The ecology of British upland peatlands: climate change, drainage, keystone insects and breeding birds

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Abstract

Northern peatlands provide important ecosystem services and support species adapted to cold, wet conditions. However, drainage and climate change could cause peatlands to become drier, threatening ecosystem functions and biodiversity. British blanket bogs occur towards the southern extent of northern peatlands and have been extensively drained, so present an excellent opportunity to examine climate change and drainage impacts.

Craneflies (Diptera: Tipulidae) are a major component of upland peatland invertebrate communities and provide a key food resource to breeding birds. However, larvae are highly susceptible to desiccation, so environmental changes that dry peat surfaces could harm cranefly populations and, in turn, bird populations. This thesis aims to examine effects of soil moisture, drainage and climate change on craneflies, and the relationship between craneflies and birds.

A large-scale field experiment showed that adult cranefly abundance increased with soil moisture. Areas with blocked drainage ditches showed significantly higher soil moisture and cranefly abundance than areas with active drainage.

A model of monthly peatland water tables driven by simple climate data was developed. The model accurately predicted water table position, and predicted up to two thirds of water table variation over time. Performance declined when modelling drained sites.

The water table model was combined with empirical relationships to model cranefly abundance under climate change. Falling summer water tables were projected to drive cranefly population declines. Drain blocking would increase abundance and slow declines, thus aiding population persistence.

Finally, modelled cranefly abundance was found to be a significant predictor of observed Golden Plover abundance, extinctions and colonisations on a large spatial scale. Across multiple species, variation explained by cranefly abundance was positively correlated with the proportion of craneflies in the diet.

Managing peatlands to maintain and increase cranefly abundance could be an important part of conserving upland bird populations.

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Declaration

I declare that the work presented in this thesis is my own, and is written by me, expect where outlined below:

Chapter 2

This chapter has been published as:

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The publication is reproduced in full here. The text was written with the co-authors, based on an initial draft produced by me. All data collection and analyses were performed by me.

Chapter 3

The MILLENNIA peat cohort model was originally developed by Dr. Andreas Heinemeyer and coded by Simon Croft. C++ coding to develop the monthly model was carried out by Dr. Chris West, under direction from Dr. Andreas Heinemeyer and me. I carried out further C++ coding and parameterisation of runoff equations, with guidance from Dr. Andreas Heinemeyer. I carried out all model testing and analyses.

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Chapter 1

General Introduction

> “In farm country, the plover has only two real enemies: the gully and the drainage ditch. Perhaps we shall one day find that these are our enemies, too.”
>
> **Aldo Leopold, *A Sand County Almanac*, 1949**

1.1 Rationale

Peatlands are a very important global terrestrial carbon store (Gorham, 1991; Limpens *et al*., 2008), and provide many other ecosystem services, such as supplying water, mitigating flood risks, and supporting biodiversity (Joosten & Clarke, 2002; Whitfield *et al*., 2011). Many of the world’s peatlands are found in the cold-temperate zones of the northern hemisphere (Moore, 2002), so are associated with cool, wet climates and high water tables (Rydin & Jeglum, 2006). Accordingly, much northern peatland biodiversity is adapted to low temperatures and wet conditions. However, land uses such as agricultural drainage and afforestation cause water tables to fall and lead to peatland degradation (Joosten & Clarke, 2002; Joosten *et al*., 2012). Warmer, drier conditions under climate change could cause further degradation of peatlands (Gorham, 1991), leading to increased greenhouse gas emissions (Davidson & Janssens, 2006), and impacts on other ecosystem services, such as reduced water quality (e.g., Clark *et al*., 2009). Further, these warmer, drier conditions could lead to abundance and distribution changes in cold-adapted or moisture-dependent species (e.g., Briones *et al*., 1997; Bale *et al*., 2002), thus affecting peatland biodiversity.

The UK provides an excellent opportunity to study effects of land management and climate change on peatland ecosystems. The cool, oceanic climate of the British uplands has led to the development of extensive blanket peatlands, constituting up to 13% of the world’s total blanket bog area (Ratcliffe & Thompson, 1988). However, large areas have been drained for agriculture (Holden *et al*., 2004), and Britain is towards the southern extent of northern peatland occurrence (Moore, 2002). Consequently, land use impacts are already visible, and climate change impacts could be experienced earlier than in other northern peatlands.

Although relatively species-poor, the British blanket peatland flora and fauna contain unique species assemblages (Thompson *et al*., 1995). The bird assemblage in particular is of great conservation interest due to its mixture of boreal, arctic and temperate species, and the large populations of species such as Golden Plover (Pearce-Higgins *et al*., 2009a). The blanket peatland invertebrate fauna is dominated by relatively few species, with craneflies (Diptera: Tipulidae) a major component (Coulson & Butterfield, 1985; Coulson, 1988). Craneflies are important in ecosystem functions (Coulson & Whittaker, 1978) and provide a major food source to upland breeding birds (Buchanan *et al*., 2006a; Pearce-Higgins, 2010). For some bird species, chick survival, adult abundance, breeding locations and foraging locations could be linked to cranefly availability (e.g., Whittingham *et al*., 2001; Pearce-Higgins & Yalden, 2003a; Pearce-Higgins & Yalden, 2004). Therefore, craneflies could be seen as keystone invertebrates of British blanket bogs.

Peatland drainage and climate change could threaten cranefly populations. Cranefly eggs and larvae are highly susceptible to desiccation, and droughts have been observed to cause substantial population reductions (Coulson, 1962; Milne *et al*., 1965). If peatlands become drier, increased larval cranefly mortality could reduce emerging adult abundance, in turn reducing food availability for upland breeding birds (Pearce-Higgins *et al*., 2010). However, the exact nature of the relationship between abundance and moisture for peatland craneflies remains unknown. Improving understanding of this relationship would aid models of climate change impacts by reducing reliance on surrogate drivers of abundance. Further, by examining drainage and restoration impacts, effects of land management and their interaction with climate change could also be examined.

In this thesis, I aim to examine the relationship between craneflies and soil moisture, the impacts of drainage and climate change on cranefly abundance, and the relationship between cranefly abundance and breeding bird distributions. The work presented here will focus directly on impacts of land management and climate change on craneflies, and will explore implications for upland bird species. However, findings could have wider implications, as changes to peatland soil moisture could affect more ecosystem services. The following sections of this chapter will review the wider scientific literature to give a more complete introduction to the concepts discussed above, before presenting an overview of the contents of the thesis.

1.2 Climate change, biodiversity and conservation

Anthropogenic climate change is one of the greatest threats to biological systems of recent times, and will continue to put pressure on global ecosystems in the coming decades (Fischlin *et al.*, 2007; Rosenzweig *et al.*, 2007). Since the Industrial Revolution, humans have burned fossil fuels at an unprecedented rate, thus increasing atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and other gases (Forster *et al.*, 2007). This change in atmospheric composition, along with land use change, has led to an increase in radiative forcing, a metric that indicates changes in global radiation balance (Forster *et al.*, 2007). A primary consequence of this is that global mean surface temperature increased by 0.74°C between 1906 and 2005, but with the rate of warming between 1956 and 2005 almost double the overall rate (Trenberth *et al.*, 2007). Further, the land is warming faster than the oceans, with Northern Hemisphere land surface temperatures increasing at around 0.3°C per decade between 1979 and 2005, compared to increases of around 0.2°C per decade for ocean temperatures over the same period (Trenberth *et al.*, 2007). Additionally, global atmospheric circulation and precipitation have been affected, but in a less predictable manner, with some areas experiencing drier conditions, but others wetter, whilst both heavy rainfall and drought frequency have increased (Trenberth *et al.*, 2007). These changes are already affecting physical, biological and human systems (Rosenzweig *et al.*, 2007), and effects will continue to develop for the foreseeable future. Understanding and predicting climate change impacts is therefore an important and necessary aspect of current research.

Projections of future climate change are made using General Circulation Models (GCMs) and Regional Climate Models (RCMs). These represent large-scale climatic processes and feedbacks, and are driven using changes in atmospheric gas concentration and other forcing influences (Meehl *et al.*, 2007). In this way, model projections can be tied into Special Report on Emission Scenarios (SRES) scenarios, which describe alternative political and economic trajectories for gas emissions. In the most recent Intergovernmental Panel on Climate Change (IPCC) report, mean projections derived from multiple GCMs indicate that by 2090–99, mean global surface temperatures could rise by as little as 1.8°C (SRES scenario B1), and as much as 4.0°C (A1FI scenario), with a concurrent increase in the frequency of extremely warm temperatures (Meehl *et al.*, 2007). Global mean precipitation is projected to increase, and the hydrological cycle to intensify, although uncertainties are greater than those for temperature projections (Meehl *et al.*, 2007); multimodel analyses show that GCMs may not even agree on whether precipitation will increase or decrease across large areas of the globe (Solomon *et al*., 2009). There is also substantial regional variation in projections, with Europe projected to experience faster warming than the global mean (Christensen *et al*., 2007). Within Europe, existing regional gradients could strengthen, with wetter winters in the north and drier summers in the south, and particularly strong summer warming in the Mediterranean (Christensen *et al*., 2007). Within the United Kingdom, regional and seasonal gradients are also projected to intensify, with summer warming and precipitation decreases stronger in the south and east, and with drier summers occurring along with wetter winters (Murphy *et al*., 2009).

Biological systems are already responding to the changing climate. The timing of events, or phenology, is often subject to seasonal triggers, so may be rapidly affected by increasing temperatures (Rosenzweig *et al*., 2007). Across 203 northern hemisphere plant and animal species, spring events were found to have advanced by a mean of 2.8 days decade^{-1} over the 20th Century, but with substantial variation in rate estimates between different groups of organisms (Parmesan, 2007). This highlights a key problem arising from phenological shifts: if species that interact, such as predators and prey, or insects and host plants, experience phenological shifts at different rates, events may no longer overlap, creating a ‘phenological mismatch’ that reduces species’ fitness (e.g., Visser & Both, 2005; Visser *et al*., 2012). An analysis of 726 UK taxa showed that spring and summer events have advanced by different amounts at different trophic levels, with primary producers and consumers advancing approximately twice as fast as secondary consumers, indicating that phenological mismatches may be occurring on broad scales (Thackeray *et al*., 2010).

Warmer conditions have also driven species poleward and upward as they track suitable climatic conditions. A meta-analysis has indicated that, globally, species’ ranges have shifted poleward at 6.1 km (or upward by 6.1 m) decade^{-1} (Parmesan & Yohe, 2003), although a more recent meta-analysis has shown that the rates may be much higher, at 16.9 km decade^{-1} poleward and 11.0 m decade^{-1} upward (Chen *et al*., 2011). Further, the extent of range shifts appears to be positively correlated with the degree of warming (Chen *et al*., 2011). Within Britain, over 80% of 329 species showed northward range shifts in the 20th Century, with a mean shift of 31 – 60 km (Hickling *et al*., 2006). In the tropics, montane moths were found to have increased mean altitude by 67 m in only 42 years (Chen *et al*., 2009).

Climate change is predicted to lead to extinctions and changes in species assemblages. Climatic shifts could reduce the area that is suitable for species to occur in: model estimates suggest that without dispersal, 38–52% of species could be consigned to extinction by 2050, while 21–32% would be even with universal dispersal (Thomas *et al*., 2004). For terrestrial birds, models indicate that by 2050 at least 400 species, and as many as 1,800 species, could suffer range contractions of over 50% due to climate and land use change (Jetz *et al*., 2007). Using estimates of physiological tolerance, models suggest that for terrestrial insects, extinction risk is greatest in the tropics even though warming is greater in temperate latitudes (Deutsch *et al*., 2008). Although soil-dwelling organisms may be buffered from some temperature change (Bale *et al*., 2002), moisture changes could be important, with experiments showing that abundance and vertical distributions change under warmer, drier conditions, leading to local extinctions and creating new species assemblages (Briones *et al*., 1997).

Multiple climate change effects could interact with one another, as well as interacting with non-climatic drivers, meaning that realised responses may not match predictions (Mustin *et al*., 2007). For example, populations of terrestrial species at southern range margins may face different pressures, such as incoming competitors, from populations at northern range margins, which are likely to respond more to increasing temperatures (Sunday *et al*., 2012). Further, experimental manipulation and comparison of different microhabitats has shown that for sea shore invertebrates, warmer conditions interact with species' physiological tolerances to influence predator-prey relationships and contribute to localised population extinctions (Harley, 2011). Hence, although climate change is a major threat to biodiversity, specific predictions of impacts are often hard to make.

