peat decomposition and carbon mobilisation (Ise et al. 2008), leading to greater concentrations of DOC in peatland surface and soil pore waters (Freeman et al. 2001, Fig. 11.10). The mobilised DOC can be mineralised and released to the atmosphere as CO_2 (e.g. Silvola et al. 1996; Lafleur et al. 2005) or CH_4 (e.g. Dunfield et al. 1993; Moore and Dalva 1993; Daulat and Clymo 1998; Hargreaves and Fowler 1998; Fig. 11.11) depending on the reduction-oxidation status of the organic soils. It can also be laterally exported with the peatland discharge into limnic systems (Tipping et al. 1999; Worrall et al. 2003). Warming-induced increases in soil carbon emissions result partly from the direct temperature effect on soil microbial physiological processes and growth and partly from better substrate availability in the soil pore water caused by higher plant productivity (Mikkelä et al. 1995; Joabsson et al. 1999; Van den Pol-van Dasselaar et al. 1999).

These findings from field and laboratory studies have been incorporated in local, regional and global soil process models (e.g. Walter et al. 2001; van Huissteden and van den Bos 2006; Bohn et al. 2007; Meng et al. 2012). The models predict considerable increases in CH_4 emissions from peatlands over the coming century due to warming as long as wetland area and soil moisture conditions remain unchanged. However, several global models tested within the Wetland and Wetland CH_4 Intercomparison of Models Project (WETCHIMP) predict a decrease in wetland area in the North Sea region in response to higher temperatures, which is likely to lead to lower CH_4 emissions (Melton et al.
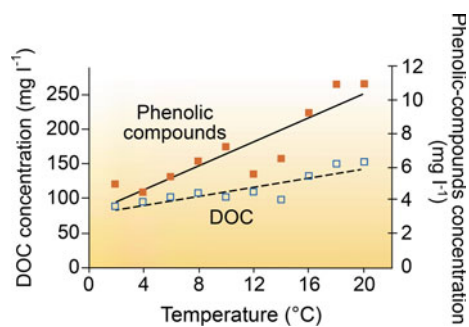
Fig. 11.10 Laboratory observations of increased concentrations of dissolved organic carbon (DOC) and phenolic compounds in peat soil in response to rising temperature (Freeman et al. 2001)

Fig. 11.11 Effects of temperature on methane (CH_4) efflux from 30 cm diameter *Sphagnum papillosum* mire cores. Flux measurements were performed in dark conditions (after Daulat and Clymo 1998)

peatlands with typical mire vegetation, peat accumulation is expected to increase in response to higher mean annual temperatures because the benefit to primary productivity will be higher than for ecosystem respiration (Loisel et al. 2012; Charman et al. 2013). Longer growing seasons (higher winter temperatures, shorter snow-cover duration) allows the vegetation to take up more photons over the year leading to higher plant productivity and peat accumulation. This increase in net carbon uptake under a warming climate—a negative feedback on climate warming—will be modulated by cloud cover and levels of photosynthetically active radiation (Yu et al. 2010; Loisel et al. 2012; Charman et al. 2013).

If peatland water tables become significantly lower due to increased evapotranspiration and/or decreased summer precipitation, peat decomposition and the release of CO_2 will be enhanced (e.g. Silvola et al. 1996; Laine et al. 2009). Higher N_2O emissions can also be expected with lower peatland water levels (Martikainen et al. 1993; Regina et al. 1996; Goldberg et al. 2010). On the other hand, CH_4 production and emission will decrease, while CH_4 oxidation will be enhanced (e.g. Daulat and Clymo 1998; Hargreaves and Fowler 1998; Nykänen et al. 1998; Le Mer and Roger 2001; Laine et al. 2007, 2009).

The impact of water table drawdown on net ecosystem productivity depends on the response of peatland vegetation, which is difficult to predict and can vary strongly with the micro-topography of mires (Malmer et al. 1994; Strack and Waddington 2007; Lindsay 2010). Since *Sphagnum* mosses have neither roots nor vessels to transport water from deeper soil layers, they rely on high water tables. Water that is lost at the soil surface through evaporation can be replaced by precipitation and capillary rise in *Sphagnum* peat and vegetation. But—depending on the *Sphagnum* species present and the degree of peat decomposition—capillary rise is only efficient in this regard if water tables are not lower than 0.5 m below the land surface (Clymo 1984). Thus, long-lasting drought may damage the vitality of *Sphagnum* mosses (Gerdol et al. 1996; Bragazza 2008; Breeuwer et al. 2009; Robroek et al. 2009).

Medium- to long-term changes in climatic variables such as temperature and precipitation have complex effects on mire vegetation composition that interact with changes in CO_2 concentration and nutrient availability (e.g. Heijmans et al. 2008; Breeuwer et al. 2010, see also Sect. 11.6.3). In a *Sphagnum*-dominated bog in southern Sweden, significant shifts in vegetation composition since the 1950s indicate higher nutrient availability, higher productivity, and drier and shadier conditions due to enhanced tree and shrub growth, which have probably all been triggered by warming (Kapfer et al. 2011). Projected climate change, particularly higher summer temperatures and lower summer precipitation may reduce the bio-climatologically suitable space for blanket

2013); however, it should be noted that these models show a very wide range of responses.

Whether increased peat decomposition and carbon mobilisation due to higher temperatures leads to lower net ecosystem productivity and to higher net carbon emissions, will depend on the land use of peatlands. For the period 1978–2003, Bellamy et al. (2005) reported carbon losses from all soil types across England and Wales, with particularly strong losses from peat soils. However, it is not clear from such data whether carbon was lost due to climate change or to concomitant changes in atmospheric chemistry and land use (see Sect. 11.4.1 and 11.6.3). Likewise, mapping of peat soils in the Dutch province of Drenthe showed that 42 % of the area of peat soils was converted to mineral soils in the last 30–40 years by carbon loss due to drainage and agricultural management; on average 1 cm peat thickness was lost per year (De Vries et al. 2008). In near-natural

Fig. 11.12 Area covered by the bioclimatic envelope of blanket peatlands as predicted by the model PeatStash using the bioclimatic thresholds associated with the 1961–1990 baseline climate for the UKCIP02 high and low emissions scenarios ('High' and 'Low', respectively) for three time periods: 2020s, 2050s and 2080s. An Ordnance Survey/EDINA supplied service (© Crown Copyright/database 2009) and Met Office/UKCIP gridded climate data (UKCIP02 © Crown Copyright 2002) (Gallego-Sala et al. 2010)
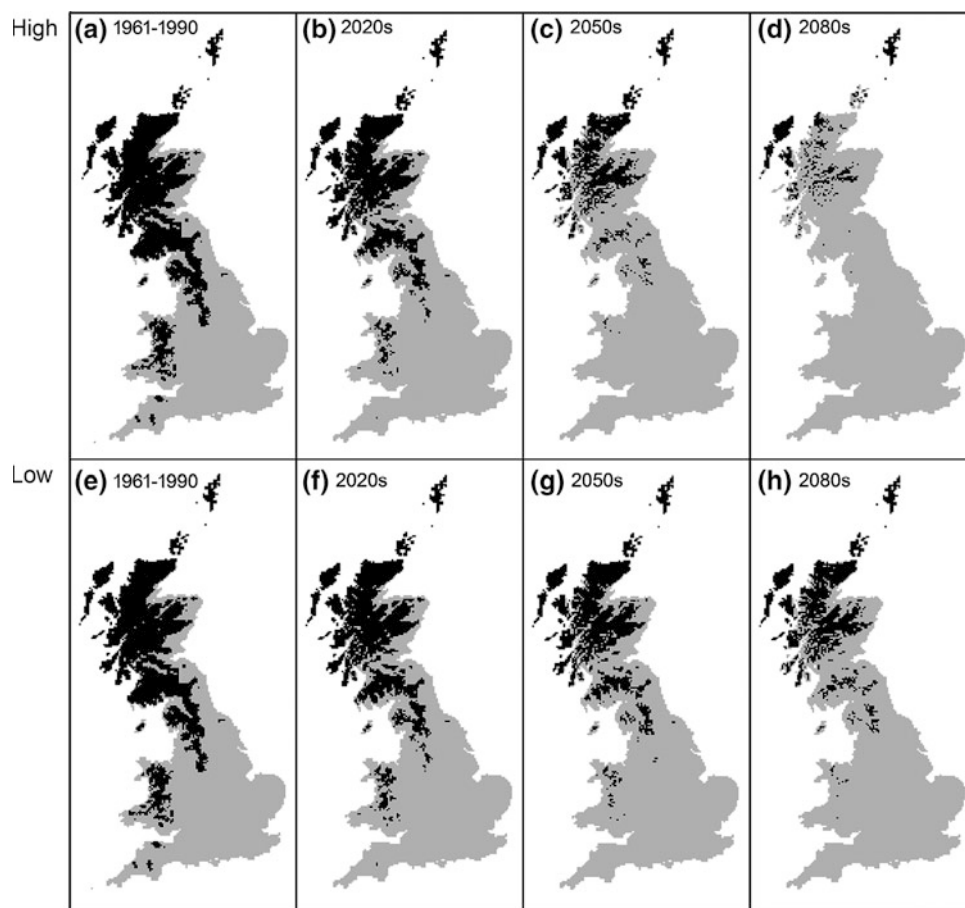
bogs in the UK (Clark et al. 2010; Gallego-Sala et al. 2010; Gallego-Sala and Prentice 2013, Fig. 11.12). Berry and Butt (2002) suggested that the dominant species in lowland raised bogs of Scotland would find suitable conditions, but that some rare species will probably lose suitable climate space under the expected future climatic conditions. Since lower summer precipitation and higher summer temperatures are projected for the entire North Sea region (Chap. 5), mires on the European continent—especially ombrogenous mires—are likely to experience falling summer water levels with negative impacts on typical mire plant communities. However, Lindsay (2010) cautioned that the climate envelope approaches applied might underestimate the importance of local atmospheric humidity, cloud cover and mist frequency for mire occurrence. Other studies even propose—on the basis of biogeographical, bioclimatological and ecophysiological reasoning—that northern oceanic peatlands will expand owing to the increased oceanicity of the future climate (Crawford 2000; Crawford et al. 2003). Lindsay (2010) also stated that mires with a well-developed acrotelm and microtopography might be able to react to climate change without losing their ability to grow and sequester carbon. Mires that are already degraded will have much less resilience to the projected changes in climate (Lindsay 2010).

11.6.3 Competing Effects of Climate Change and Other Influences

In addition to the changes in climate, there have also been changes in the intensity of land use and atmospheric chemistry (such as CO_2 concentration, and atmospheric deposition of nitrogen and sulphur) over recent decades, with strong impacts on near-natural and degraded peatlands. These may intensify, mask or reverse the effects of climate change on peatlands.

11.6.3.1 Atmospheric Chemistry
Research in *Sphagnum* bogs found that elevated atmospheric CO_2 concentrations did not affect NPP due to the strong N-limitation of these ecosystems (Berendse et al. 2001). However, CH_4 emission (Dacey et al. 1994; Hutchin et al. 1995) and DOC export (Freeman et al. 2004; Van Groenigen et al. 2011) from peatlands were enhanced under elevated CO_2 concentrations. Increased N-deposition promotes microbial peat decomposition and thus CO_2 and CH_4 emissions (Aerts et al. 1992; Aerts and de Caluwe 1999) and DOC export fluxes (Bragazza et al. 2006). Large shifts in mire vegetation composition may also occur in response to elevated CO_2 concentrations and increased N-deposition

(Van der Heijden et al. 2000; Berendse et al. 2001; Fenner et al. 2007; Heijmans et al. 2008). Deposition of nitrogen and sulphur leads to acidification of top soils and thus changes the solubility and mobilisation of dissolved organic matter. The rise in DOC concentrations in limnic water bodies observed in the latter half of the 20th century in Great Britain and Sweden seems to have been mainly driven by decreasing S-deposition with the warming effect of minor importance (Freeman et al. 2001; Worrall et al. 2002; Evans et al. 2005, 2006a, 2007; Monteith et al. 2007; Erlandsson et al. 2008). However, S-deposition has also been shown to suppress CH_4 emissions because sulphate reduction is energetically favourable compared to methanogenesis (Dise and Verry 2001). Heavy air pollution can even lead to die-off of *Sphagnum* mosses, triggering for example peat erosion in blanket mires (e.g. Tallis 1985).

11.6.3.2 Land Use

Drained and degraded peatlands are hotspots of greenhouse gas emissions (e.g. Oleszczuk et al. 2008; Couwenberg 2011; Joosten et al. 2012). Mineralisation of peat organic matter and the respective CO_2 emissions are strongly related to drainage depth and management intensity (Aerts and Ludwig 1997; Dirks et al. 2000; Beetz et al. 2013; Leiber-Sauheitl et al. 2013; Schrier-Uijl et al. 2014). A project on peatlands in Germany has shown that the annual greenhouse gas balance of managed peatland areas can be estimated well from two predictor variables—mean annual water level and carbon exported by harvest—which together can be used as a proxy for management intensity (Drösler et al. 2011, 2012). Within the set of managed peatlands, greenhouse gas emissions from deeply-drained peatlands such as cropland or intensively-used pastureland are especially large (Veenendaal et al. 2007; Drösler et al. 2011; Elsgaard et al. 2012; Leiber-Sauheitl et al. 2013). Greenhouse gas emissions can stay high at such sites even when management intensity is moderated by nature conservancy measures (Best and Jacobs 1997; Schrier-Uijl et al. 2010; Hahn-Schöfl et al. 2011). Intensively-used peatlands are more common in lowlands than in uplands due to better accessibility and suitability for high-intensity agriculture. Burning peatland vegetation as a management practice in the UK may strongly affect carbon sequestration and dissolved organic matter export (Garnett et al. 2000; Clutterbuck and Yallop 2010; Yallop et al. 2010) although the evidence is not conclusive (cf. Worrall et al. 2007; Clay et al. 2009; Allen et al. 2013). It should be stressed that change in land use is the primary driver of changes in peatland hydrology and biogeochemistry, and probably has a stronger impact than climate change. However, some climate change effects will exacerbate the impact of human activities such as drainage, grazing, burning and peat mining (e.g. Petrescu et al. 2009).

On the other hand, land use-related effects on peatlands often make them more vulnerable to climate change impacts (e.g. Parish et al. 2008).

11.7 Inland Ecosystems and the Wider North Sea System

Inland ecosystems have important functions within the coupled land-ocean-atmosphere system of the North Sea region. Major functions of inland ecosystems are freshwater storage and transmission, carbon storage, carbon sequestration, greenhouse gas emission and the export of dissolved and particulate organic matter to aquatic systems. While forests in the North Sea region currently sequester carbon and act as greenhouse gas sinks (Ciais et al. 2008; Luyssaert et al. 2010), agricultural systems are greenhouse gas sources through CO_2 and N_2O emissions from soils and CH_4 emissions from enteric fermentation of livestock and manure management (Schulze et al. 2009). Greenhouse gas emissions from degraded and agriculturally-used peatlands are significant in several countries of the North Sea region when compared to their total national greenhouse gas emissions, with contributions of about 5 % in Germany and Denmark, 2–3 % in the Netherlands and about 1 % in the UK (Cannell et al. 1999; Van den Bos 2003; Drösler et al. 2008, 2011; Verhagen et al. 2009; Joosten 2010; Worrall et al. 2011; Nielsen et al. 2013). On the other hand, CO_2 uptake by the few remaining near-natural peatlands in the North Sea region is negligible compared to CO_2 release by degraded peatlands or CO_2 uptake by forests. This means that reducing emissions from reclaimed peatlands is more important than the possible contribution of natural peatland to carbon sequestration.

The export of dissolved and particulate organic matter from inland ecosystems has important effects on the biogeochemistry and ecology of the receiving aquatic systems (i.e. lakes, rivers, estuaries and the North Sea) and supplies them with inputs of carbon, nitrogen, phosphorus and other important nutrient elements (e.g. Evans et al. 2005). Because export of DOC and POC is controlled by many interacting factors (e.g. temperature, nutrient supply, precipitation, evapotranspiration, run-off), its future behaviour is difficult to predict. Run-off is projected to increase in the northern part of the North Sea region and to decrease in the south (Alcamo et al. 2007). However, due to the projected warming and higher frequency of heavy rain events in the North Sea region (Chap. 5), enhanced mobilisation of soil organic matter and transport of terrestrial DOC to the limnic ecosystems and the North Sea are likely. Dissolved organic matter affects ecosystem nutrient availability (Carpenter et al. 2005), acidification of limnic systems (Oliver et al.

1983) and solubility, transport and toxicity of heavy metals and organic pollutants (Carter and Suffet 1982; Pokrovsky et al. 2005). It also regulates the photochemistry of natural waters (Zafiriou et al. 1984) and influences aquatic production of algae and bacteria (Wetzel 1992; Carpenter and Pace 1997). The export of organic matter into limnic systems can affect human health adversely since these organic substances support bacterial proliferation and lead to the formation of carcinogens when they react with disinfectants (such as chlorine) during water treatment (Nokes et al. 1999; Sadiq and Rodriguez 2004). The magnitude of DOC fluxes in rivers correlates with organic matter storage in the soils of their catchments (e.g. Hope et al. 1997). Riverine organic matter is modified strongly and largely removed through mineralisation and sedimentation during transport in rivers and estuaries (e.g. Raymond and Bauer 2000; Wiegner and Seitzinger 2001; Abril et al. 2002; Raymond et al. 2013). Thomas et al. (2005) estimated that about one million tons of DOC and POC are transported into the North Sea by rivers each year. Only 10 % of the riverine input of organic carbon is probably buried in the shelf sediments (Hedges et al. 1997; Schlünz and Schneider 2000), with the rest incorporated in the food webs of coastal seas.

Flood risk mitigation is an important issue in coastal and fluvial lowlands bordering the North Sea, especially given the projected acceleration in sea-level rise in the future due to climate change (Chap. 5). Peat soil degradation causes land subsidence by a combination of peat oxidation and compaction after drainage (Schothorst 1977). Historical subsidence—caused by drainage since medieval times—often combined with peat extraction for fuel, in coastal peatlands of the Netherlands, Germany and eastern Britain may have resulted in up to several metres of subsidence (Godwin 1978; Borger 1992; Verhoeven 1992; Hoogland et al. 2012). In the eastern British fenlands, compaction and peat oxidation has resulted in up to 4 m of subsidence in 150 years (Godwin 1978). In Dutch managed peatlands, subsidence is ongoing at up to one centimetre per year (Hoogland et al. 2012, and references therein). Under a warmer climate, peat decomposition would be even faster, particularly in drained peatlands. This would increase flood risk, induce costs for creating and managing flood protection systems and ever deeper drainage, and threaten the economic viability of agriculture. Subsidence also influences peatland hydrology and hydrochemistry. The need for increasingly deeper drainage enhances the upwelling of sulphate-rich brackish or salt water (Hoogland et al. 2012). This in turn may enhance peat decomposition by sulphate reduction, with adverse impacts on water quality by increasing dissolved and particulate organic matter and nutrient mobilisation (Smolders et al. 2006). Replenishing surface water with alkaline river water in agriculturally managed peatlands in dry periods may have a similar effect on peat decomposition.

11.8 Summary

The expected future impacts of climate change on terrestrial ecosystems are summarised in Table 11.1.

Future climate change is likely to increase NPP in the North Sea region due to warmer conditions and longer growing seasons, at least if future climate change is moderate and summer precipitation does not decrease as strongly as projected in some of the more extreme climate scenarios. The physiological effects of increasing atmospheric CO_2 levels and increasing N-mineralisation in the soil may also play a significant role, but to an as yet uncertain extent.

The effects of total carbon storage in terrestrial ecosystems are highly uncertain, due to the inherent complexity of the processes involved. For example, water table effects in mires, large uncertainties in soil carbon modelling, the unknown fate of additional carbon taken up through CO_2 fertilisation, and other important drivers, such as changes in land use (e.g. forest harvest and wetland drainage). For moderate climate change, land use effects are often more important drivers of total ecosystem carbon accumulation than climate change.

Across a wide range of organism groups, range expansions to higher latitudes and altitudes, changes in phenology, and in the case of butterflies and birds, population increases in warm-adapted species and decreases in cold-adapted species have occurred in response to recent climate change. Regarding range expansions, some studies suggest substantial differences between organism groups; for example, herbaceous plants show only small or no responses while variability within other groups is large. Habitat specialists with restricted ranges have generally responded very little or even shown range contractions. Many of these often already threatened species could therefore be particularly vulnerable to climate change. Cold-adapted mountain top species are at particular risk because they have very limited habitat space in which to track climate change.

Overall effects of recent climate change on forest ecosystems within the region are limited, and major impacts on forest type distribution and forest functioning are unlikely if future warming is moderate and summer precipitation does not decrease as much as is projected in some of the more extreme climate scenarios. However, current models simulating potential impacts of climate change on forests rarely include a number of drivers of potentially rapid changes in forest functioning, such as forest pests and diseases (e.g. Kirilenko and Sedjo 2007; Jönsson et al. 2009). As a result, projections of climate-driven changes in future forest productivity, biomass and carbon storage are highly uncertain.