Integrating climate change into attempts to conserve biodiversity is a key challenge for the 21st Century (Heller & Zavaleta, 2009). Given projected shifts in species' ranges, problems with existing conservation methods may arise, such as species moving out of established protected areas (Araújo *et al*., 2004). A commonly-cited response is to increase connectivity between habitats, so that species are not forced into extinctions by a lack of suitable habitat (e.g., Vos *et al*., 2008). To allow for large-scale range shifts, a network of protected areas with high connectivity would require global coordination (Hannah, 2010). However, not all species will be able to track climate, with high-latitude and high-altitude species threatened because there is no further land to move into (e.g., Jetz *et al*., 2007; Dirnböck *et al*., 2011; Renwick *et al*., 2012), and other species threatened because their dispersal speed may not match the speed of climatic warming (Schloss *et al*., 2012). Therefore, conservation management within sites, aiming to make populations more resistant or resilient to climate change, will also be required (Heller & Zavaleta, 2009). This could involve direct management to offset climate-induced effects, such as irrigation or drainage to control moisture (Peters & Darling, 1985), general restoration of habitats in key sites, or removing other local threats to target populations (Mawdsley *et al*., 2009). To aid conservation management, modelling could play a key role, projecting species' range shifts (Pearson & Dawson, 2003) and, as model complexity increases, integrating information on dispersal and interactions (Mokany & Ferrier, 2011). Such information could be used to ensure that appropriate conservation actions are taken to provide longer-term benefits under climate change.

1.3 Peatlands

Peatlands (defined as areas with peat over 30 cm deep) cover around 4 million km^2 worldwide, which is around 3% of global land area (Rydin & Jeglum, 2006). Around 80% of peatlands are in cold-temperate latitudes of the northern hemisphere, with other significant peat deposits occurring in the tropics (Figure 1.1; Limpens *et al*., 2008). Peat deposits are found in many countries of the world (Joosten & Clarke, 2002), so peatlands are a truly global resource. Peatlands are major carbon stores: an estimated 270 – 455 PgC are held in boreal and subarctic peatlands (Gorham, 1991; Turunen *et al*., 2002), and an estimated 81 – 92 PgC are held in tropical peatlands (Page *et al*., 2011); this compares to around 550 PgC in vegetation, 805 PgC in the atmosphere and 700 – 1000 PgC in surface oceans (Houghton, 2007). Consequently, peatlands, and particularly those in cool, temperate regions of the northern hemisphere, are one of the most important terrestrial carbon stores (Gorham, 1991; Worrall *et al*., 2010). Although peatlands can be sources of CO_2 and CH_4, over thousands of years northern peatlands have been a net carbon sink, exerting an overall cooling effect on global temperatures (Frolking & Roulet, 2007). Ensuring that peatland carbon stores are maintained over time will therefore play an important role in global climate change mitigation.

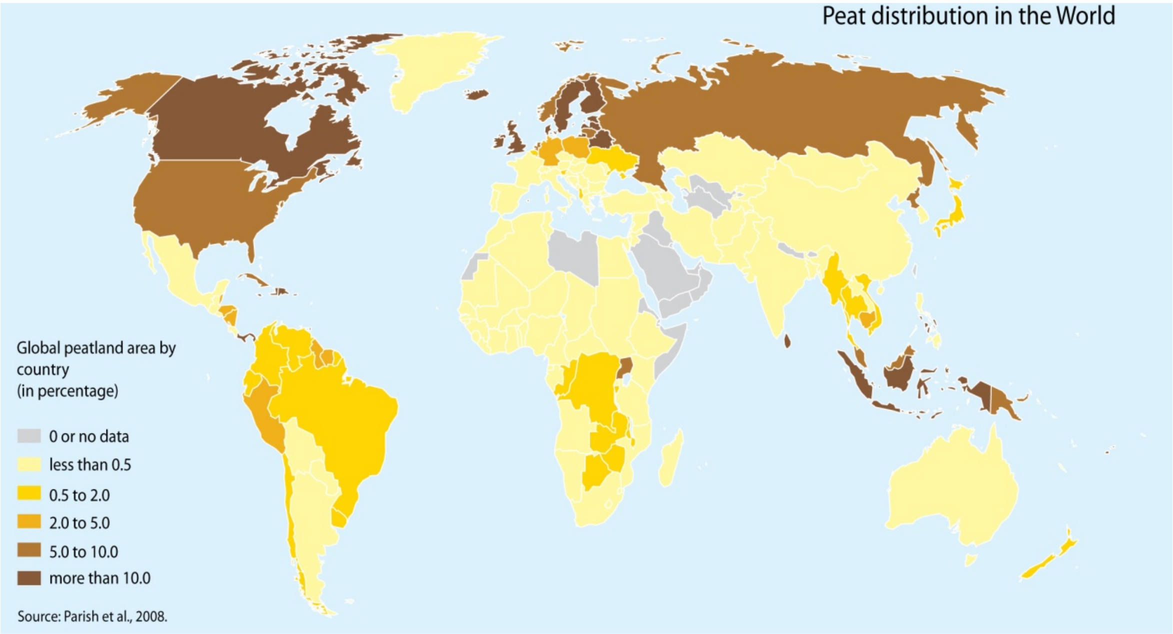

Figure 1.1. Global distribution of peatlands (reproduced courtesy of Riccardo Pravettoni, UNEP/GRID-Arendal, available at http://www.grida.no/graphicslib/detail/peat-distribution-in-the-world_8660).

Peat forms where high water tables create anoxic soil conditions, slowing decomposition of plant material and allowing organic-rich material to accumulate (Gorham, 1957). Appropriate conditions occur due to high rainfall or poor drainage leading to waterlogged soils; if peat-forming plants are present, peat may start to form (Rydin & Jeglum, 2006). In northern peatlands and in Tierra del Fuego, *Sphagnum* mosses are the most important peat-forming plants (Rydin & Jeglum, 2006). In the tropics, peat is mostly made of material from trees (Page *et al*., 1999), whilst in New Zealand, plants of the Restionaceae family are the primary peat-forming species (Rydin & Jeglum, 2006). Peat growth is slow, taking thousands of years to reach depths observed today (e.g., Tallis, 1998; Page *et al*., 1999; Yu *et al*., 2009). Peat depths vary widely: northern peatlands are estimated to have a mean depth of 2.5 m (Clymo *et al*., 1998), with some areas containing deposits over 5 m deep (e.g., Tallis, 1998; Turunen *et al*., 2002), while tropical peatlands may contain deposits over 10 m deep on average (Page *et al*., 1999). As peat accumulates, conditions become increasingly acidic and nutrient-poor, slowing decomposition and, in northern peatlands, favouring further *Sphagnum* growth (Gorham, 1957; Rydin & Jeglum, 2006). Peatlands fed by groundwater are classified as swamps or fens; if peat accumulation isolates the surface from groundwater, the peatland becomes ombrotrophic, or rain-fed, and is classified as a bog (Rydin & Jeglum, 2006).

Exploitation of peatlands has led to widespread degradation. Globally, over 450,000 km^2 of non-tropical peatlands have been lost to agriculture, forestry and extraction (Joosten & Clarke, 2002). Carbon storage is strongly affected by degradation, with drained peatlands emitting around 1,300 TgC in 2008 (Joosten, 2010), thus making peatland restoration a key component of climate change mitigation (Joosten *et al*., 2012). In Britain, blanket peatlands were extensively drained in the 20th Century with the aim of improving agriculture (Holden *et al*., 2004; Ramchunder *et al*., 2009); impacts of drainage are discussed below. Afforestation damages peatlands through artificial drainage and trees drawing up water, leading to drying, shrinking and cracking of peat and changed runoff regimes (Holden *et al*., 2007c). Around 9% of UK upland peatlands have been afforested (Holden *et al*., 2007c), although in other countries this rate may be much higher, such as Finland, where 60% of active peatlands have been afforested since the 1950s (Chapman *et al*., 2003). In southeast Asia, the high economic value of palm oil is driving drainage of peatlands and conversion to oil palm plantations (Koh *et al*., 2009). Further, agricultural conversion of southeast Asian peatlands often involves burning to clear native forest, but fires can become uncontrolled, damaging the peatland and releasing stored carbon; in 1997, an estimated 0.8 – 2.6 PgC was released into the atmosphere due to burning of peat and the overlying vegetation (Page *et al*., 2002). Harvesting accounts for less peatland loss globally (Chapman *et al*., 2003), but it can be locally very important, such as in Ireland, where 5 Mt year^{-1} are extracted for fuel (Moore, 2002). Not all degradation involves exploitation: SO_2 deposition from atmospheric pollution is responsible for the loss of *Sphagnum* in the South Pennines (Moore, 2002).

Peatlands are also threatened by climate change. Warmer, drier conditions could cause water tables to fall, turning peatlands into net carbon sources, with the zone of active peat formation shifting north as temperatures increase (Gorham, 1991). Within the UK, which is towards the southern margin of cool temperate bog occurrence (Moore, 2002), climate suitable for blanket peats could be restricted to northern Scotland by the 2080s, driven primarily by temperature increases (Clark *et al*., 2010b); extensive blanket peats in northern England could therefore stop accumulating carbon (Gallego-Sala *et al*., 2010). Model results suggest that ombrotrophic bogs in central Europe are also threatened by the loss of suitable climate space (Essl *et al*., 2012). Historical water table reconstructions support model findings, with summer temperature appearing to exert dominant controls over hydrology, and therefore bog growth, over hundreds of years (Hendon & Charman, 2004). As well as gradual effects on bog growth, climate change could also increase the risk of summer wildfires, which can cause dramatic damage to peatland habitats (Albertson *et al*., 2010). The loss of stored carbon from peatlands, through release of greenhouse gases, could accelerate climate change, thus creating a positive feedback loop (Davidson & Janssens, 2006).

Mechanisms involved in peatland responses to climate change are subject to much recent research effort. Droughts stimulate microbial growth and affect enzymatic processes, stimulating the decomposition of carbon compounds and leading to carbon being lost first as CO_2 and then as dissolved organic carbon (DOC) (Fenner & Freeman, 2011). Drought increases both the amount of DOC produced and the temperature sensitivity of DOC production, such that much greater increases could be seen as summers become warmer and drier (Clark *et al*., 2009). Water table drawdown will also affect gas emissions, with decreased CH_4 and increased CO_2 fluxes (Moore & Knowles, 1989), although the balance of these may be mediated by microtopography in a complex manner (Strack & Waddington, 2007). Peat structure also changes as water tables fall, becoming denser and changing pore size distributions, which will have significant impacts on hydrology (Whittington & Price, 2006). Even the *Sphagnum* that forms peat could be affected, with different species responding differently to temperature and moisture changes, thus changing the species composition (Robroek *et al*., 2007).

The UK contains around 18,000 km^2 of peatlands, corresponding to around 7% of the land surface (Rydin & Jeglum, 2006). Blanket bogs account for over 90% of peatland area in Great Britain (Clark *et al*., 2010b), representing 7 – 13% of the world's blanket bog (Ratcliffe & Thompson, 1988). Blanket peats develop in cool, wet, oceanic climates, and differ from other peatland types in being able to form on steeper slopes (Gorham, 1957). Underlying woody peat formation started up to 10,000 years ago, but blanket peat development typically started 2000 – 8000 years ago, and was triggered by the climate becoming wetter and humans clearing forests, leading to waterlogging of soils (Tallis, 1998). Mire vegetation communities, which comprise the peat-forming plant species, are associated with annual rainfall of at least 800 mm (Holden *et al*., 2007c), although blanket bogs are associated with annual rainfall over 1200 mm and warmest monthly mean temperatures under 15°C (Tallis, 1998). Given these climatic limitations, blanket peats are typically found in northern and western Britain and at higher altitudes, but in northern

Scotland they are found closer to sea level (Tallis, 1998). Mean depth of blanket peat is around 2 m, but can locally grow to over 5 m depending on topography (Tallis, 1998).