For grasslands, significant range expansion of thermophilous animal species (e.g. Parmesan et al. 1999), changes in flowering phenology (e.g. Fitter and Fitter 2002), and population increases (e.g. Poniatowski et al. 2012) are

Table 11.1 Climate change impacts on terrestrial ecosystems of the North Sea region

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Phenology			
Shift towards earlier spring and summer phases in plants	Spring events advanced on average by 6.3 days ✓✓✓	Further advancement depending on temperature increase ✓✓	Modified responses due to non-linear effects of further increasing temperatures early in the year
Shift towards later autumn phases in plants	Autumn events delayed by on average 4.5 days ✓	Further delay depending on temperature increase ✓	Limited data quality
Extension of growing period	Extension of growing season by about 20 days ✓	Further extension depending on temperature increase	Limited data quality
Earlier onset of reproduction in animals	Earlier onset of first spawning in amphibians by 10–20 days ✓✓✓; Advances of dates of first clutches in bird species by on average 8.8 days ✓✓	No studies	
Changed migratory patterns and behaviour	Advances in the arrival of migratory birds ✓✓✓; Shift in winter distribution of waterfowl and waders to the North-East ✓✓✓	No studies	
Biogeography and community structure			
Range shifts in vascular plants and cryptogams	Plants: range extensions lagging warming due to dispersal and/or habitat limitation ✓✓	Strongly limited range filling due to dispersal limitation in fragmented landscapes ✓✓	Impact of other abiotic factors (e.g. nutrients); Dispersal and recruitment limitation; Habitat limitation and landscape fragmentation; Changed biotic interactions (e.g. competition, herbivory, pathogens); Changing land-use and disturbance regimes; Impact of climate extremes
	Lichens: cold-adapted species declining and warm-adapted expanding their ranges northwards	Decline of cold-adapted species at the rear edge and at lower mountain elevations ✓	Poorly known phenotypic plasticity and evolutionary capacity
Range shifts in animals	Substantial range extension to the north in many mobile, generalist animal species ✓✓✓	Continuing range expansion to the north in mobile, generalist species ✓✓	Impact of other abiotic factors (e.g. nutrients); Dispersal and recruitment limitation; Habitat limitation and landscape fragmentation; Changed biotic interactions (e.g. competition, herbivory, pathogens); Changing land-use and disturbance regimes; Impact of climate extremes
	No or minor range extension or range contraction in many habitat specialists		
	Decline in some northern species in the south	Decline of cold-adapted species at the rear edge ✓	Poorly known phenotypic plasticity and evolutionary capacity

(continued)

Table 11.1 (continued)

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Changed composition in plant communities	Limited evidence for primarily climate-induced changes so far ✓	Relatively slow shifts in species composition	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
			Impact of climate extremes
			Poorly known phenotypic plasticity and evolutionary capacity
			Few studies, 'new' biotic interactions
Changed biome distribution	Upward shift of tree-line in the southern Scandes into arctic-alpine Tundra ecosystems ✓✓	Moderate shifts mostly in the northern part of the region between nemoral and boreal forests (spread of broadleaved trees) and boreal forests and arctic-alpine tundra (spread of shrubs and trees) ✓✓	Impact of other abiotic factors (e.g. nutrients)
			Dispersal and recruitment limitation
			Habitat limitation and landscape fragmentation
			Changed biotic interactions (e.g. competition, herbivory, pathogens)
			Changing land-use and disturbance regimes
			Impact of climate extremes
		Reduction of bioclimatologically suitable space for blanket bogs ✓	Poorly known phenotypic plasticity and evolutionary capacity
Biotic mismatch	Few well documented examples for birds and insects ✓	Increasing spatial mismatches between butterflies and host plants, particularly for those butterflies that are already constrained by specific host plants ✓	
Physiological tolerance and stress			
Tree stress and forest dieback	Limited evidence for drought stress in southern part of the region ✓	Increasing drought risk especially in the southern part of the region ✓	Ecological complexity and lack of process understanding
			Other abiotic factors
	Role of pests and pathogens still rather uncertain. ✓	Increasing risk of pathogens and pests ✓	Species-specific reactions and genetic variability within species

(continued)

Table 11.1 (continued)

Class of impact	Impact of recent climate change	Projected impact of future climate change	Uncertainties
Ecosystem functioning			
Net primary productivity and forest growth	Increased growing season length and NPP ✓✓✓	Further increase of NPP especially in the north of the region ✓✓	Impact of other drivers such as N-deposition and enhanced mineralisation, acidification and potential CO_2 'fertilisation'
		Mixed effects on NPP in the southern part of the region, depending on water supply ✓	Impacts of drought stress and disturbance events poorly captured in vegetation
	Increasing forest growth especially in northern regions and at sites without moisture limitation ✓✓✓	Increased NPP in mires and drained peatlands ✓	Tree species selection and forest management practices
Carbon sequestration capacity	Enhanced vegetation carbon fixation due to increased forest growth ✓✓	Northern areas remain net carbon sinks, southern areas may eventually turn into small to moderate sources ✓	Relative importance and interplay of raised soil respiration and NPP
			Feedbacks of changed hydrology on carbon exchange in wetlands
			Human alterations in land cover and land use
		Increased peat accumulation in mires, accelerated peat decay in drained peatlands ✓	Only one regional modelling study included total terrestrial carbon cycle
Greenhouse gas release from mineral and organic soils	Increased soil respiration and CH_4 release from hydrologically intact peatlands. ✓✓	Enhanced carbon release especially from desiccated peat soils and other humus-rich soils ✓✓	Unpredictable hydrological changes associated with climate warming
			Competing effects of climate change and other influences (atmospheric chemistry, land use)
	Increased C-release from desiccated and degraded peat soils, especially in the south ✓✓		Large uncertainties in soil carbon modelling
Lateral waterborne export fluxes of elements	Increased run-off in northern part, decreased run-off in the southern North Sea region ✓✓	Further enhanced mobilisation of DOC, especially from drained peatlands ✓✓	Unpredictable hydrological changes associated with climate warming
			Competing effects of climate change and other influences (atmospheric chemistry, land use)
	Increased export of DOC ✓		Large uncertainties in soil carbon modelling

✓✓✓ strong evidence; ✓✓ moderate evidence; ✓ minor evidence

currently more obvious signs of climate change, than changes in plant community composition and ecosystem processes. Even in experimental studies simulating drought and warming, responses to treatments were modest (Bates et al. 2005; Grime et al. 2008; Kreyling 2010). Evidence from observational and correlative studies is weak and speculative due to many confounding effects such as eutrophication and changes in management practice (e.g. Gaudnik et al. 2011; McGovern et al. 2011).

For heathlands, overall evidence for effects of recent climate change from experimental warming and drought treatments is also weak, variable and inconsistent, suggesting that now and in the near future, climate warming is of low significance compared to other predominant drivers of ecological change in heathland ecosystems such as eutrophication, acidification and altered management practices (e.g. Härdtle et al. 2006). For more extreme climate scenarios, however, substantial effects could be expected in heathlands. Projections of the exact nature of these future effects are highly uncertain.

The projected climatic changes for the North Sea region are likely to have significant impacts on abiotic and biotic processes in mires and drained peatlands. However, the consequences will vary widely between mires and drained peatlands. Higher temperatures and longer growing seasons will increase NPP, but also ecosystem respiration, CH_4 emission and DOC export in mires and drained peatlands. The net effect is expected to result in increased peat accumulation in mires but accelerating peat decay in drained peatlands. In mires, lower water tables due to less summer precipitation and/or higher evapotranspiration will enhance NPP but also—and to a much greater degree—ecosystem respiration, leading to a net loss of peat organic matter and the release of CO_2. On the other hand, CH_4 emission will also be reduced, while effects on DOC export are less clear. In drained peatlands, climatic changes will have less effect on the water budget and biogeochemical fluxes since water tables are regulated.

Low summer precipitation and/or high evapotranspiration can make conditions unsuitable for some mire types. However, well-developed natural mires may have considerable resilience to climate change. The status of peatlands, namely the level of drainage and soil degradation will determine whether peatlands mitigate or exacerbate climate change.

Besides their function as a sink for atmospheric carbon, the export of dissolved and particulate organic carbon and nutrients from terrestrial ecosystems is probably the most significant process directly affecting the North Sea system. Because this export is controlled by many interrelating factors (temperature, precipitation, evapotranspiration, run-off, human impact), its future development is very uncertain and therefore difficult to predict.

References

Abril G, Nogueira E, Hetcheber H, Cabec-adas G, Lemaire E, Brogueira MJ (2002) Behaviour of organic carbon in nine contrasting European estuaries. Estuar Coast Shelf Sci 54:241–262

Aerts R, de Caluwe H (1999) Nitrogen deposition effects on carbon dioxide and methane emissions from temperate peatland soils. Oikos 84:44–54

Aerts R, Ludwig F (1997) Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. Soil Biol Biochem 29:1691–1698

Aerts R, Wallen B, Malmer N (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J Ecol 80:131–140

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol 165:351–372

Alberto FJ, Aitken SN, Alia R, Gonzalez-Martinez SC, Hanninen H, Kremer A, Lefevre F, Lenormand T, Yeaman S, Whetten R, Savolainen O (2013) Potential for evolutionary responses to climate change evidence from tree populations. Glob Change Biol 19:1645–1661

Alcamo J, Flörke M, Märker M (2007) Future long-term changes in global water resources driven by socio-economic and climatic changes. Hydrol Sci J 52:247–275

Allen KA, Harris MPK, Marrs RH (2013) Matrix modelling of prescribed burning in *Calluna vulgaris*-dominated moorland: short burning rotations minimize carbon loss at increased wildfire frequencies. J Appl Ecol 50:614–624

Arp WJ, Van Mierlo JEM, Berendse F, Snijders W (1998) Interactions between elevated CO_2 concentration, nitrogen and water: effects on growth and water use of six perennial plant species. Plant Cell Environ 21:1–11

Bates JW, Thompson K, Grime JP (2005) Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. Glob Change Biol 11:757–769

Beebee TJC (1995) Amphibian breeding and climate. Nature 374:219–220

Beetz S, Liebersbach H, Glatzel S, Jurasinski G, Buczko U, Höper H (2013) Effects of land use intensity on the full greenhouse gas balance in an Atlantic peat bog. Biogeosciences 10:1067–1082

Bellamy PH, Loveland PJ, Bradley RI, Lark RM, Kirk GJD (2005) Carbon losses from all soils across England and Wales 1978-2003. Nature 437:245–248

Belyea LR, Malmer N (2004) Carbon sequestration in peatland: patterns and mechanisms in response to climate change. Glob Change Biol 10:1043–1052

Berendse F, Van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. Glob Change Biol 7:591–598

Berger S, Soehlke G, Walther GR, Pott R (2007) Bioclimatic limits and range shifts of cold-hardy evergreen broad-leaved species at their northern distributional limit in Europe. Phytocoenologia 37:523–539

Berry PM, Butt N (2002) CHIRP – Climate change impacts on raised bogs: a case study of Thorne Crowle, Goole and Hatfield Moors. English Nature Research Report No 457

Berry PM, Dawson TP, Harrison PA, Pearson RG (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. Glob Ecol Biogeogr 11:453–462

Bertrand R, Lenoir J, Piedallu C, Riofrio-Dillon G, de Ruffray P, Vidal C, Pierrat JC, Gegout JC (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature 479:517–520

Best EPH, Jacobs FHH (1997) The influence of raised water table levels on carbon dioxide and methane production in ditch-dissected peat grasslands in the Netherlands. Ecol Engineer 8:129–144

Betts RA, Boucher O, Collins M, Cox PM, Falloon PD, Gedney N, Hemming DL, Huntingford C, Jones CD, Sexton DMH, Webb MJ (2007) Projected increase in continental runoff due to plant responses to increasing carbon dioxide. Nature 448:1037–1041

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemuller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354

Billett MF, Palmer SM, Hope D, Deacon C, Storeton-West R, Hargreaves KJ, Flechard C, Fowler D (2004) Linking land-atmosphere-stream carbon fluxes in a lowland peatland system. Glob Biogeochem Cy 18:GB1024

Billett MF, Charman D, Clark JM, Evans CD, Evans MG, Ostle NG, Worrall F, Burden A, Dinsmore KJ, Jones T, McNamara NP, Parry L, Rowson JG, Rose R (2010) Carbon balance of UK peatlands: current state of knowledge and future research challenges. Climate Res 45:13–29

Blodau C (2002) Carbon cycling in peatlands: A review of processes and controls. Environ Rev 10:111–134

Bohn U, Neuhäusle R, Gollub G, Hettwer C, Neuhäuslová Z, Raus T, Schlüter H, Weber H (2003) Map of the natural vegetation of Europe. Landwirtschaftsverlag, Münster

Bohn TJ, Lettenmaier DP, Sathulur K, Bowling LC, Podest E, McDonald KC, Friborg T (2007) Methane emissions from western Siberian wetlands: heterogeneity and sensitivity to climate change. Env Res Lett 2:045015

Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution area of European beech - A review. Forestry 80:413–429

Bolte A, Ammer C, Löf M, Madsen P, Nabuurs GJ, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. Scand J Forest Res 24:473–482

Bolte A, Hilbrig L, Grundmann B, Kampf F, Brunet J, Roloff A (2010) Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. Eur J For Res 129:261–276

Borger GJ (1992) Draining, digging, dredging; the creation of a new landscape in the peat areas of the low countries. In: Verhoeven JTA (ed) Fens and Bogs in the Netherlands: Vegetation, history, nutrient dynamics and conservation. Kluwer

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in long-distance migrant bird. Nature 411:296–298

Both C, Artemyev AV, Blaauw B et al (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. P Roy Soc Lond B 271:1657–1662

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83

Both C, Van Asch M, Bijlsma RG, Van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations. J Anim Ecol 78:73–83

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. P Roy Soc B 277:1259–1266

Bower M (1960) The erosion of blanket peat in the southern Pennines. East Midland. Geographer 13:22–33

Bower MM (1961) The distribution of erosion in blanket peat bogs in the Pennines. Trans Inst Brit Geogr 29:17–30

Bowman WD, Cleveland CC, Halada L, Hresko J, Baron JS (2008) Negative impact of nitrogen deposition on soil buffering capacity. Nat Geosci 1:767–770

Bragazza L (2008) A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. Glob Change Biol 14:2688–2695

Bragazza L, Freeman C, Jones T, Rydin H, Limpens J, Fenner N, Ellis T, Gerdol R, Hajek M, Hajek T, Iacumin P, Kutnar L, Tahvanainen T, Toberman H (2006) Atmospheric nitrogen deposition promotes carbon loss from peat bogs. PNAS 103:19386–19389

Bragg OM (2002) Hydrology of peat-forming wetlands in Scotland. Sci Tot Environ 294:111–129

Breeuwer A, Robroek BJ, Limpens J, Heijmans MM, Schouten MG, Berendse F (2009) Decreased summer water table depth affects peatland vegetation. Basic Appl Ecol 10:330–339

Breeuwer A, Heijmans MMPD, Robroek BJM, Berendse F (2010) Field simulation of global change: transplanting northern bog mesocosms southward. Ecosystems 13:712–726

Bridgham SD, Pastor J, Updegraff K, Malterer TJ, Johnson K, Harth C, Chen J (1999) Ecosystem control over temperature and energy flux in northern peatlands. Ecol Appl 9:1345–1358

Broadmeadow MSJ, Ray D, Samuel CJA (2005) Climate change and the future for broadleaved tree species in Britain. Forestry 78:145–161

Buckland SM, Grime JP, Hodgson JG, Thompson K (1997) A comparison of plant responses to the extreme drought of 1995 in Northern England. J Ecol 85:875–882

Buckland SM, Thompson K, Hodgson JG, Grime JP (2001) Grassland invasions: effects of manipulations of climate and management. J Appl Ecol 38:301–309

Bullock JM, Jefferson RG, Blackstock TH, Pakeman RJ, Emmett BA, Pywell RF, Grime JP, Silvertown J (2011) Semi-natural grasslands. The UK National Ecosystem Assessment Technical Report. UNEP-WCMC, Cambridge

Bullock JM, White SM, Prudhomme C, Tansey C, Perea R, Hooftman DAP (2012) Modelling spread of British wind-dispersed plants under future wind speeds in a changing climate. J Ecol 100:104–115

Cannell MGR, Milne R, Hargreaves KJ, Brown TAW, Cruickshank MM, Bradley RI, Spencer T, Hope D, Billett MF, Adger WN, Subak S (1999) National inventories of terrestrial carbon sources and sinks: the UK experience. Climatic Change 42:505–530

Carpenter SR, Pace ML (1997) Dystrophy and eutrophy in lake ecosystems: implications of fluctuating inputs. Oikos 78:3–14

Carpenter SR, Cole JJ, Pace ML, Van de Bogert M, Bade DL, Bastviken D, Gille CM, Hodgson JR, Kitchell JF, Kritzberg ES (2005) Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. Ecology 86:2737–2750

Carroll EA, Sparks TH, Collinson N, Beebee TJC (2009) Influence of temperature on the spatial distribution of first spawning dates of the common frog (Rana temporaria) in the UK. Glob Change Biol 15:467–473

Carter CW, Suffet IH (1982) Binding of DDT to dissolved humic materials. Environ Sci Technol 16:735–740

Charman DJ, Beilman DW, Blaauw M et al (2013) Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences 10:929–944

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Christensen JH, Carter TR, Rummukainen M, Amanatidis G (2007) Evaluating the performance and utility of regional climate models: the PRUDENCE project. Climatic Change 81:1–6

Ciais P, Schelhaas MJ, Zaehle S, Piao SL, Cescatti A, Liski J, Luyssaert S, Le-Maire G, Schulze ED, Bouriaud O, Freibauer A, Valentini R, Nabuurs GJ (2008) Carbon accumulation in European forests. Nat Geosci 1:425–429

Clark J, Gallego-Sala AV, Allott TEH, Chapman SJ, Farewell T, Freeman C, House JI, Orr HG, Prentice IC, Smith P (2010) Assessing the vulnerability of blanket peat to climate change using an ensemble of statistical bioclimatic envelope models. Climate Res 45:131–150

Clay GD, Worrall F, Fraser ED (2009) Effects of managed burning upon dissolved organic carbon (DOC) in soil water and runoff water following a managed burn of a UK blanket bog. J Hydrol 367:41–51

Clutterbuck B, Yallop AR (2010) Land management as a factor controlling dissolved organic carbon releases from upland peat soils 2: changes in DOC productivity over four decades. Sci Tot Environ 408:6179–6191

Clymo RS (1984) The limits to peat bog growth. P Trans Roy Soc B 303:605–654

Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichefet T, Friedlingstein P, Gao X, Gutowski WJ, Johns T, Krinner G, Shongwe M, Tebaldi C, Weaver AJ, Wehner M (2013) Long-term climate change: Projections, commitments and irreversibility. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Doschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp 1029-1136

Cotton PA (2003) Avian migration phenology and global climate change. Proc Nat Acad Sci USA 100:12219–12222

Couwenberg J (2011) Greenhouse gas emissions from managed peat soils: is the IPCC reporting guidance realistic? Mires and Peat 8:1–10

Crawford RMM (2000) Tansley Review No. 114: Ecological hazards of oceanic environments. New Phytol 147:257–281

Crawford RMM, Jeffree CE, Rees WG (2003) Paludification and forest retreat in northern oceanic environments. Ann Bot 91:213–226

Crick HQ, Dudley C, Glue DE (1997) UK birds are laying eggs earlier. Nature 388:526

Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science 331:324–327

Dacey JWH, Drake BG, Klug MJ (1994) Stimulation of methane emission by carbon dioxide enrichment of marsh vegetation. Nature 370:47–49

Daulat WE, Clymo RS (1998) Effects of temperature and water table on the efflux of methane from peatland surface cores. Atmos Environ 32:3207–3218

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Davies GM, Gray A, Rein G, Legg CJ (2013). Peat consumption and carbon loss due to smouldering wildfire in a temperate peatland. Forest Ecol Manage 308:169–177

De Vries F, Hendriks RFA, Kemmers RH, Wolleswinkel R (2008) Het veen verdwijnt uit Drenthe. Omvang, oorzaken en gevolgen. Alterra-rapport 1661. Alterra, Wageningen (in Dutch)

Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliola J, Herrando S, Julliard R, Kuussaari M, Lindstrom A, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C, Vermouzek Z, WallisDeVries M, Wynhoff I, Jiguet F (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nat Clim Change 2:121–124

Dinsmore KJ, Billett MF, Skiba UM, Rees RM, Drewer J, Helfter C (2010) Role of the aquatic pathway in the carbon and greenhouse gas budgets of a peatland catchment. Glob Change Biol 16:2750–2762