UK peatlands provide multiple ecosystem services. A major service is carbon storage, with the current best estimate suggesting that peatlands hold around 2,300 TgC (Billett *et al.*, 2010), representing the UK's largest terrestrial carbon store (Whitfield *et al.*, 2011). Upland peat-covered catchments provide a large proportion of the country's drinking water, and peatland condition and management play important roles in determining water quality (e.g., Mitchell & McDonald, 1995). Related to this, peatlands strongly influence catchment hydrology, so inappropriate management can lead to problems such as increased flood risk (e.g., Holden *et al.*, 2004; Holden, 2005b). Peatlands provide important agricultural land, supporting livestock grazing in upland moorlands, although overgrazing can cause habitat degradation through vegetation changes and erosion (Holden *et al.*, 2007c). Upland peatlands support unique bird assemblages and mixtures of vegetation communities, so are important for biodiversity (See Section 1.5; Thompson *et al.*, 1995; Littlewood *et al.*, 2010). Social ecosystem services are also provided, with considerable recreation, sport and cultural value (Whitfield *et al.*, 2011). Although managing land for multiple ecosystem services is challenging, appropriate peatland management can lead to concurrent improvements in several ecosystem services (Maltby, 2010). Therefore, as UK peatlands provide important ecosystem services, but are located towards the southern margins of northern peatland occurrence (Moore, 2002) and are degraded due to human actions (Holden *et al.*, 2007c), they provide an ideal opportunity to study the effects of climate change on peatland functioning and to test restoration methods.

1.4 Peatland hydrology

According to Rydin and Jeglum (2006), "the hydrology of wetlands, mires and peatlands is…probably the single most important condition influencing peatland ecology, development, functions and processes." This is undoubtedly true, as peat may only develop when the ground becomes saturated, and once peat does develop, hydrological processes may become very different from those in mineral soils (Evans & Warburton, 2007). Here, the focus will be on ombrotrophic bogs, which constitute most British peatlands, and for which the only water input is precipitation, meaning that there is less water supply per unit area, lower mineral concentration and lower pH than peats supplied by groundwater (Holden, 2005b). This peat is typically over 90% water by mass, but may be as much as 98% in saturated peat (Holden, 2005b). Understanding peatland hydrology is therefore of great importance in understanding peatland ecosystems and their responses to environmental change.

Perhaps the most important concept in peatland hydrology is that of water table depth. The water table is defined as the level to which water rises to balance atmospheric pressure (Rydin & Jeglum, 2006). In blanket peats, the water table may be within 5 cm of the surface for over 80% of the year (Evans *et al*., 1999), meaning that high water tables are a key feature. The high water table influences hydrological processes, but also peatland ecology, with vegetation form, community composition and growth responding to water table depth (Rydin & Jeglum, 2006), and soil invertebrate communities dominated by species that can tolerate wet conditions (Coulson & Whittaker, 1978).

To understand peatland processes, water table position is often used to define layers where properties and processes differ (see Figure 1.2 for sketch). The acrotelm is traditionally defined as peat above the deepest water table depth during drought (Morris *et al*., 2011b). The acrotelm experiences oxic conditions, leading to higher decay rates (Clymo, 1984), lower and more variable water content (Holden, 2005b) and higher hydraulic conductivity that in turn leads to greater through-flow and runoff generation (Holden & Burt, 2003b). Within the acrotelm, bulk density increases and hydraulic conductivity decreases with depth due to decay of plant materials in the peat (Clymo, 1984; Morris *et al*., 2011a). The acrotelm is also the zone relevant to ecology, as it supports most plant roots, microbial activity, and invertebrate activity (Clymo, 1984; Moore, 2002). The zone beneath the deepest water table position is the catotelm. As this is always saturated, conditions are anoxic, decay rates are very low (Clymo, 1984) and hydraulic conductivity may be 3–5 orders of magnitude lower than in the acrotelm (Evans & Warburton, 2007). This two-layer model oversimplifies the system (Morris *et al*., 2011b), missing out processes such as flow through soil pipes and macropores, and spatial variation in runoff production (Holden & Burt, 2003b; Holden, 2005b). However, it is still a useful concept in understanding variation in peat properties and hydrological processes with depth (Holden & Burt, 2003b), and highlights the importance of water table depth.

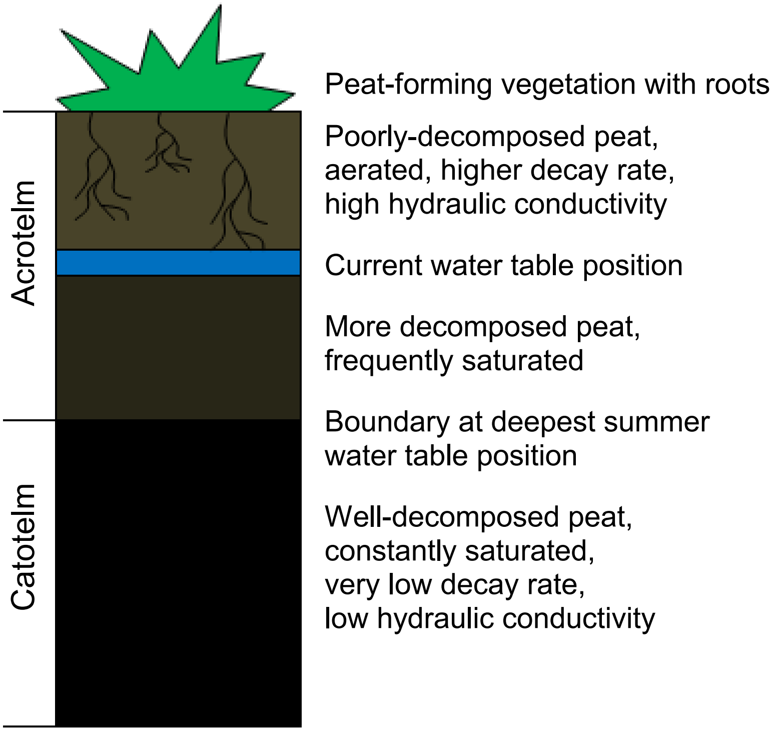

Figure 1.2. Sketch of distinction between acrotelm and catotelm, showing key properties.

Water fluxes are also a key component of understanding peatland hydrology. Ombrotrophic peatlands only receive water input from precipitation, which then enters pores within the peat via infiltration (Rydin & Jeglum, 2006). This raises the water table, but as water tables are usually already high, surface runoff may be quickly generated (Holden, 2005b); antecedent water table depths therefore exert dominant control over runoff production (Daniels *et al.*, 2008). Although peatlands may generally be seen as sponge-like, this low storage capacity means that runoff generation is actually very flashy (Evans *et al.*, 1999). Runoff from blanket peats is the dominant source of water loss, with estimates indicating it to be around 3 times greater than evaporative loss (Evans *et al.*, 1999; Evans & Warburton, 2007). Runoff may account for as much as around 90% of precipitation when the water table is near the surface, or as little as 10% when the water table is deep (over 20 cm) (Evans *et al.*, 1999). As a further consequence of precipitation being the only input, evapotranspiration becomes important in determining water table depth, especially during dry periods (Evans & Warburton, 2007). Within a day, the water table may vary by 10 – 20 mm, driven only by evapotranspiration, and a seasonal pattern of summer water table drawdown and winter recharge is observed (Evans & Warburton, 2007). Therefore, changes to precipitation and temperature regimes under climate change could substantially affect peatland hydrology.

The processes described above have been incorporated into models of peatland hydrology that allow examination of various aspects of peatland systems. These models are reviewed in Chapter 3, so are not discussed here.

Humans have strongly influenced peatland hydrology. Grazing and burning regimes can affect water table depth, acting via vegetation composition and evapotranspiration rates (Clay *et al*., 2009). However, the dominant human influence on peatland hydrology is through drainage. In the UK, after the Second World War peatlands were extensively drained for agriculture, with a key concern being maximising drainage effectiveness (e.g., Burke, 1961). Peatland drainage occurred on small scales for centuries, but new ploughs developed in the 1930s allowed large-scale drainage to occur, aided by agricultural subsidies (Stewart & Lance, 1983). The main aim was to increase runoff, thus drying peat surfaces and improving conditions for grouse and sheep (Coulson *et al*., 1990). However, drainage did not provide agricultural benefits (Coulson *et al*., 1990; Stewart & Lance, 1991), with authors commenting, “The usefulness of moor-draining may seem self-evident. However, this confuses need with result,” (Stewart & Lance, 1983).

In the longer term, drainage damages peatlands. Early studies suggested that shrub cover increased and *Sphagnum* cover decreased within 2 m of drains, and that erosion increased (Stewart & Lance, 1983). Other studies showed that the invertebrate assemblage changed and that nutrient content increased near drains (Coulson *et al*., 1990). However, more recently, studies have shown that drains have more negative effects. Numerous hydrological processes are affected: water storage initially increases, but decreases in the longer term (Holden *et al*., 2004); peat structural changes lead to increased flow through natural pipes and macropores (Holden, 2005a); the seasonality of water table fluctuations is lost (Holden *et al*., 2011); peak flows following storms become synchronised, potentially leading to increased flood risk (Holden, 2005b). Drains also increase sediment load (Holden *et al*., 2007b), DOC concentrations (Wallage *et al*., 2006) and water colouration (Mitchell & McDonald, 1995). Ecological impacts have also been detected, with lower abundance and species richness of stream invertebrates (Ramchunder *et al*., 2012).

To reduce drainage impacts, drain blocking programmes are becoming increasingly common. By 2009, it was estimated that over €250 million had been spent on blocking peatland drains in the UK (Armstrong *et al*., 2009). Several methods have been established, with peat, heather, wood and plastic used as dams, and with drain re-profiling and water redistribution used to re-wet surrounding peat more effectively (Armstrong *et al*., 2009). After drain blocking, water tables rise, although natural water table behaviour may not be restored (Wilson *et al*., 2010; Holden *et al*., 2011). Drain blocking also appears to buffer flow levels against droughts and storm events (Wilson *et al*., 2011a), reduce DOC, particulate organic carbon (POC) and water colouration (Wallage *et al*., 2006; Armstrong *et al*., 2010; Wilson *et al*., 2011b), and lead to increased *Sphagnum* cover (Bellamy *et al*., 2011). Therefore, restoring peatland hydrology is a key part of managing degraded peatlands for multiple ecosystem services. However, much drain blocking may be occurring without a full understanding of effects (Holden *et al*., 2007c), suggesting that more research into impacts of drain blocking is required.

1.5 The British uplands

Most of the UK's blanket peatlands are located in the British uplands (Clark *et al*., 2010b), so changes to peatlands will predominantly be influenced by upland land use and policy. The physical environment, biological systems, ecosystem services, land uses and political and economic drivers of change are often specific to upland ecosystems (e.g., Ratcliffe & Thompson, 1988; Condliffe, 2009), so the uplands should be considered separately from the warmer, drier, flatter, more populated lowlands. Therefore, to understand changes in blanket peatlands, it is necessary to understand the British uplands.

The uplands may be defined in several ways, with the definition chosen influencing the amount of land the uplands constitute (Clark *et al*., 2010c). At a basic level, they are the areas above the limit of enclosed farmland, comprising 27–30% of Great Britain (Thompson *et al*., 1995). Commonly, an altitudinal limit of 300 m is set, covering around 17% of Britain (Clark *et al*., 2010c). The uplands may also be defined as areas classified by the EU as Severely Disadvantaged Areas, covering 42% of Britain (Clark *et al*., 2010c). Here, the broad definition of Sim *et al*. (2005) will be used, defining uplands as "unenclosed land, generally greater than 300 m above sea level but at lower altitudes in north and west Scotland." Under this definition, much of Scotland and Wales is classified as upland, but uplands in England are restricted to the south-west and north.

The uplands have a relatively unusual oceanic climate, with high precipitation, low temperature, high cloudiness and relatively little seasonal variation in weather (Ratcliffe & Thompson, 1988). Generally, soils are acidic podsols and peats (Thompson *et al*., 1995), with increasing coverage of blanket peats to the north and west as the climate becomes cooler and wetter (Ratcliffe & Thompson, 1988). A dominant feature of the uplands is the extensive heather moorland cover (Thompson *et al*., 1995), which developed after forest clearance for grazing in the Neolithic period (Bevan, 2009). There are also extensive upland grasslands, many of which developed through grazing and burning of dwarf shrub heath (Ratcliffe & Thompson, 1988).