Dirks BOM, Hensen A, Goudriaan J (2000) Effect of drainage on CO_2 exchange patterns in an intensively managed peat pasture. Climate Res 14:57–63

Dise NB (2009) Peatland response to global change. Science 326:810–811

Dise NB, Verry ES (2001) Suppression of peatland methane emission by cumulative sulfate deposition in simulated acid rain. Biogeochemistry 53:143–160

Doswald N, Willis SG, Collingham YC, Pain DJ, Green RE, Huntley B (2009) Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European Sylvia warblers. J Biogeogr 36:1194–1208

Doxford SW, Freckleton RP (2012) Changes in the large-scale distribution of plants: extinction, colonisation and the effects of climate. J Ecol 100:519–529

Drösler M, Freibauer A, ChristensenT, Friborg T (2008) Observation and status of peatland greenhouse gas emission in Europe. In: Dolman H, Valentini R, Freibauer A (eds) The Continental-Scale Greenhouse Gas Balance of Europe. Ecological Studies 203. Springer

Drösler M, Freibauer A, Adelmann W et al (2011) Klimaschutz durch Moorschutz in der Praxis. Schlussbericht des BMBF-Verbundprojekts „Klimaschutz - Moornutzungsstrategien 2006-2010. Arbeitsberichte aus dem Thünen-Institut für Agrarklimaschutz. Eigenverlag des vTi, Braunschweig

Drösler M, Schaller L, Kantelhardt J, Schweiger M, Fuchs D, Tiemeyer B, Augustin J, Wehrhan M, Förster C, Bergmann L, Kapfer A, Krüger GM (2012) Beitrag von Moorschutz- und Revitalisierungsmaßnahmen zum Klimaschutz am Beispiel von Naturschutzgroßprojekten. Natur Landsch 87:70–76

Dunfield P, Dumont R, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol Biochem 25:321–326

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen, 6th edn. Ulmer

Elsgaard L, Görres CM, Hoffmann CC, Blicher-Mathiesen G, Schelde K, Petersen SO (2012) Net ecosystem exchange of CO_2

and carbon balance for eight temperate organic soils under agricultural management. Agr Ecosyst Environ 162:52–67

Emmett BA, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Peñuelas J, Schmidt I, Sowerby A (2004) The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. Ecosystems 7:625–637

Enquist F (1924) Sambandet mellan klimat och växtgränser. Geol Fören Förhandl 46:202–213

Erlandsson M, Buffam I, Folster J, Laudon H, Temnerud J, Weyhenmeyer GA, Bishop K (2008) Thirty-five years of synchrony in the organic matter concentrations of Swedish rivers explained by variation in flow and sulphate. Glob Change Biol 14:1191–1198

EUROSTAT (2014) CORINE land cover types 2006, www.eea.europa.eu/data-and-maps/figures/corine-land-cover-types-2006. Accessed 24.4.2014

EUROSTAT (2015) Land cover/use statistics (LUCAS), Statistics illustrated, Land over overview2012. http://ec.europa.eu/eurostat/web/lucas/statistics-illustrated. Accessed 10.3.2015

Evans M, Warburton J (2010) Geomorphology of Upland Peat: Erosion, form and landscape change. Wiley and Sons

Evans CD, Monteith DT, Cooper DM (2005) Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. Environ Poll 137:55–71

Evans CD, Chapman PJ, Clark JM, Monteith DT, Cresser MS (2006a) Alternative explanations for rising dissolved organic carbon export from organic soils. Glob Change Biol 12:2044–2053

Evans M, Warburton J, Yang J (2006b) Eroding blanket peat catchments: Global and local implications of upland organic sediment budgets. Geomorphology 79:45–57

Evans CD, Freeman C, Cork LG, Thomas DN, Reynolds B, Billett MF, Garnett MH, Norris D (2007) Evidence against recent climate-induced destabilisation of soil carbon from ^{14}C analysis of riverine dissolved organic matter. Geophys Res Lett 34:L07407

Fenner N, Ostle NJ, McNamara N, Sparks T, Harmens H, Reynolds B, Freeman C (2007) Elevated CO_2 effects on peatland plant community carbon dynamics and DOC production. Ecosystems 10:635–647

Finkelstein SA, Cowling SA (2011) Wetlands, temperature, and atmospheric CO_2 and CH_4 coupling over the past two millennia. Glob Biogeochem Cy 25:GB1002

Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME, Ledford J, Liberloo M, Oren R, Polle A, Pritchard S, Zak DR, Schlesinger WH, Ceulemans R (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. Proc Nat Acad Sci USA 104:14014–14019

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science 296:1689–1691

Francis IS (1990) Blanket peat erosion in a mid-Wales catchment during two drought years. Earth Surf Proc Land 15:445–456

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412:785

Freeman C, Fenner N, Ostle NJ, Kang H, Dowrick DJ, Reynolds B, Lock MA, Sleep D, Hughes S, Hudson J (2004) Dissolved organic carbon export from peatlands under elevated carbon dioxide levels. Nature 430:195–198

Fridley JD, Grime JP, Askew AP, Moser B, Stevens CJ (2011) Soil heterogeneity buffers community response to climate change in species-rich grassland. Glob Change Biol 17:2002–2011

Friedrichs DA, Buntgen U, Frank DC, Esper J, Neuwirth B, Löffler J (2009) Complex climate controls on 20th century oak growth in Central-West Germany. Tree Phys 29:39–51

Frolking S, Roulet NT (2007) Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Glob Change Biol 13:1079–1088

Gaillard MJ, Sugita S, Mazier F, Kaplan JO, Trondman AK, Broström A, Hickler T, Kjellström E, Kuneš P, Lemmen C, Olofsson J, Smith B, Strandberg G (2010) Holocene land-cover reconstructions for studies on land cover-climate feedbacks. Clim Past Discuss 6:307–346

Gallego-Sala AV, Prentice IC (2013) Blanket peat biome endangered by climate change. Nat Clim Change 3:152–155

Gallego-Sala A, Clark J, House J, Orr H, Prentice IC, Smith P, Farewell T, Chapman S (2010) Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. Clim Res 45:151-162

Garnett MH, Ineson P, Stevenson AC (2000) Effects of burning and grazing on carbon sequestration in a Pennine blanket bog, UK. Holocene 10:729–736

Gaudnik C, Corcket E, Clément B, Delmas CEL, Gombert-Courvoisier S, Muller S, Stevens CJ, Alard D (2011) Detecting the footprint of changing atmospheric nitrogen deposition loads on acid grasslands in the context of climate change. Glob Change Biol 17:3351–3365

Gerdol R, Bonora A, Gualandri R, Pancaldi S (1996) CO_2 exchange, photosynthetic pigment composition, and cell ultrastructure of Sphagnum mosses during dehydration and subsequent rehydration. Can J Botany 74:726–734

Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch S (2004) Terrestrial vegetation and water balance– Hydrological evaluation of adynamic global vegetation model. J. Hydrol 286:249– 270

Godwin H (1978) Fenland: Its Ancient Past and Uncertain Future. Cambridge University Press

Goldberg SD, Knorr KH, Blodau C, Lischeid G, Gebauer G (2010) Impact of altering the water table height of an acidic fen on N_2O and NO fluxes and soil concentrations. Glob Change Biol 16:220–233

Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kielty JP (2000) The response of two contrasting limestone grasslands to simulated climate change. Science 289:762–765

Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. Proc Nat Acad Sci USA 105:10028–10032

Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: A meta analysis. Glob Change Biol 8:345–360

Hahn-Schöfl M, Zak D, Minke M, Gelbrecht J, Augustin J, Freibauer A (2011) Organic sediment formed during inundation of a degraded fen grassland emits large fluxes of CH_4 and CO_2. Biogeosciences 8:1539–1550

Hanewinkel M, Cullmann DA, Schelhaas MJ, Nabuurs GJ, Zimmermann NE (2013). Climate change may cause severe loss in the economic value of European forest land. Nat Clim Change 3:203–207

Härdtle W, Niemeyer M, Niemeyer T, Aßmann T, Fottner S (2006) Can management compensate for atmospheric nutrient deposition in heathland ecosystems? J Appl Ecol 43:759–769

Härdtle W, Niemeyer T, Aßmann T, Aulinger A, Fichtner A, Lang AC, Leuschner C, Neuwirth B, Pfister L, Quante M, Ries C, Schuldt A, Oheimb G (2013) Climatic responses of tree-ring width and δ^{13}C signatures of sessile oak (Quercus petraea Liebl.) on soils with contrasting water supply. Plant Ecol 214:1147–1156

Hargreaves KJ, Fowler D (1998) Quantifying the effects of water table and soil temperature on the emission of methane from peat wetland at the field scale. Atmos Environ 32:3275–3282

Hauck M (2009) Global warming and alternative causes of decline in arctic-alpine and boreal-montane lichens in north-western Central Europe. Glob Change Biol 15:2653–2661

Hedges JI, Keil RG, Benner R (1997) What happens to terrestrial organic matter in the ocean? Org Geochem 27:195–212

Heijmans MMPD, Mauquoy D, van Geel B, Berendse F (2008) Long-term effects of climate change on vegetation and carbon dynamics in peat bogs. J Veg Sci 19:307–320

Hemery GE (2008) Forest management and silvicultural responses to projected climate change impacts on European broadleaved trees and forests. Int For Rev 10:591–607

Hemery GE, Clark JR, Aldinger E, Claessens H, Malvolti ME, O'Connor E, Raftoyannis Y, Savill PS, Brus R (2010) Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. Forestry 83:65–81

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Glob Chang Biol 12:450–455

Hickler T, Vohland K, Feehan J, Miller P, Fronzek S, Giesecke T, Kuehn I, Carter T, Smith B, Sykes M, (2012) Projecting tree species-based climate-driven changes in European potential natural vegetation with a generalized dynamic vegetation model. Glob Ecol Biogeogr 21:50–63

Hickler T, Rammig A, Werner C (2015) Modelling CO_2 impacts on forest productivity. Curr Forestry Rep I:69–80

Hill JK, Thomas CD, Huntley B (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proc Roy Soc Lond B 266:1197–1206

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. Proc Roy Soc Lond B 269:2163–2172

Hochkirch A, Damerau M (2009) Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. Biol J Linnean Soc 97:118–127

Holden J (2005) Peatland hydrology and carbon release: why small-scale process matters. P Trans Roy Soc B 363:2891–2913

Holden J, Shotbolt L, Bonn A, Burt TP, Chapman PJ, Dougill AJ, Fraser EDG, Hubacek K, Irvine B, Kirkby MJ, Reed MS, Prell C, Stagl S, Stringer LC, Turner A, Worrall F (2007) Environmental change in moorland landscapes. Earth Sci Rev 82:75–100

Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecol Lett 5:525–530

Hoogland T, van den Akker JJH, Brus DJ (2012) Modeling the subsidence of peat soils in the Dutch coastal area. Geoderma 171-172:92–97

Hope D, Billett MF, Cresser MS (1997) Exports of organic carbon in two river systems in NE Scotland. J Hydrol 193:61–82

Horswill P, O'Sullivan O, Phoenix GK, Lee JA, Leake JR (2008) Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. Environ Poll 155:336–349

Hulme PE (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? J Appl Ecol 42:784–794

Huntley B, Collingham YC, Willis SG, Green RE (2008) Potential impacts of climatic change on European breeding birds. PLOS ONE 3,1:e1439. doi:10.1371/journal.pone.0001439

Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. P Roy Soc Lond B 270:233–240

Hutchin PR, Press MC, Lee JA Ashenden TW (1995) Elevated concentrations of CO_2 may double methane emissions from mires. Glob Change Biol 1:125–128

Isaac-Renton MG, Roberts DR, Hamann A, Spiecker H (2014) Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. Glob Change Biol 20:2607–2617

Ise T, Dunn AL, Wofsy SC, Moorcroft PR (2008) High sensitivity of peat decomposition to climate change through watertable feedback. Nat Geosci 1:763–766

Iversen J (1944) Viscum, Hedera and Ilex as climatic indicators. A contribution to the study of past-glacial temperature climate. Geol Fören Förhandl 66:463–483

Jacob D, Petersen J, Eggert B, Alias A, Christensen O, Bouwer L, Braun A, Colette A, Déqué M, Georgievski G, Georgopoulou E, Gobiet A, Menut L, Nikulin G, Haensler A, Hempelmann N, Jones C, Keuler K, Kovats S, Kröner N, Kotlarski S, Kriegsmann A, Martin E, Meijgaard E, Moseley C, Pfeifer S, Preuschmann S, Radermacher C, Radtke K, Rechid D, Rounsevell M, Samuelsson P, Somot S, Soussana J-F, Teichmann C, Valentini R, Vautard R, Weber B, Yiou P (2014) EURO-CORDEX: new high-resolution climate change projections for European impact research. Reg Environ Change 14:563–578

Janssens IA, Freibauer A, Ciais P, Smith P, Nabuurs G-J, Folberth G, Schlamadinger B, Hutjes RWA, Ceulemans R, Schulze E-D, Valentini R, Dolman AJ (2003) Europe's terrestrial biosphere absorbs 7 to 12 % of European Anthropogenic CO_2 emissions. Science 300:1538–1542

Janssens IA, Freibauer A, Schlamadinger B, Ceulemans R, Ciais P, Dolman AJ, Heimann M, Nabuurs GJ, Smith P, Valentini R, Schulze E-D (2005) The carbon budget of terrestrial ecosystems at country-scale. A European case study. Biogeosciences 2:15–27

Jensen K, Beier C, Michelsen A, Emmett BA (2003) Effects of experimental drought on microbial processes in two temperate heathlands at contrasting water conditions. Appl Soil Ecol 24:165–176

Joabsson A, Christensen TR, Wallén B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol Evol 14:385–388

Jönsson AM, Appelberg G, Harding S, Bärring L (2009) Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, Ips typographus. Glob Change Biol 15:486–499

Joosten H (2010) The Global Peatland CO_2 Picture: Peatland status and drainage related emissions in all countries of the world. Wetlands International

Joosten H, Clarke D (2002) Wise use of peatlands. International Mire Conservation Group, International Peat Society, Jyväskylä, Finland

Joosten H, Tapio-Biström ML, Tol S (2012) Peatlands-guidance for climate change mitigation through conservation, rehabilitation and sustainable use. UN Food and Agriculture Organization, and Wetlands International

Kapfer J, Grytnes J-A, Gunnarson U, Birks JB (2011) Fine-scale changes in vegetation composition in a boreal mire over 50 years. J Ecol 99:1179–1189

Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. Quat Sci Rev 28:3016–3034

Kellner E (2001) Surface energy fluxes and control of evapotranspiration from a Swedish Sphagnum mire. Agr Forest Meteorol 110:101–123

King D, Daroussin J, Tavernier R (1994) Development of a soil geographical database from the soil map of the European Communities. Catena 21:37–56

King D, Jones RJA, Thomasson AJ (1995) European Land Information Systems for Agroenvironmental Monitoring. EUR 16232 EN, Office for Official Publications of the European Communities

Kirilenko AP, Sedjo RA (2007) Climate change and food security special feature: Climate change impacts on forestry. Proc Nat Acad Sci USA 104:19697–19702

Köhl M, Hildebrandt R, Olschofksy K, Köhler R, Rötzer T, Mette T, Pretzsch H, Köthke M, Dieter M, Abiy M, Makeschin F, Kenter B (2010) Combating the effects of climatic change on forests by

mitigation strategies. Carbon Bal Manage 5:doi:10.1186/1750-0680-5-8

Körner C, Asshoff R, Bignucolo O, Hattenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362

Körner C, Morgan JA, Norby R (2007) CO_2 fertilisation: when, where, how much? In: Canadell SG, Pataki DE, Pitelka LF (eds) Terrestrial Ecosystems in a Changing World. Springer

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, Sykes MT, de Winter W (2010) Modelling exploration of the future of European beech (Fagus sylvatica L.) under climate change – range, abundance, genetic diversity and adaptive response. Forest Ecol Manag 259:2213–2222

Kreyling J (2010) Winter climate change: a critical factor for temperate vegetation performance. Ecology 91:1939–1948

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. J Ecol 90:68–77

Lafleur PM, Moore TR, Roulet NT, Frolking S (2005) Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. Ecosystems 8:619–629

Laine A, Wilson D, Kiely G, Byrne KA (2007) Methane flux dynamics in an Irish lowland blanket bog. Plant Soil 299:181–193

Laine AM, Byrne KA, Kiely G, Tuittila ES (2009) The short-term effect of altered water level on carbon dioxide and methane fluxes in a blanket bog. Suo 60:65–83

Le Mer J, Roger P (2001) Production, oxidation, emission and consumption of methane by soils: a review. Eur J Soil Biol 37:25–50

Lebourgeois F, Cousseau G, Ducos Y (2004) Climate–tree growth relationships of Quercus petraea Mill. stand in the Forest of Berce ('Futaie des Clos', Sarthe, France). Ann For Sci 61:361–372

Lebourgeois F, Breda N, Ulrich E, Granier A (2005) Climate–tree-growth relationships of European beech (Fagus sylvatica L.) in the French permanent plot network (RENECOFOR). Trees Struct Funct 19:385–401

Lehikoinen A, Jaatinen K, Vähätalo AV, Clausen P, Crowe O, Deceuninck B, Hearn R, Holt CA, Hornman M, Keller V, Nilsson L, Langendoen T, Tománková I, Wahl J, Fox AD (2013) Rapid climate driven shifts in wintering distributions of three common waterbird species. Glob Change Biol 19:2071–2081

Leiber-Sauheitl K, Fuß R, Voigt C, Freibauer A (2013) High greenhouse gas fluxes from grassland on histic gleysol along soil carbon and drainage gradients. Biogeosci Discuss 10:11283–11317

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

Leuzinger S, Bader M (2012) Experimental versus modelled water use in mature Norway spruce (Picea abies) exposed to elevated CO_2. Front Plant Sci 3:229. doi:10.3389/fpls.2012.00229

Leuschner C, Backes K, Hertel D, Schipka F, Schmitt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive Fagus sylvatica L. and Quercus petraea (Matt.) Liebl. trees in dry and wet years. Forest Ecol Manag 149:33–46

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

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolstrom M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecol Manage 259:698–709

Lindsay R (2010) Peatbogs and Carbon: A critical synthesis. RSPB Scotland

Loisel J, Gallego-Sala AV, Yu Z (2012) Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. Biogeosciences 9:2737–2746

Lükewille A, Wright R (1997) Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. Glob Change Biol 3:13–21

Luyssaert S, Ciais P, Piao SL, Schulze ED, Jung M, Zaehle S, Janssens IA et al (2010) The European carbon balance. Part 3: forests. Glob Change Biol 16:1429–1450

Maclean IMD, Austin GE, Rehfisch MM, Blew J, Crowe O, Delany S, Devos K, Deceuninck B, Günther K, Laursen K, Van Roomen M, Wahl J (2008) Climate change causes rapid changes in the distribution and site abundance of birds in winter. Glob Change Biol 14:2489–2500

Malmer N, Svensson BM, Wallén B (1994) Interactions between Sphagnum mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot Phytotx 29:483–496

Martikainen PJ, Nykänen H, Crill P, Silvola J (1993) Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366:51–53

McCarthy HR, Oren R, Finzi AC, Johnsen KH (2006) Canopy leaf area constrains CO_2-induced enhancement of productivity and partitioning among aboveground carbon pools. Proc Nat Acad Sci USA 103:19356–19361

McGovern S, Evans CD, Dennis P, Walmsley C, McDonald MA (2011) Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. J Veg Sci 22:346–356

Meier IC, Leuschner C (2008) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob Change Biol 14:2081–2095

Melillo JM, Butler S, Johnson J, Mohan J, Steudler P, Lux H, Burrows E, Bowles F, Smith R, Scott L, Vario C, Hill T, Burton A, Zhou YM, Tang J (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. Proc Nat Acad Sci USA 108:9508–9512

Melton JR, Wania R, Hodson EL, Poulter B, Ringeval B, Spahni R, Bohn T, Avis CA, Beerling DJ, Chen G, Eliseev AV, Denisov SN, Hopcroft PO, Lettenmaier DP, Riley WJ, Singarayer JS, Subin ZM, Tian H, Zürcher S, Brovkin V, van Bodegom PM, Kleinen T, Yu ZC, Kaplan JO (2013) Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP). Biogeosciences 10:753–788

Meng L, Hess PGM, Mahowald NM, Yavitt JB, Riley WJ, Subin ZM, Lawrence DM, Swenson SC, Jauhiainen J, Fuka DR (2012) Sensitivity of wetland methane emissions to model assumptions: application and model testing against site observations. Biogeosciences 9:2793–2819

Menzel A (2000) Trends in phenological phases in Europe between 1951 and 1996. Int J Biometeorol 44:76–81

Menzel A, Fabian P (1999) Growing season extended in Europe. Nature 397:659

Menzel A, Estrella N, Fabian P (2001) Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. Glob Change Biol 7:657–666