Much of the uplands are above the limit of enclosed farming, due to their marginal climate and poor soils (Ratcliffe & Thompson, 1988). Upland moors were traditionally common land, used for grazing, peat cutting, quarrying and foraging (Bevan, 2009). However, technological improvements and land ownership changes have led to dominant land uses becoming grazing, grouse shooting and forestry (Bevan, 2009). In the 20th Century, extensive areas of the uplands were opened to the public, making tourism another key land use (Curry, 2008). All of these land uses have the potential to harm upland ecosystems. Overgrazing promotes the conversion of heath to grassland (Usher & Gardner, 1988) and can increase erosion (Holden *et al*., 2007c). Grouse moors are managed with rotational burning, which if done inappropriately can cause soil desiccation and erosion (Ramchunder *et al*., 2009). Both burning and grazing change vegetation communities, in turn reducing the carbon stored in vegetation and litter, and increasing CO_2 fluxes, thus affecting peatland carbon storage capacity (Ward *et al*., 2007). Illegal persecution of raptors on grouse moors is an ongoing problem, and can severely harm upland biodiversity (Thirgood *et al*., 2000). Afforestation changes hydrological processes (Holden *et al*., 2007c), and can lead to forest species replacing upland moorland species (Usher & Gardner, 1988). Finally, recreational disturbance can damage vegetation and wildlife, although provision of specific walking routes can reduce the scale of disturbance, providing subsequent benefits for bird species (Pearce-Higgins & Yalden, 1997; Finney *et al*., 2005). Therefore, the uplands are used in several ways, but these uses often conflict with one another and with biodiversity, making appropriate management a complex problem.

A key ecosystem service of the British uplands is that they support important biodiversity. The upland flora is relatively species poor (Thompson *et al*., 1995), and few individual plant species are of regional or global conservation importance, although one higher plant and three moss species found in blanket bogs are listed as UK Biodiversity Action Plan (BAP) priority species (Littlewood *et al*., 2010). However, the mix of plant species present gives the uplands their importance, with six heath and mire communities confined to the UK and Ireland and a further seven better developed in the UK than anywhere else (Thompson *et al*., 1995). As a result, blanket bogs are listed as priority habitats in the UK BAP (Littlewood *et al*., 2010), and the UK has special responsibilities within the EU for conserving habitats including blanket bog and Atlantic wet heath with *Erica tetralix* (McLeod *et al*., 2005).

The upland fauna is also species poor compared to the lowlands (Coulson & Butterfield, 1978), but the bird and invertebrate faunas make the uplands important for animal biodiversity (Ratcliffe & Thompson, 1988; Thompson *et al*., 1995). The breeding bird species present are not individually rare, but upland peatlands support 11 UK BAP priority species and several species included in Annex I of the EC Birds Directive (Littlewood *et al*., 2010). Further, several species, including Red Grouse (*Lagopus lagopus scotius*) and Curlew (*Numenius arquata*), have regionally-important populations in the uplands (Ratcliffe & Thompson, 1988; Pearce-Higgins *et al*., 2009a). However, arguably the key aspect of the upland bird fauna is the unique mixture of boreal, arctic and temperate species (Thompson *et al*., 1995), which has been described as having “no counterpart elsewhere” (Ratcliffe & Thompson, 1988). Upland breeding birds are discussed in Chapter 5 so will not be discussed further here.

The British upland invertebrate assemblage is also unique, comprising arctic-alpine, alpine and boreal-British assemblages (Thompson *et al*., 1995). Due to the cold, wet climate, the soil invertebrate fauna is particularly rich, with abundances of Lumbricidae, Enchytraeidae, Collembola and Diptera equal to or greater than many lowland communities (Coulson & Whittaker, 1978). Although some rare invertebrate species occur in the uplands (Coulson & Butterfield, 1985), few species are internationally rare (Usher & Thompson, 1993). Seven UK BAP priority species are found on blanket bogs, and three red data book-listed spiders are confined to blanket bogs (Littlewood *et al*., 2010). However, the invertebrate fauna is dominated by relatively few taxa: excluding enchytraeids and lumbricids, 90% of blanket bog invertebrate species come from Diptera, Coleoptera, Araneae or Opiliones (Coulson, 1988). Biomass is similarly dominated by few groups, with Lumbricids and Enchytraeids together accounting for over 60% of blanket bog invertebrate biomass, and Diptera accounting for around 20% (Coulson, 1988). Upland invertebrates perform several important ecosystem functions, such as aiding decomposition and nutrient cycling, and providing a major food source for upland breeding birds (Coulson, 1988). Given the dominance of the community by so few groups and the important functions performed by invertebrates, individual taxa (such as Tipulidae: see Section 1.6) may become particularly influential in ecosystem functioning, and thus could be described as keystone species.

Economic and political factors are drivers of change in the uplands. Agricultural policy led to increased upland grazing intensity over the 20th Century, but if subsidies decreased, stocking levels could decline or grazing land could be abandoned (Reed *et al*., 2009). Likewise, financial pressures could see grouse moor abandoned, which would lead to the loss of rotational burning (Sotherton *et al*., 2008). Although changes to agricultural practices and grouse moor management could be beneficial (e.g., Thompson *et al*., 1995), the total loss of habitat management could lead to the loss of heathland, which would have substantial water quality, biodiversity and economic impacts (Reed *et al*., 2009). Conflicting land uses in the uplands are common (Reed *et al*., 2009), such as the belief amongst grouse moor managers and farmers that blocking drainage ditches will harm their business (Armstrong *et al*., 2009); such conflicts can hinder responses to change and make appropriate land management difficult. New economic pressures are also developing, most notably the use of uplands to provide wind energy (Reed *et al*., 2009). However, new land uses bring new conflicts, such as impacts of wind farms on bird populations, although studies suggest that impacts may be limited in this instance (e.g., Pearce-Higgins *et al*., 2009b; Douglas *et al*., 2011), providing hope that land use conflicts can be minimised.

Environmental drivers of change are also a key concern. Deposition of atmospheric nitrogen and sulphur pollution has changed vegetation communities and reduced plant diversity (Caporn & Emmett, 2009). Although sulphur emissions have declined, increasing ozone emissions could damage *Sphagnum* and other important bryophytes (Potter *et al*., 1996), meaning that atmospheric pollution still presents a threat. Climate change will impact the uplands: altitudinal lapse rates and seasonality of weather are already changing (Burt & Holden, 2010), and the climate currently associated with upland habitats could move to higher latitudes and altitudes (Clark *et al*., 2010c). Climate change could also impact upland biodiversity: heather dominance could increase (Peñuelas *et al*., 2007), soil invertebrate assemblages could change (Briones *et al*., 1997) and important upland bird species could decline (Pearce-Higgins *et al*., 2010).

Interactions between environmental and economic drivers of change are possible: as the climate warms, upland valleys could become suitable for arable crops and biofuels (Reed *et al*., 2009), changing our view of upland agriculture. Atmospheric pollutant deposition and changes to grazing regimes have caused shifts in upland vegetation communities (McGovern *et al*., 2011); these processes are directly influenced by political and economic factors, highlighting the potential for interactions between drivers of change. Therefore, as well as existing drivers of change, new processes and new interactions will affect physical and biological systems in the uplands. As changes occur, appropriate management may only be achieved by understanding upland ecosystems and deciding which ecosystem services we need the uplands to provide.

1.6 Craneflies

Craneflies (Diptera: Tipulidae) are a key component of the invertebrate fauna of British upland peatlands (Coulson, 1988). As described above, Diptera constitute around 20% by weight of all soil invertebrates on blanket bog; this is almost entirely due to craneflies (Coulson, 1988). Craneflies are found throughout upland habitats, but their relative importance increases with altitude. They constitute around 5% of the invertebrate biomass of drier, lower-altitude heath and grassland (Coulson, 1988). On blanket bogs, however, their dominance is such that when adult craneflies emerge over several weeks in spring, around 75% of the annual above-ground invertebrate biomass is present (Coulson & Butterfield, 1985). On upland mineral soils, large-bodied *Tipula paludosa*, *T. varipennis* and *T. pagana* can reach densities of 30–100 final instar larvae m^{-2}; on peat, *T. subnodicornis* and the small-bodied *Molophilus ater* can reach final instar densities of over 100 m^{-2} and over 3000 m^{-2} respectively (Coulson & Whittaker, 1978). This dominance, along with the roles they play in ecosystem functions, means that craneflies could be seen as keystone invertebrates of blanket bogs.

Much of the work on cranefly biology has focused on mineral soil species, notably *T. paludosa* and *T. oleracea*, due to their importance as agricultural pests (e.g., Rennie, 1917; Mayor & Davies, 1976; Blackshaw, 1990; Blackshaw & Coll, 1999). Cranefly larvae eat decomposing plants, microorganisms, mosses and liverworts; their status as agricultural pests comes from species that eat grass and roots, which can damage crops and lawns (Pritchard, 1983). The life cycle of craneflies varies between species, with most temperate species being univoltine, but with some having two generations per year or taking multiple years per generation (Pritchard, 1983). However, the progression from eggs, through four larval instars to pupation and adult emergence, appears to be common to all species (Pritchard, 1983). Eggs and larvae live in moist environments, which are commonly soils, but also include mosses, vegetation, damp wood and running water (Coulson, 1959; Freeman, 1967). Although some species can tolerate relatively dry soils, this reliance on moisture for eggs and larvae is a defining feature of cranefly biology (Pritchard, 1983). The low temperatures, wet soil and lack of flowers on blanket peats can make conditions unsuitable for some invertebrates but the adaptation of craneflies to such conditions helps to explain their dominance (Coulson & Whittaker, 1978).

When the environment becomes too dry, eggs and larvae can rapidly die due to desiccation. The exact reason for the susceptibility to desiccation is unknown, but it is likely to be linked to cuticle properties (Pritchard, 1983). Soil moisture conditions, as determined by weather, may therefore strongly affect larval mortality (e.g., Coulson, 1962; Milne *et al.*, 1965; Meats, 1967b). This has long been understood, with an early study indicating that eggs and early larval instars are, “particularly susceptible to the prevailing physical conditions,” further noting that, “a wet summer and autumn foreshadows a plentiful supply of crane-fly in the following year,” (Rennie, 1917). Moisture availability may also interact with population size to drive density-dependent mortality through cannibalism, meaning that dry conditions may both directly and indirectly cause larval mortality (Blackshaw & Petrovskii, 2007). Moisture conditions are believed to be the primary driver of larval mortality (Pritchard, 1983), thus leading to temporal (e.g., Milne *et al.*, 1965) and spatial (e.g., McCracken *et al.*, 1995) trends in abundance.

Desiccation is not the only environmental influence on cranefly growth and survival. Although desiccation presents the greater risk, larvae are also susceptible to drowning (Meats, 1970; Pritchard, 1983; Blackshaw, 1990), thus some species may avoid the wettest habitats during wet periods (Coulson, 1962). Between the extreme conditions of flood and drought, higher larval growth rates are associated with wetter conditions (Meats, 1967a). Growth rates increase at higher temperatures, although the relationship may not be a simple linear one and the optimal temperature may change with developmental stage (Laughlin, 1967; Butterfield, 1976a; Butterfield & Coulson, 1988). Photoperiod also appears to influence development, with temperature sensitivity of growth and the occurrence of diapause both related to day length (Butterfield, 1976b). Indeed, the combination of temperature and photoperiod sensitivity may act to synchronise adult emergence over the range of altitudes and temperatures present in the uplands (Butterfield, 1976a; Coulson *et al.*, 1976).

Links between craneflies and climate have previously been used to create predictive models of cranefly abundance. Meats (1974a; 1974b) modelled *T. paludosa* and *T. oleracea* populations based on physiological responses to temperature and soil moisture, considering weather effects on fecundity, egg development and larval development. The model accounted for over 85% of variation in the intrinsic population growth rate, but overpredicted the extent of population crashes (Meats, 1974b). Blackshaw (1990) developed a model based on statistical associations between climate and records of larval abundance in Northern Ireland, which was used to estimate risk to agricultural fields (Blackshaw & Perry, 1994). Tulp and Schekkerman (2008) showed that climate variables predicted arctic tundra cranefly daily abundances, and that due to springs becoming warmer, emergence may peak increasingly early. Finally, models based on statistical associations with summer temperature have shown that in Britain, upland craneflies could emerge earlier (Pearce-Higgins *et al.*, 2005) and show population declines (Pearce-Higgins *et al.*, 2010; Pearce-Higgins, 2011b) due to climate change.