Menzel A, Sparks TH, Estrella N et al (2006) European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969–1976

Merian P, Bontemps JD, Berge's L, Lebourgeois F (2011) Spatial variation and temporal instability in growth–climate relationships of sessile oak (Quercus petraea [Matt.] Liebl.) under temperate conditions. Plant Ecol 212:1855–1871

Meusel H, Jäger E, Weinert E (1965) Vergleichende Chorologie der zentraleuropäischen Flora. Jena: Fischer

Mikkelä C, Sundh I, Svensson BH, Nilsson M (1995) Diurnal variation in methane emission in relation to the water table, soil temperature, climate and vegetation cover in a Swedish acid mire. Biogeochemistry 28:93–114

Mitchell TD, Carter TR, Jones PD, Hulme M, New M (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Tyndall Centre Working Papers 55, July 2004 www.tyndall.ac.uk/publications/working_papers/wp55.pdf

Mölder I, Leuschner C, Leuschner HH (2011) $\delta^{13}C$ signature of tree rings and radial increment of *Fagus sylvatica* trees as dependent on tree neighbourhood and climate. Trees Struct Funct 25:215–229

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. P Natl Acad Sci USA 105:16195–16200

Montanarella L, Jones RJ, Hiederer R (2006) The distribution of peatland in Europe. Mires and Peat vol 1,1

Monteith DT, Stoddard JL, Evans CD, de Wit HA, Forsius M, Høgasen T, Wilander A, Skjelkvale BL, Jeffries DS, Vuorenmaa J, Keller B, Kopacek J, Vesely J (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450:537–541

Montoya JM, Raffaelli D (2010) Climate change, biotic interactions and ecosystem services. P Trans Roy Soc B 365:2013–2018

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J Soil Sci 44:651–664

Moore PA, Pypker TG, Waddington JM (2013) Effect of long-term water table manipulation on peatland evapotranspiration. Agr Forest Meteorol 178–179:106–119

Morales P, Hickler T, Smith B, Sykes MT, Rowell DP (2007) Changes in European ecosystem productivity and carbon balance driven by regional climate model outputs. Glob Change Biol 13:108–122

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW, Shaw MR (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140:11–25

Moser B, Fridley JD, Askew AP, Grime JP (2011) Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. J Ecol 99:1229–1236

Nabuurs GJ, Schelhaas MJ, Mohren GMJ, Field CB (2003) Temporal evolution of the European forest sector carbon sink from 1950 to 1999. Glob Change Biol 9:152–160

Nakićenović N, Swart R (eds) (2000) Special report on emission scenarios. A special report of working group III of the Intergovernmental Panel on Climate Change. Cambridge University Press

Nielsen OK, Plejdrup MS, Winther M et al (2013) Denmark's National Inventory Report 2013. Scientific Report from DCE No. 56. Aarhus University, Danish Centre for Environment and Energy, Denmark

Nokes CJ, Fenton E, Randall CJ (1999) Modelling the formation of brominated trihalomethanes in chlorinated drinking waters. Wat Res 33:3557–3568

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. Proc Nat Acad Sci USA 107:19368–19373

Normand S, Ricklefs RE, Skov F, Bladt J, Tackenberg O, Svenning JC (2011) Postglacial migration supplements climate in determining plant species ranges in Europe. Proc Roy Soc B 278:3644–3653

Nykänen H, Alm J, Silvola J, Tolonen K, Martikainen PJ (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Glob Biogeochem Cy 12:53–69

Oleszczuk R, Regina K, Szajdak L, Höper H, Marygnova V (2008) Impacts of agricultural utilization of peat soils on the greenhouse gas balance. Peatlands and climate change. 70. International Peat Society, Jyväskylä, Finland

Oliveira PJC, Davin EL, Levis S, Seneviratne SI (2011) Vegetation-mediated impacts of trends in global radiation on land hydrology: a global sensitivity study. Glob Change Biol 17:453–3467

Oliver B, Thurman E, Malcolm R (1983) The contribution of humic substances to the acidity of colored natural waters. Geochim Cosmochim Ac 47:2031–2035

Oliver TH, Thomas CD, Hill JK, Brereton T, Roy DB (2012) Habitat associations of thermophilous butterflies are reduced despite climatic warming. Glob Change Biol 18:2720–2729

Parish F, Sirin A, Charman D, Joosten H, Minayeva T, Silvius M, Stringer L (eds) (2008) Assessment on Peatlands, Biodiversity and Climate Change: Main Report. Global Environment Centre, Kuala Lumpur and Wetlands International, Wageningen

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. In: Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

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

Peichl M, Sagerfors J, Lindroth A, Buffam I, Grelle A, Klemedtsson L, Laudon H, Nilsson MB (2013) Energy exchange and water budget partitioning in a boreal minerogenic mire. J Geophys Res Biogeo 118:1–13

Peñuelas J, Gordon C, Llorens L, Nielsen T, Tietema A, Beier C, Bruna P, Emmett BA, Estiarte M, Gorissen A (2004) Non-intrusive field experiments show different plant responses to warming and drought among sites, seasons and species in a North–South European gradient. Ecosystems 7:598–612

Peñuelas P, Prieto P, Beier C et al (2007) Responses of shrubland species richness and primary productivity to six-years experimental warming and drought in a North–South European gradient: reductions in primary productivity in the hot and dry 2003. Glob Change Biol 13:2563–2581

Petrescu AMR, van Huissteden J, de Vries F, Bregman EPH, Scheper A (2009) Assessing CH_4 and CO_2 emissions from wetlands in the Drenthe Province, the Netherlands: a modelling approach. Neth J Geosci 88:101–116

Pokrovsky O, Dupré B, Schott J (2005) Fe-Al-organic colloids control of trace elements in peat soil solutions: Results of ultrafiltration and dialysis. Aquat Geochem 11:241–278

Pompe S, Hanspach J, Badeck F, Klotz S, Thuiller W, Kühn I (2008) Climate and land use change impacts on plant distributions in Germany. Biol Lett 4:564–567

Poniatowski D, Fartmann T (2011) Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. Agr Ecosyst Environ 145:5–9

Poniatowski D, Heinze S, Fartmann T (2012) The role of macropters during range expansion of a wing-dimorphic insect species. Evol Ecol 26:759–770

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Pretzsch H, Dursky J (2002) Growth reaction of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus silvatica* L.) to

possible climatic changes in Germany: a sensitivity study. Forstwiss Cbl 121:145–154

Raymond PA, Bauer JE (2000) Bacterial consumption of DOC during transport through a temperate estuary. Aquat Microb Ecol 22:1–12

Raymond PA, Hartmann J, Lauerwald R, Sobek S, McDonald C, Hoover M, Guth P et al (2013) Global carbon dioxide emissions from inland waters. Nature 503:355–359

Regina K, Nykänen H, Silvola J, Martikainen PJ (1996) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry 35:401–418

Robroek BJ, Schouten MG, Limpens J, Berendse F, Poorter H (2009) Interactive effects of water table and precipitation on net CO_2 assimilation of three co-occurring Sphagnum mosses differing in distribution above the water table. Glob Change Biol 15:680–691

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. Glob Change Biol 6:407–416

Ruddiman WF (2003) The anthropogenic greenhouse era began thousands of years ago. Climatic Change 61:261–293

Runkle BRK, Wille C, Gazovic M, Wilmking M, Kutzbach L (2014) The surface energy balance and its drivers in a boreal peatland fen of northwestern Russia. J Hydrol 511:359–373

Sadiq R, Rodriguez MJ (2004) Disinfection by-products (DBPs) in drinking water and predictive models for their occurrence: a review. Sci Tot Environ 321:21–46

Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, Hüppop O, Lehikoinen A, Lehikoinen E, Rainio K, Romano M, Sokolov L (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proc Roy Soc B 278:835–842

Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ, Sutherland WJ, Svenning JC (2011) The influence of Late Quaternary climate-change velocity on species endemism. Science 334:660–664

Schlünz B, Schneider RR (2000) Transport of terrestrial organic carbon to the oceans by rivers: re-estimating flux and burial rates. Int J Earth Sci 88:599–606

Schlyter P, Stjernquist I, Barring L, Jonsson AM, Nilsson C (2006) Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. Climate Res 31:75–84

Schmidt IK, Tietema A, Williams D, Gundersen P, Beier C, Emmett BA, Estiarte M (2004) Soil solution chemistry and element fluxes in three European heathlands and their responses to warming and drought. Ecosystems 7:638–649

Schothorst CJ (1977) Subsidence of low moor peat soils in the western Netherlands. Geoderma 17:265–291

Schrier-Uijl AP, Kroon PS, Leffelaar PA, Van Huissteden JC, Berendse F, Veenendaal EM (2010) Methane emissions in two drained peat agro-ecosystems with high and low agricultural intensity. Plant Soil 329:509–520

Schrier-Uijl AP, Kroon PS, Hendriks DMD, Hensen A, Van Huissteden J, Berendse F, Veenendaal EM (2014) Agricultural peatlands: towards a greenhouse gas sink – a synthesis of a Dutch landscape study. Biogeosciences 11:4559–4576

Schuch S, Bock J, Krause B, Wesche K, Schaefer M (2012a) Long-term population trends in three grassland insect groups: a comparative analysis of 1951 and 2009. J Appl Entomol 136:321–331

Schuch S, Wesche K, Schaefer M (2012b) Long-term decline in the abundance of leafhoppers and planthoppers (Auchenorrhyncha) in Central European protected dry grasslands. Biol Conserv 149:75–83

Schulze ED, Luyssaert S, Ciais P, Freibauer A, Janssens IA (2009) Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. Nat Geosci 2:842–850

Schweiger O, Settele J, Kudrna O, Klotz S, Kühn I (2008) Climate change can cause spatial mismatch of trophically interacting species. Ecology 89:3472–3479

Schweiger O, Heikkinen RK, Harpke A, Hickler T, Klotz S, Kudrna O, Kühn I, Pöyry J, Settele J (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Glob Ecol Biogeogr 21:88–99

Settele J, Scholes R, Betts R, Bunn S, Leadley P, Nepstad D, Overpeck JT, Taboada MA (2014) Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change. Cambridge University Press pp 271-359

Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ (1996) CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J Ecol 84:219–228

Simmons IG (2003) The moorlands of England and Wales: an environmental history 8000 BC to AD 2000. Edinburgh University Press

Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P, Jones CD, Prentice IC, Woodward FI (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Glob Change Biol 14:2015–2039

Skov F, Svenning JC (2004) Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27:366–380