The synchronised emergence of adults is one of the features that make craneflies important to peatland ecosystems. This is observed in the two main upland peatland species, *T. subnodicornis* and *M. ater*. Although they are from different families (Tipulidae and Limoniidae respectively) and are very different sizes [*T. subnodicornis* pupal mass ~500 mg (Coulson, 1962), *M. ater* pupal mass ~1–2 mg (Hadley, 1971)], they display remarkably similar life cycles (Coulson *et al.*, 1976). Both are univoltine; adults emerge over several weeks in May and June, and eggs are laid within days of emergence; eggs hatch within a month, then three larval instars are passed through, each taking around one month; overwintering occurs in the fourth instar, with pupation occurring in April and May (Coulson, 1962; Hadley, 1971; Coulson *et al.*, 1976). Numbers emerging are substantial, with recorded daily emergence densities of over 14 m^{-2} for *T. subnodicornis* (Coulson, 1962) and 200–350 m^{-2} for *M. ater* (Hadley, 1969). Because of their high availability and biomass, adult craneflies are an important food source for breeding birds present on upland peatlands, such as Golden Plover, Dunlin and Red Grouse (e.g., Yalden, 1974; Butterfield & Coulson, 1975; Pearce-Higgins, 2010); this is discussed further in Chapters 4 and 5.

Craneflies are not only important as prey for upland birds. Across various habitats, they are prey items for farmland birds (Holland *et al.*, 2012), House Sparrows (Klvaňová *et al.*, 2012), Red-billed Choughs (Kerbiriou & Julliard, 2007), bats (Williams *et al.*, 2011), shrews (Churchfield, 1982), badgers (Cleary *et al.*, 2011), frogs (Houston, 1973) and spiders (Coulson & Whittaker, 1978). Craneflies also play roles in ecosystem functions. In mineral soils, cranefly larvae affect hydrological processes such as infiltration and water flow routes (Holden & Gell, 2009), aid leaf litter processing (Pritchard, 1983) and affect soil carbon compounds and microbial communities (Grayston *et al.*, 2001). On blanket bogs, cranefly larvae aid decomposition of plant material (Coulson & Butterfield, 1978; Standen, 1978) and may be the most important herbivores after sheep (Coulson & Whittaker, 1978). Furthermore, after the spring emergence peak, dead adult craneflies account for a significant release of nutrients to the upper soil layers (Coulson & Whittaker, 1978). Therefore, craneflies play an important role in soils and, due to their biomass and numerical dominance, play a particularly important role on upland blanket bogs.

1.7 Thesis overview

British upland peatlands are an important habitat within the UK, but inappropriate land management and climate change threaten their continued provision of ecosystem services. Upland peatlands support important biodiversity, in particular the unique bird assemblage. Several bird species of conservation or economic importance rely on synchronised adult cranefly emergence for food during breeding, but due to the sensitivity of cranefly larvae to drought, drier conditions could reduce populations. Smaller cranefly populations could harm breeding birds and affect other ecosystem processes. Models based on statistical relationships with climate can be used to project population trends, but these often rely on surrogate variables rather than soil moisture, which is the direct driving factor. As peatland restoration often seeks to raise water tables, understanding how soil moisture affects cranefly abundance, and how widely-used restoration methods impact soil moisture, could provide valuable information. Further, if cranefly populations could be modelled as a function of peatland moisture, climate change impacts could be examined. Understanding such issues could prove essential for longer-term conservation and land management in the uplands, where individual areas are expected to provide multiple ecosystem services.

This primary aims of this thesis are:
1) Explore the relationships between cranefly abundance, moisture and peatland drainage.
2) Use field-derived relationships to develop a predictive model of cranefly abundance that can be used to examine effects of moisture variation on cranefly populations.
3) Use the model to explore spatial relationships between peatland cranefly abundance and upland breeding bird populations.
Therefore, this thesis will provide information on how an important environmental driver affects the abundance of keystone upland invertebrates, and will explore how land management and climate change could affect their population sizes. Further, by examining links between cranefly abundance and bird populations, it will explore how species of conservation interest at higher trophic levels are influenced by prey species, which in turn may be strongly influenced by environmental conditions. Together, these aims could help to identify threats to upland peatland biodiversity and opportunities for adaptation management under climate change. Figure 1.3 shows how ideas and processes are developed throughout the thesis, and how the different chapters relate to one another.

The contents of the remaining chapters are as follows:

- Chapter 2 describes a large-scale field experiment that examines the relationship between cranefly abundance and soil moisture in upland peatlands. The key hypothesis tested is that cranefly abundance increases with soil moisture. Areas with active drainage are compared to those that have had drains blocked; this is used to test the hypotheses that 1) blocking drains increases soil moisture, and 2) that drain blocking should lead to higher cranefly abundances.
- Chapter 3 presents an extension of an existing model of peatland processes, allowing water table depth predictions to be made on a monthly scale, driven only by easily-available climate data and without extensive local parameterisation. This development is important because biodiversity and ecosystem functions may be affected by water tables at particular times of year. Model output is evaluated against data from four blanket bogs in England and Wales, with success judged on two criteria: 1) Can the model accurately predict water table position, as defined by mean, maximum and minimum water table depths? 2) Can the model predict a large proportion of the variation in water table depth over time?

- Chapter 4 combines the model developed in Chapter 3 with field data from Chapter 2 to allow projections of cranefly abundance to be made, driven by variation in soil moisture. The model is validated by examining 1) whether modelled water table depth is a significant predictor of observed soil moisture, and 2) whether modelled cranefly abundance is positively correlated with observed abundance. The model is then used to make projections of cranefly abundance under climate change, comparing landscapes subject to drainage and those for which drains have been blocked. These projections are used to test the hypotheses that 1) climate change will drive cranefly abundance declines by causing peat to become drier, and 2) blocking peatland drains will reduce the magnitude of climate-driven declines. Model results will therefore identify whether climate change does threaten cranefly populations, and whether drain blocking is a viable option for adaptation management.
- Chapter 5 uses the modelling process developed in Chapter 4 to make large-scale spatial estimates of cranefly abundance; these projections are used to explore relationships between expected cranefly abundance and observed breeding bird distributions, using data from two years of regional-scale bird surveys. For Golden Plover, the hypotheses are tested that 1) bird abundance is significantly and positively associated with cranefly abundance, and 2) changes in bird distributions over time (i.e., extinctions, colonisations and abundance change) are significantly associated with cranefly abundance. The predictive ability of modelled cranefly abundance is compared to other possible drivers of bird distributions, to establish how well food availability compares to observed environmental surrogates. Finally, by examining the relationship between modelled cranefly abundance and observed bird abundance across multiple species, the hypothesis is tested that bird species with a larger proportion of craneflies in the diet are more strongly influenced by variation in cranefly abundance.
- Finally, Chapter 6 discusses findings from the thesis in the context of the wider literature, considering directions for future work, and land management and conservation implications.

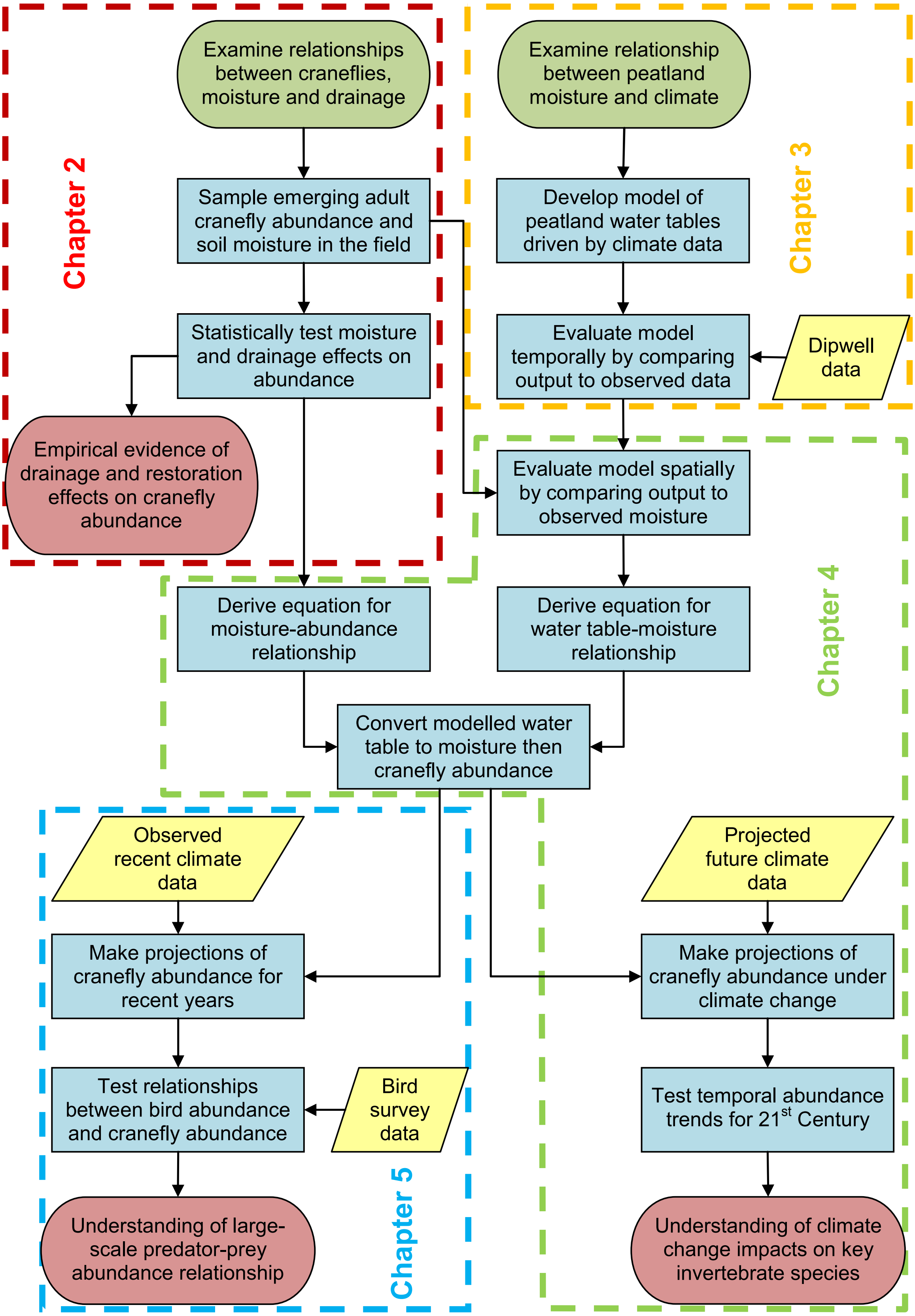

Figure 1.3. Flow chart showing initial concepts (green boxes), processes (blue boxes), main outputs (red boxes) and external input data (yellow boxes) from the thesis. Dashed boxes show which chapter the material is covered in.

Chapter 2

Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies

2.1 Abstract

The capacity of peatlands in the northern hemisphere to provide carbon storage, maintain water quality and support northern biodiversity is threatened by a combination of climate change and inappropriate land management. Historical drainage and increasing temperatures threaten the maintenance of the high water tables required for effective peatland functioning, and there is an urgent need to develop appropriate adaptation strategies. Here we use a large-scale replicated experimental design to test the effects of artificial drainage and drain blocking upon soil moisture and cranefly (Diptera: Tipulidae) abundance. Craneflies constitute a key component of peatland biological communities; they are important herbivores and a major prey item for breeding birds. However, they are also susceptible to drought, so are at risk from future climate change. We found that cranefly abundance increased with soil moisture, in a wedge-shaped relationship; high soil moisture is a necessary condition for high cranefly abundance. Blocking drains increased both soil moisture (by 0.06 $m^3.m^{-3}$ in 2009 and 0.23 $m^3.m^{-3}$ in 2010) and cranefly abundance (1.3-fold in 2009, 4.5-fold in 2010), but the strength and significance of the effects varied between years. The benefits of restoring ecosystem moisture levels are likely to be greatest during dry years and at dry sites. This study provides some of the first evidence that adaptation management can potentially reduce some of the negative effects of climate change on vulnerable peatland systems. Management to maintain or increase soil moisture in peatlands can therefore be expected to increase populations of craneflies and their avian predators (which are of conservation and economic interest), but also increase the resilience of the ecosystem to future warming and increasingly frequent droughts, and improve carbon storage and water quality.

2.2 Introduction

Environmental and conservation agencies across the world are faced with the need to develop adaptation strategies for climate change, but such strategies are contentious and often based on limited biological information (Heller & Zavaleta, 2009). Much discussion of adaptation in the literature has focussed on accommodating change so that species and habitats may shift their distributions polewards and upwards in order to track the changing climate (Vos *et al.*, 2008; Willis *et al.*, 2009). However, this option may not be appropriate for high-latitude (hereafter "northern") and montane (hereafter "upland") systems limited by available land-area to shift into. Therefore, management to increase the resistance of northern species and habitats to change may be the only viable option, but is largely untested (Pearce-Higgins *et al.*, 2011). Northern peatland ecosystems represent one of the systems where these issues are particularly urgent for both biodiversity and climate change mitigation reasons. They contain the greatest concentration of stored carbon in terrestrial ecosystems, a portion of which could be converted to greenhouse gases under climate change (Gorham, 1991; Freeman *et al.*, 1992; Holden, 2005b; Worrall & Evans, 2009). This creates the potential for positive feedback between climate warming and greenhouse gas emissions, which may cause peatlands to become major sources of carbon (Dorrepaal *et al.*, 2009). Northern peatlands also support important biological communities and unique species (Chapman *et al.*, 2003). These are particularly vulnerable to detrimental climate change effects, as there is little colder land available to which such species could retreat (e.g., Jetz *et al.*, 2007). The relatively warm, southern margins of northern peatlands could be expected to be the first areas to exhibit degradation under climate warming, and there may already be signs of ecosystem impacts (Hendon & Charman, 2004; Caporn & Emmett, 2009). Some of the most extensive and southernmost peatlands occur in the UK, which supports 7–13% of the world's blanket bog area, and a range of internationally important habitats and bird populations (Ratcliffe & Thompson, 1988; Thompson *et al.*, 1995; Pearce-Higgins *et al.*, 2009a). Consequently, the development of climate change adaptation strategies for these ecosystems is particularly relevant.

Peatlands are formed where waterlogging slows decay of plant materials, allowing peat to accumulate; key peat-building *Sphagnum* species are particularly sensitive to moisture availability (Gorham & Rochefort, 2003). Maintaining soil moisture is therefore critical to peatland survival, but their hydrological systems are under threat from both climate change and intensification of land use (Bragg & Tallis, 2001). Throughout the world, peatlands have been drained for agriculture, forestry and extraction, including the USA, Canada, Finland, Sweden and Ireland (Burke, 1961; Fisher *et al*., 1996; Huttunen *et al*., 2003; Vasander *et al*., 2003). In the UK, drainage of blanket bogs for agriculture was particularly prevalent during the latter part of the 20th Century (Usher & Gardner, 1988; Holden *et al*., 2004); this resulted in widespread habitat degradation (Bragg & Tallis, 2001; Holden *et al*., 2007c). Climate change projections of drier summers and increased temperatures are also likely to be detrimental, for both abiotic peatland processes and for the biological communities that live there (Holden *et al*., 2007c). Historical drainage and future climate change may interact to increase rates of peatland degradation and biodiversity loss through reductions in soil moisture; drying effects of drainage ditches may already be greater in drier areas (Coulson *et al*., 1990). Blocking drainage ditches should raise soil moisture levels (Wilson *et al*., 2010); this could potentially ameliorate the future drying effects of climate change. However, recent enthusiasm for blocking drains on degraded peatlands has not been matched by direct evidence of its capacity to restore the ecosystem and its associated biodiversity (Wallage *et al*., 2006; Holden *et al*., 2007c).

Craneflies (Diptera: Tipulidae) are a keystone invertebrate of peatland ecosystems, particularly in blanket bog. They are a dominant component of the macro-invertebrate community and play an important role in litter decomposition and herbivory, in the UK and elsewhere (Coulson & Whittaker, 1978; Standen, 1978; Coulson, 1988; Tulp & Schekkerman, 2008). In the UK, the most important of these species is *Tipula subnodicornis*, whose adults undergo a mass emergence in May and June that constitutes nearly 75% of annual above-ground invertebrate biomass for blanket bog (Coulson, 1962; Coulson & Butterfield, 1985). *Tipula subnodicornis* and another common upland species, *Molophilus ater*, share a similar life-cycle. Eggs are laid in peat, hatching after three to four weeks; three larval instars are passed through, each lasting three to four weeks; overwintering occurs in a fourth larval instar, lasting from October to April; and pupation occurs in April and May, with adults emerging after around three weeks (Coulson, 1962; Hadley, 1971). Therefore, the whole life-cycle, other than the few days spent above ground as adults, is spent in the upper layers of peat.

Due to their high availability and nutrient content, craneflies are a vital component of the diet of many of the bird species associated with peatland ecosystems (Butterfield & Coulson, 1975; Park *et al*., 2001; Buchanan *et al*., 2006a; Pearce-Higgins, 2010). Cranefly abundance therefore influences productivity for birds of both economic and conservation importance (Red Grouse, Park *et al.*, 2001; Golden Plover, Pearce-Higgins & Yalden, 2004). They may also influence bird habitat selection (Whittingham *et al.*, 2001; Pearce-Higgins & Yalden, 2004). However, the size of cranefly populations is influenced by soil conditions, as the eggs and larvae (leatherjackets) of many species are highly susceptible to mortality through desiccation (e.g., Coulson, 1962; Meats, 1967b; Pritchard, 1983). Indeed, in lowland cranefly species, dramatic population crashes have been observed following droughts, and peatland cranefly abundance is lower following hotter summers, with subsequent effects on their avian predators (Milne *et al.*, 1965; Pearce-Higgins *et al.*, 2010).

Given the urgent need to test whether blocking drainage ditches is an effective management strategy to preserve ecosystem functions and biodiversity (Gorham & Rochefort, 2003), we test the effects of soil moisture and drainage on cranefly populations. Uniquely, we use a large-scale experimental approach to test the following hypotheses:
1) Cranefly abundance increases with soil moisture.
2) Blocking drainage ditches increases soil moisture and restores cranefly abundance, relative to areas in which drainage remains active.
Combined, these hypotheses examine the extent to which peatland cranefly populations are likely to be negatively impacted by projected increases in drought frequency and test the potential for restorative management to provide effective climate change adaptation. The implications of these impacts for peatland conservation, and for peatland bird populations, are discussed.

2.3 Materials and Methods

2.3.1 Study sites

The study was conducted over two years. In 2009, sampling was conducted at Lake Vyrnwy RSPB reserve in Wales (52°47'N, 3°34'W), in four experimental paired river sub-catchments (altitude 440 – 550m a.s.l.; area 40 – 80 ha); one member of each pair had blocked drainage ditches, while the other had unblocked drains (Figure 2.1). Drains were established during 1940 to 1980; drains were blocked in autumn/winter 2007 by inserting heather bales at 5 – 10 m intervals. In 2010, in addition to resampling one paired sub-catchment at Lake Vyrnwy, we sampled across a greater environmental gradient by including two additional sites: Wood Moss, part of Leek Moors SSSI in the South Pennines (5°13'N, 2°00'W; altitude 410 – 470m a.s.l.; area 10 ha) and Bransdale Moor in the North York Moors (5°24'N, 1°03'W; altitude 400 – 450m a.s.l.; area 75 ha) (Figure 2.1). At Wood Moss, drains were cut around 1945 to 1955 and blocked in 2006, using peat turves; blocked and unblocked drains were in discrete areas. At Bransdale Moor, drains were cut during the 1960s, and blocked in March 2008, also using peat turves; blocked and unblocked drains were mostly in discrete areas, but with some unblocked drains interspersed with blocked ones.

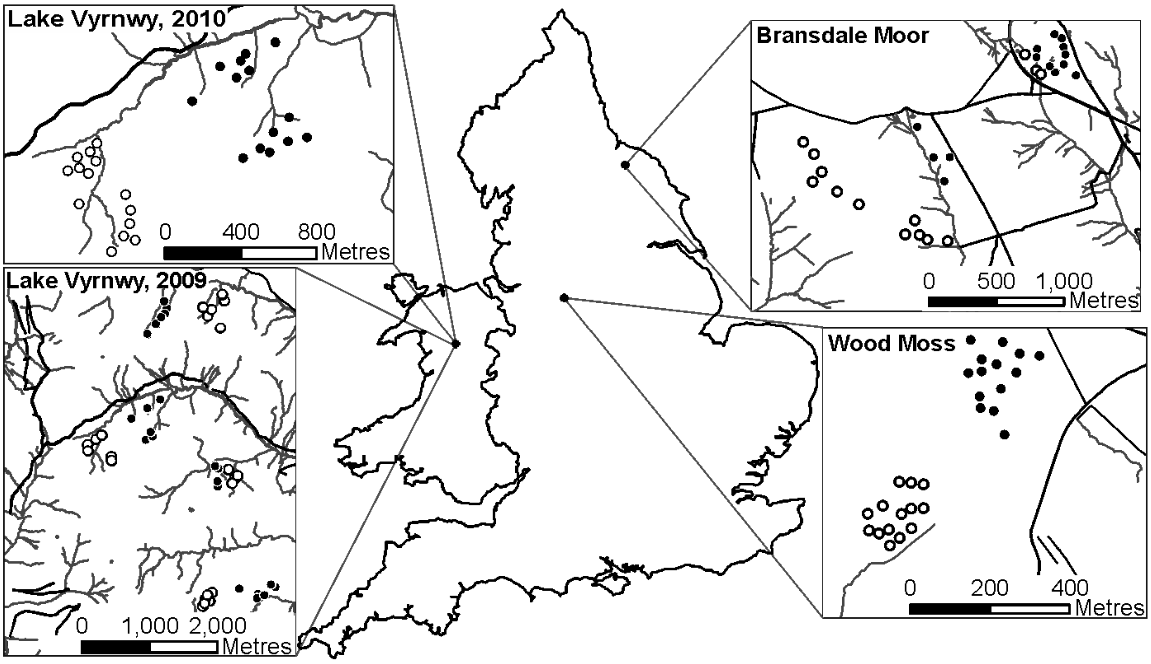

Figure 2.1. Map of England and Wales showing locations of field sites, and sampling locations at blocked drains (●) and unblocked drains (○) within each. Within site maps, black lines denote roads and paths; grey lines denote water courses. Each sampling location held four traps. The country map was created using 'blighty' R package (Lucy, 2010). Site maps © Crown Copyright/database right 2010. An Ordnance Survey/EDINA supplied Service: License 100018355.

Vegetation at Lake Vyrnwy was primarily blanket bog vegetation, with *Eriophorum vaginatum*, *Calluna vulgaris* and *Scirpus cespitosus* widely found, but with *Molinia caerulea*-dominated grassland and dry heath also present. At Wood Moss, vegetation around blocked drains was *Eriophorum vaginatum* and *Deschampsia flexuosa*-dominated blanket mire, with some *Vaccinium myrtillus*, whereas around unblocked drains *Molinia caerulea* was dominant, with minor amounts of *Eriophorum vaginatum*. At Bransdale Moor, *Calluna vulgaris* and *Vaccinium myrtillus* were dominant, with *Eriophorum vaginatum* becoming common in wetter areas, and with the peat surface exposed in some areas.

2.3.2 Sampling procedure

Sampling locations were placed at random points along drains, but were constrained to be separated by a radius of ≥50 m. At Wood Moss, where there were fewer drains, the condition was relaxed so that only sampling locations on the same drain had to be ≥50 m apart. In 2009, 44 sampling locations were selected at Lake Vyrnwy, spread amongst four experimental sub-catchments (22 at blocked drains, 22 at unblocked drains; Figure 2.1). In 2010, 28 sampling locations were selected at each site (14 at blocked drains, 14 at unblocked drains; Figure 2.1), giving 84 locations in total. Four traps were set at each location, totalling 176 traps in 2009 and 336 traps in 2010.

Emergence traps sampled adult craneflies. Traps consisted of a plastic basket (L41 cm × W28 cm × H17 cm) pegged onto the peat, open end down, with yellow sticky traps on every inner surface. Traps were set by 3rd May, and were active for three consecutive periods of around 20 days, covering the *Tipula subnodicornis* emergence season. At the end of each period, craneflies were counted and sticky traps replaced. Counts from all three periods were summed to give a total for each trap. The most common species caught were *T. subnodicornis*, *Limonia dilutior, Molophilus ater*, *Molophilus sp.* (probably *M. occultus*) and *Tricyphona immaculata*. We consider the total abundance of all craneflies within the analyses.