Smith JU, Smith P, Wattenbach M, Zaehle S, Hiederer R, Jones RJA, Montanarella L, Rounsevell MDA, Reginster I, Ewert F (2005) Projected changes in mineral soil carbon of European croplands and grasslands, 1990–2080. Glob Change Biol 11:2141–2152

Smith P, Chapman SJ, Scott WA, et al (2007) Climate change cannot be entirely responsible for soil carbon loss observed in England and Wales, 1978–2003. Glob Change Biol 13:2605–2609

Smolders AJP, Lamers LPM, Lucassen ECHET, van der Velde G, Roelofs JGM (2006) Internal eutrophication: How it works and what to do about it – a review. Chem Ecol 22:93–111

Sottocornola M, Kiely G (2010) Energy fluxes and evaporation mechanisms in an Atlantic blanket bog in southwestern Ireland. Wat Resour Res 46:W11524

Soussana JF, Loiseau P, Vuichard N, Ceschia E, Balesdent J, Chevallier T, Arrouays D (2004) Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use Manage 20:219–230

Sowerby A, Emmett BA, Tietema A, Beier C (2008) Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils. Glob Change Biol 14:2388–2404

Sparks TH, Bairlein F, Bojarinova JG, Hüppop O, Lehikoinen EA, Rainio K, Sokolov LV, Walker D (2005) Examining the total arrival distribution of migratory birds. Glob Change Biol 11:22–30

Stampfli A, Zeiter M (2004) Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. J Ecol 92:568–576

Strack M, Waddington JM (2007) Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. Global Biogeochem Cy 21,1:GB1007

Svenning JC, Skov F (2004) Limited filling of the potential range in European tree species. Ecol Lett 7:565–573

Tallis JH (1985) Mass movement and erosion of a Southern Pennine blanket peat. J Ecol 73:283–315

Tamis WLM, Van't Zelfde M, Van Der Meijden R, Udo De Haes HA (2005) Changes in vascular plant biodiversity in the Netherlands in

the 20th century explained by their climatic and other environmental characteristics. Climatic Change 72:37–56

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright, PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16:3304–3313

Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Func Ecol 13:55–64

Thomas H, Bozec Y, de Baar HJW, Elkalay K, Frankignoulle M, Schiettecatte L-S, Kattner G, Borges AV (2005) The carbon budget of the North Sea. Biogeosciences 2:87–96

Thornton P, Lamarque JF, Rosenbloom NA, Mahowald NM (2007) Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. Glob Biochem Cy 21: GB4018. doi:10.1029/2006GB002868

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. Proc Nat Acad Sci USA 102:8245–8250

Tingley MW, Koo MS, Moritz C, Rush AC, Beissinger SR (2012) The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Glob Change Biol 18:3279–3290

Tipping E, Woof C, Rigg E, Harrison AF, Ineson P, Taylor K, Benham D, Poskitt J, Rowland AP, Bol R, Harkness DD (1999) Climatic influences on the leaching of dissolved organic matter from upland UK moorland soils, investigated by a field manipulation experiment. Environ Int 25:83–95

Tørseth K, Aas W, Breivik K, Fjæraa AM, Fiebig M, Hjellbrekke AG, Lund Myhre C, Solberg S, Yttri KE (2012) Introduction to the European Monitoring and Evaluation Programme (EMEP) and observed atmospheric composition change during 1972-2009. Atmos Chem Phys 12:5447–5481

Tranvik LJ, Jansson M (2002) Terrestrial export of organic carbon. Nature 415:861–862

Urban NR, Bayley SE, Eisenreich SJ (1989) Export of dissolved organic carbon and acidity from peatlands. Wat Resour Res 25:1619–1628

Van Breemen N, Jenkins, A Wright RF, Beerling DJ, Arp WJ, Berendse F, Beier C, Collins R, van Dam D, Rasmussen L, Verburg PSJ, Wills MA (1998) Impacts of elevated carbon dioxide and temperature on a boreal forest ecosystem (CLIMEX project). Ecosystems 1:345–351

Van den Bos RM (2003) Restoration of former wetlands in the Netherlands; effect on the balance between CO_2 sink and CH_4 source. Neth J Geosci 82:325–332

Van den Pol-van Dasselaar A, Van Beusichem ML, Oenema O (1999) Determinants of spatial variability of methane emissions from wet grasslands on peat soil. Biogeochemistry 44:221–237

Van der Heijden E, Jauhiainen J, Silvola J, Vasander H, Kuiper PJC (2000) Effects of elevated atmospheric CO_2 concentration and increased nitrogen deposition on growth and chemical composition of ombrotrophic *Sphagnum balticum* and oligo-mesotrophic *Sphagnum papillosum*. J Bryol 22:175–182

Van der Wal R, Bonn A, Monteith D, Reed M, Blackstock K, Hanley N, Thompson D, Evans D, Alonso I (2011) Mountains, moorlands and heaths. The UK National Ecosystem Assessment Technical Report. UNEP-WCMC, Cambridge

Van Groenigen KJ, Osenberg CW, Hungate BA (2011) Increased soil emissions of potent greenhouse gases under increased atmospheric CO_2. Nature 475:214–216

Van Herk CM, Aptroot A, van Dobben HF (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. Lichenologist 34:141–154

Van Huissteden J, Van den Bos R (2006) Modelling the effect of water-table management on CO_2 and CH_4 fluxes from peat soils. Neth J Geosci 85:3–18

Van Nouhuys S, Lei G (2004) Parasitoid-host metapopulation dynamics: the causes and consequences of phenological asynchrony. J Anim Ecol 73:526–35

van Vliet AJH, Bron WA Mulder S, van der Slikke W, Ode B (2014) Observed climate-induced changes in plant phenology in the Netherlands. Reg Environ Change 14:997–1008

Veenendaal EM, Kolle O, Leffelaar PA, Schrier-Uijl AP, Van Huissteden J, Van Walsem J, Möller F, Berendse F (2007) CO_2 exchange and carbon balance in two grassland sites on eutrophic drained peat soils. Biogeosciences 4:1027–1040

Verhagen A, van den Akker JJH, Blok C, Diemont WH, Joosten JHJ, Schouten MA, Schrijver RAM, den Uyl RM, Verweij PA, Wösten JHM (2009) Climate change scientific assessment and policy analysis. Peatlands and carbon flows. Outlook and importance for the Netherlands. Report 500102 02. Netherlands Environmental Assessment Agency, Bilthoven

Verhoeven JTA (ed) (1992) Fens and Bogs in the Netherlands. Series Geobotany, vol 18. Kluwer

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proc Roy Soc B 272:2561–2569

Visser ME, Perdeck AC, van Balen JH, Both C (2009) Climate change leads to decreasing bird migration distances. Glob Change Biol 15:1859–1865

Voss N, Welk E, Durka W, Eckstein RL (2012) Biological Flora of Central Europe: *Ceratocapnos claviculata* (L) Lidén. Pers Plant Ecol 14:61–77

Walker AP, Hanson PJ, De Kauwe MG, Medlyn BE, Zaehle S, Asao S, Dietze M, Hickler T, Huntingford C, Iversen CM et al. (2014) Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO_2 enrichment experiments: model performance at ambient CO_2 concentration. J Geophy Res: Biogeosci 119:937–964

Walter H, Straka H (1970) Arealkunde—Floristischhistorische Geobotanik, 2nd edn. Ulmer

Walter BP, Heimann M, Matthews E (2001) Modeling modern methane emissions from natural wetlands: 2. Interannual variations 1982–1993. J Geophys Res 106:34207–34219

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Walther GR, Berger S, Sykes MT (2005) An ecological 'footprint' of climate change. P Roy Soc B 272:1427–1432

Warburton J (2003) Wind-splash erosion of bare peat on UK upland moorlands. Catena 52:191–207

Warren MS, Hill JK, Thomas JA, Asher J, Fos R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–68

Webb NR (1998) The traditional management of European heathlands. J Appl Ecol 35:987–990

Werkman BR, Callaghan TV, Welker JM (1996) Responses of bracken to increased temperature and nitrogen availability. Glob Change Biol 2:59–66

Wesche K, Krause B, Culmsee H, Leuschner C (2012) Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. Biol Conserv 150:76–85

Wessel WW, Tietema A, Beier C, Emmett BA, Peñuelas J, Riis-Nielsen T (2004) A qualitative ecosystem assessment for different shrublands in Western Europe under impact of climate change using the results of the CLIMOOR research project. Ecosystems 7:662–671

Wetzel RG (1992) Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems. Hydrobiologia 229:181–198

Wiegner TN, Seitzinger SP (2001) Photochemical and microbial degradation of external dissolved organic matter inputs to rivers. Aquat Microb Ecol 24:27–40

Wild M, Gilgen H, Roesch A, Ohmura A, Long CN, Dutton EG, Forgan B, Kallis A, Russak V, Tsvetkov A (2005) From dimming to brightening: Decadal changes in solar radiation at Earth's surface. Science 308:847–850

Williams TA, Abberton MT (2004) Earlier flowering between 1962 and 2002 in agricultural varieties of white clover. Oecologia 138:122–126

Worrall F, Burt T, Jaeban RY, Warburton J, Shedden R (2002) Release of dissolved organic carbon from upland peat. Hydrol Process 16:3487–3504

Worrall F, Burt T, Shedden R (2003) Long term records of riverine dissolved organic matter. Biogeochemistry 64:165–178

Worrall F, Armstrong A, Adamson JK (2007) The effects of burning and sheep-grazing on water table depth and soil water quality in a upland peat. J Hydrol 339:1–14

Worrall F, Chapman P, Holden J, Evans C, Artz R, Smith P, Grayson R (2011) A review of current evidence on carbon fluxes and greenhouse gas emissions from UK peatland. JNCC Rep 442, Peterborough, UK

Wu J, Kutzbach L, Jager D, Wille C, Wilmking M (2010) Evapotranspiration dynamics in a boreal peatland and its impact on the water and energy balance. J Geophys Res: Biogeo 115:G04038

Yallop AR, Clutterbuck B, Thacker J (2010) Increases in humic dissolved organic carbon export from upland peat catchments: the role of temperature, declining sulphur deposition and changes in land management. Climate Res 45:43–56

Yu Z, Loisel J, Brosseau DP, Beilman, DW, Unt SJ (2010) Global peatland dynamics since the Last Glacial Maximum. Geophys Res Lett 37:L13402

Zafiriou OC, Joussot-Dubien J, Zepp RG, Zika RG (1984) Photochemistry of natural waters. Environ Sci Technol 18:358–371

Zeiter M, Stampfli A, Newbery DM (2006) Recruitment limitation constrains local species richness and productivity in dry grassland. Ecology 87:942–951