Stewart and Lance (1991) showed that water tables were lowered up to 2 m downslope of drains, but that there was no significant drying midway between drains; to reflect this, four traps were placed at each sampling location (Figure 2.2). The first two traps were at the drain edge. At blocked drains, one was immediately ‘upstream’ of a dam, and one was between dams; in 2009, these had mean distance apart of 4.66 m (standard deviation $\sigma = 1.18$ m, this variation reflecting varying distances between dams); in 2010, Lake Vyrnwy traps were 2.56 m apart ($\sigma = 0.32$ m), Wood Moss traps were 4.43 m apart ($\sigma = 0.86$ m), and Bransdale traps were 4.67 m apart ($\sigma = 1.13$ m). At unblocked drains, the traps were 5 m apart. The second two traps were parallel to the first two, but 10 m downslope. This design enabled the magnitude of drainage effects to be derived from the comparison between the drain edge and 10 m away.

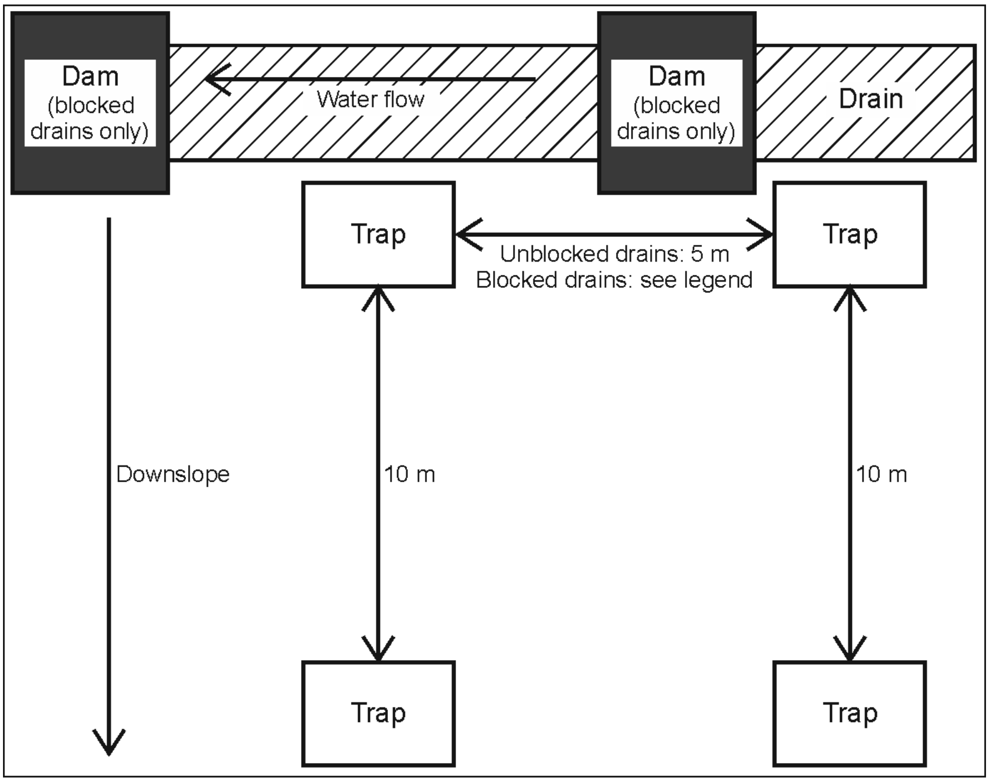

Figure 2.2. Diagram showing the positions of the four traps at sampling points. Diagram shows the layout at a blocked drain. The first trap is placed immediately upstream of a dam, and the next is placed midway between that dam and the next dam downstream, meaning that the distance between these traps varies slightly between drains due to variation in dam spacing. At unblocked drains, there were no dams, so these traps were always 5 m apart.

At the end of each trapping period, a ThetaProbe ML2 (Delta-T Devices Ltd., Cambridge) was used to take five soil moisture readings from under each trap, giving 15 readings per trap in total. The mean value was then calculated for each trap. Raw data were converted to volumetric soil moisture (m^3 water per m^3 soil) content using the calibration curve for organic soils from the ThetaProbe manual; the highest values imply a local water table at or above the peat surface. Although moisture at the time of sampling is unlikely to influence emerged cranefly abundance directly (the strongest influence should be on egg and early larval instars), spatial variation in soil moisture was consistent (i.e., the driest locations were always the driest; Spearman's ρ correlations varied between 0.77 and 0.86 when comparing sampling periods).

2.3.3 Analysis

Analysis was completed in R v2.11 (R Development Core Team, 2010). The dependent variable in count data analyses was total cranefly abundance for each trap. As this was a discrete value, the ‘vcd’ R package (Meyer *et al.*, 2010), was used to establish a suitable distribution for modelling. In both years, abundance data did not differ significantly from a negative binomial distribution (2009, mean = 2.53, $\theta = 0.909$; 2010, mean = 3.24, $\theta = 0.540$), so this was specified in all models.

Random effects were required to account for spatial clustering of data. Consequently, Generalized Linear Mixed Models (GLMMs) with negative binomial error and log link were used. As the experimental design varied between years (one site in 2009, multiple sites in 2010), the two years were analysed separately. Random effects for 2009 were ‘sampling location’ (a unique code for each quartet of traps) nested within ‘sub-catchment’, and for 2010 were ‘sampling location’ nested within ‘site’. To fit models, the ‘MASS’ R package (Venables & Ripley, 2002) was used, which fits GLMM parameters using penalised quasi-likelihood (Bolker *et al.*, 2009).

Grazing animals occasionally tipped the traps over; in 2009, 27 trap sessions were lost in this way (25 from blocked drains, 2 from unblocked); in 2010, 25 trap sessions were lost (all from blocked drains). Counts from interrupted trapping periods were excluded from the calculation of total abundance for that trap. To account for this, an offset of ln(completed trapping periods) was entered into abundance models.

For soil moisture analysis, the dependent variable was mean soil moisture for each trap. These data were also modelled within a mixed model framework, initially specifying Gaussian error and identity link. Shapiro-Wilk tests indicated that 2009 residuals differed significantly from a Normal distribution, but 2010 residuals did not. However, linear mixed models are relatively robust to misspecification of the error distribution (Jacqmin-Gadda *et al.*, 2007), so modelling proceeded with the Gaussian error and identity link. The model fitting algorithm and random effects structures were identical to those used for abundance models.

To test the effect of soil moisture on abundance, the fixed effect was mean volumetric soil moisture. To test the effects of drain blocking and proximity to drains on cranefly abundance and soil moisture, two fixed effects, ‘blocked’ (blocked or unblocked) and ‘proximity’ (drain edge or 10 m back) were entered, along with the interaction of these two effects.

2.4 Results

2.4.1 Relationship between abundance and moisture

Cranefly abundance increased with mean soil moisture (Figure 2.3). In both years, the relationship was wedge-shaped: abundances were low at relatively dry sites but could be high or low at relatively wet sites. GLMMs describing abundance as a linear function of mean soil moisture indicated that overall, the relationship was positive and significant in both years (Table 2.1). When blocked and unblocked drains were modelled separately, no significant relationship was found for blocked drains (most had high soil moisture; see below) but cranefly abundance increased significantly with soil moisture at unblocked drains (Table 2.1).

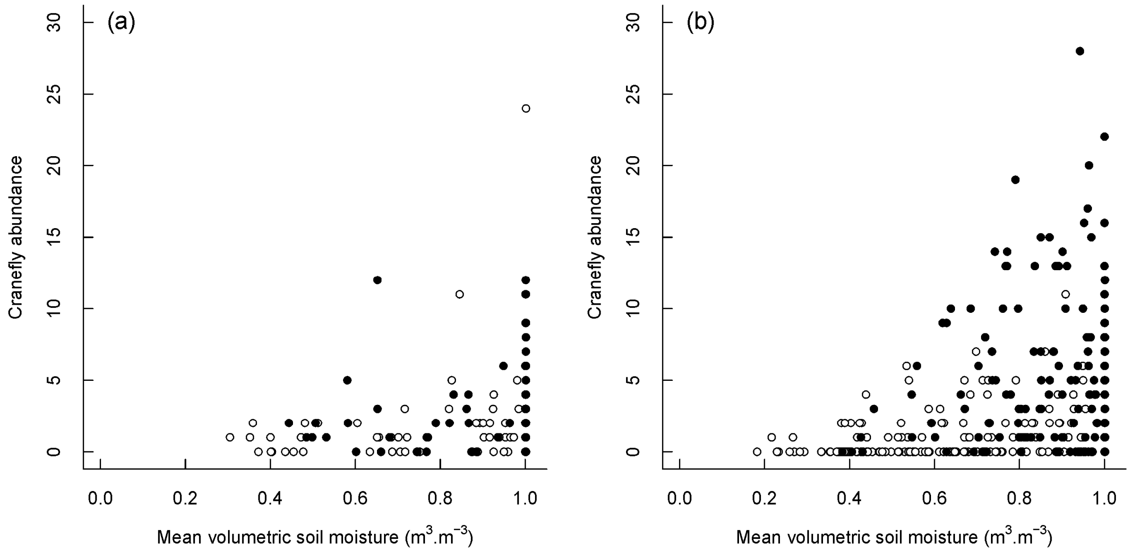

Figure 2.3. Relationship between mean volumetric soil moisture and cranefly abundance, for sampling locations at blocked drains (●) and unblocked drains (○), in a) 2009 and b) 2010.

Table 2.1. Results from GLMMs with negative binomial error and log link, describing cranefly abundance as a function of mean soil moisture. An offset of ln (number of completed trapping sessions) was entered to account for the exclusion of traps that were damaged (tipped over). Random effects were location nested within catchment in 2009, and location nested within site in 2010. Bold font highlights moisture slope significantly different from 0 at *P*<0.05. Coefficients represent slope of relationship.

Data subset	Standard deviations of random effects		Fixed effects				
			Coefficient	Standard error	DF	t-value	*P*-value
	Catchment	Location					
2009, all data	**0.329**	**0.752**	**1.025**	**0.439**	**131**	**2.332**	**0.021**
2009, blocked	0.220	0.758	0.311	0.653	65	0.477	0.635
2009, unblocked	**0.586**	**0.602**	**1.518**	**0.584**	**65**	**2.600**	**0.012**
	Site	Location					
2010, all data	**0.299**	**0.840**	**2.602**	**0.400**	**251**	**6.504**	**<0.001**
2010, blocked	0.486	0.495	0.485	0.564	125	0.859	0.392
2010, unblocked	**<0.001**	**0.637**	**2.631**	**0.558**	**125**	**4.719**	**<0.001**

2.4.2 Effects of drains: soil moisture

Soil moisture was increased where drains were blocked (Table 2.2a; Figure 2.4). The blocked*proximity interaction was significant and positive in both years (Table 2.3), implying that soil moisture behaves in different ways at blocked and unblocked drains: soil moisture levels were strongly reduced at unblocked drain edges, whereas distance from the drain edge had little impact at blocked drains (Figure 2.4). However, the strength of effects varied with year. In the wetter of the two years (2009; at Lake Vyrnwy), moisture levels were reduced adjacent to free-flowing, unblocked drains, but not 10 m away. In 2010, however, this drying effect extended to 10 m from unblocked drains (hence the significant "Blocked" main effect, as well as the significant interaction; Table 2.3; Figure 2.4).

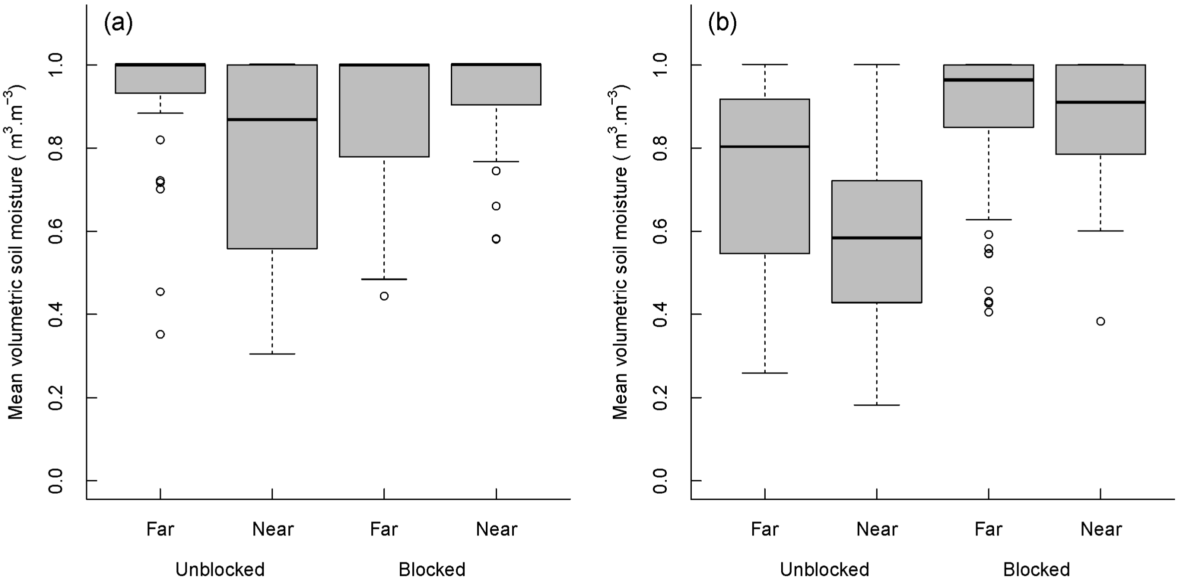

Figure 2.4. Comparison of mean volumetric soil moisture, between blocked and unblocked drains, and at the drain edge (Near) and 10m from the drain (Far), for a) 2009 and b) 2010. Box midline indicates median, box edges indicate interquartile range. Whiskers indicate range of data; points indicate data outside 1.5× the interquartile range.

Table 2.2. Mean values and standard deviations (σ) of a) volumetric soil moisture and b) cranefly abundance at sampling locations in both years of the study, showing the overall mean, means from blocked/open drains, and means from drain edge/10 m from drain trap positions.

(a)	Soil moisture ($m^3.m^{-3}$)		
	Overall	Drain edge	10 m from drain
2009	0.882 (σ = 0.187)		
Blocked	0.912 (σ = 0.155)	0.940 (σ = 0.117)	0.884 (σ = 0.182)
Unblocked	0.852 (σ = 0.212)	0.769 (σ = 0.239)	0.934 (σ = 0.142)
2010	0.770 (σ = 0.218)		
Blocked	0.883 (σ = 0.145)	0.874 (σ = 0.131)	0.892 (σ = 0.157)
Unblocked	0.657 (σ = 0.221)	0.578 (σ = 0.196)	0.736 (σ = 0.216)

(b)	Cranefly abundance (individuals per trap)		
	Overall	Drain edge	10 m from drain
2009	2.528 (σ = 3.104)		
Blocked	2.841 (σ = 2.932)	2.818 (σ = 2.943)	2.864 (σ = 2.954)
Unblocked	2.216 (σ = 3.253)	1.864 (σ = 2.398)	2.568 (σ = 3.926)
2010	3.235 (σ = 4.394)		
Blocked	5.298 (σ = 5.192)	5.833 (σ = 5.327)	4.762 (σ = 5.027)
Unblocked	1.173 (σ = 1.795)	1.202 (σ = 1.893)	1.143 (σ = 1.701)

Table 2.3. Results from Linear Mixed Models of mean volumetric soil moisture, with Gaussian error and identity link. Random effects were location nested in catchment (2009) or location nested in site (2010). Fixed effects were blocked/unblocked and proximity (drain edge/10 m away). Intercepts represent the expected per-trap moisture value at ‘far’ traps at unblocked drains; ‘Blocked’ represents the difference between the intercept and ‘far’ traps at blocked drains; ‘Proximity’ represents the difference between the intercept and ‘near’ traps at unblocked drains; ‘Blocked*Proximity’ represents the difference at ‘near’ traps at blocked drains, that is not explained by summing ‘Blocked’ and ‘Proximity’ main effects. *P*-values refer to a test of the coefficient being 0; bold font highlights results significant at *P*<0.05.

	Coefficient	Standard error	DF	t-value	*P*-value
(a) 2009					
Intercept	**0.934**	**0.036**	**130**	**26.152**	**<0.001**
Blocked	-0.050	0.037	39	-1.347	0.186
Proximity	**-0.165**	**0.035**	**130**	**-4.726**	**<0.001**
Blocked * Proximity	**0.221**	**0.049**	**130**	**4.485**	**<0.001**
Random effects: catchment, σ = 0.048; location in catchment, σ = 0.042					
(b) 2010					
Intercept	**0.736**	**0.055**	**250**	**13.494**	**<0.001**
Blocked	**0.157**	**0.029**	**80**	**5.463**	**<0.001**
Proximity	**-0.158**	**0.018**	**250**	**-8.728**	**<0.001**
Blocked * Proximity	**0.139**	**0.026**	**250**	**5.444**	**<0.001**
Random effects: site, σ = 0.087, location in site, σ = 0.102					

2.4.3 Effects of drains: cranefly abundance

In 2009, 445 craneflies were caught; 250 at blocked drains and 195 at unblocked drains. In 2010, 1087 craneflies were caught; 890 at blocked drains and 197 at unblocked drains. As counts from traps tipped over by animals were excluded from total counts, and as the damage happened more frequently at blocked drains, if anything, the differences reported here could be slightly conservative. Effects on cranefly abundance were not as strong as those observed for soil moisture (Table 2.2b), and only attained significance in 2010 (Table 2.4; Figure 2.5). In 2010, there was significantly higher abundance at blocked drains; an overall mean of 5.30 per trap ($\sigma = 5.192$) at blocked drains and 1.17 per trap ($\sigma = 1.795$) at unblocked drains, representing a 4.5-fold difference in density. There was no significant difference between the drain edge and 10 m away at unblocked drains, but the blocked*proximity interaction term was marginally non-significant (Table 2.4; see Figure 2.5b). In 2009, the coefficients (Table 2.4) and trends (Figure 2.5) were in the same direction as those from 2010, but the effect (if any) was much weaker (2.84 per trap, $\sigma = 2.932$, at blocked drains; 2.22 per trap, $\sigma = 3.253$, at unblocked drains, representing a 1.3-fold difference) and no coefficient was significantly different from 0.

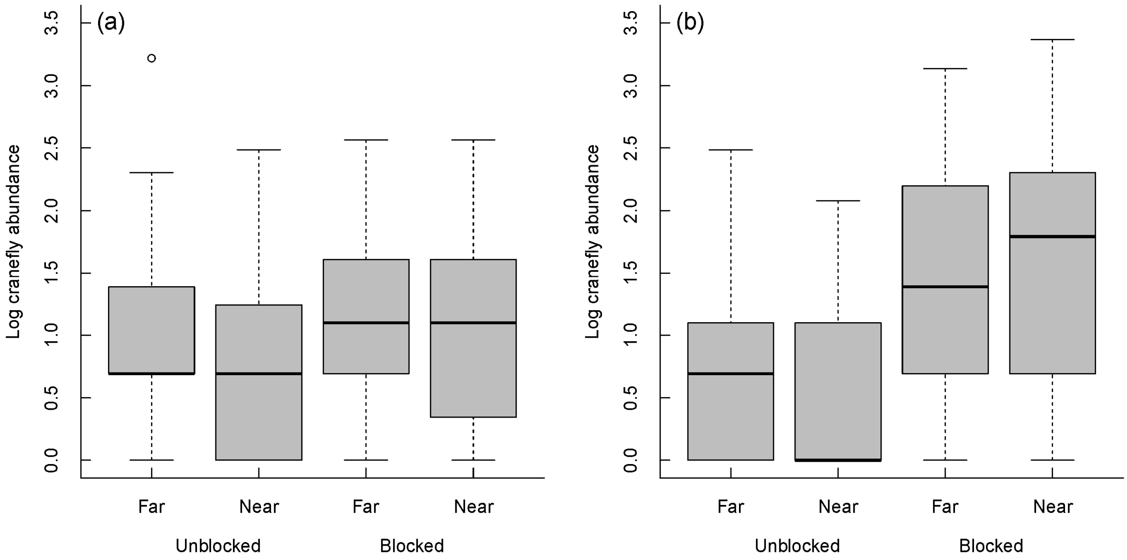

Figure 2.5. Comparison of log cranefly abundance between blocked and unblocked drains, and at traps at the drain edge (Near) and 10m from the drain (Far), for a) 2009 and b) 2010. Data were transformed as log(1+abundance) before plotting. Box midline indicates median, box edges indicate interquartile range. Whiskers indicate range of data within 1.5× the interquartile range; points indicate data outside 1.5× the interquartile range.

Table 2.4. Results from GLMMs of cranefly abundance, with negative binomial error and log link. Random effects were location nested in catchment (2009) or location nested in site (2010). Fixed effects were blocked/unblocked and proximity (drain edge/10 m away). An offset of ln(number of completed trapping sessions) was entered to account for the exclusion of traps that were damaged (tipped up). Coefficients represent expected effects on the predictor scale (i.e., log-transformed) after the offset has been taken into account: intercepts represent the expected per-trap abundance at 'far' traps at unblocked drains; 'Blocked' represents the difference between the intercept and 'far' traps at blocked drains; 'Proximity' represents the difference between the intercept and 'near' traps at unblocked drains; 'Blocked*Proximity' represents the difference at 'near' traps at blocked drains, that is not explained by summing 'Blocked' and 'Proximity' main effects. *P*-values refer to a test of the coefficient being 0; bold font highlights results significant at $P<0.05$; italic font highlights results marginally not significant at $0.05 \leq P < 0.1$.

	Coefficient	Standard error	DF	t-value	*P*-value
(a) 2009					
Intercept	*-0.572*	*0.289*	*130*	*-1.975*	*0.050*
Blocked	0.348	0.293	39	1.187	0.243
Proximity	-0.261	0.190	130	-1.372	0.172
Blocked * Proximity	0.223	0.261	130	0.855	0.394
Random effects: catchment, σ = 0.393; location in catchment, σ = 0.747					
(b) 2010					
Intercept	**-1.519**	**0.289**	**250**	**-5.255**	**<0.001**
Blocked	**1.403**	**0.217**	**80**	**6.452**	**<0.001**
Proximity	-0.136	0.174	250	-0.781	0.436
*Blocked * Proximity*	*0.408*	*0.227*	*250*	*1.798*	*0.073*
Random effects: site, σ = 0.413, location in site, σ = 0.667					

2.5 Discussion

2.5.1 Relationship between abundance and moisture

The results showed that the abundance of craneflies, keystone peatland invertebrates, is positively related to soil moisture. The mechanism generating the relationship is likely to be the susceptibility of cranefly eggs and larvae to desiccation, which increases mortality and reduces growth (Laughlin, 1958; Coulson, 1962; Meats, 1967b; Meats, 1967a; Meats, 1968). This presumably underpins the observed decline in cranefly abundance following high summer temperatures (Pearce-Higgins *et al*., 2010); hotter summers are usually associated with a drier peat surface. As the UK uplands are expected to experience hotter, drier summers in the future (Holden *et al*., 2007c), climate change is likely to reduce the abundance of craneflies substantially. Our results confirm the critical role of soil moisture in driving such declines.

Cranefly abundance was consistently low where the peat was dry, suggesting that soil moisture is limiting in such locations. In contrast, abundance was highly variable in wet locations, creating a wedge-shaped relationship between abundance and moisture availability (Figure 2.3). Abundance was generally higher in wet areas, but the aggregated nature of cranefly populations, along with additional factors such as dispersal ability, food availability and predation, may cause variation in abundance where moisture is not limiting (Coulson, 1962; Freeman, 1967; Freeman, 1968).

Interestingly, the abundance-moisture relationship was significant at unblocked drains, but not at blocked drains. This may indicate that cranefly abundance has not yet reached equilibrium with soil moisture in areas of drain blocking. Alternatively, water table fluctuations are smaller after drain blocking (Wilson *et al*., 2010), which may provide a buffering effect against decreases in soil moisture; even during relatively dry periods, there may be sufficient soil moisture to reduce the risk of desiccation mortality. To clarify these possibilities, it may be instructive to conduct a mesocosm and additional field experiments, whereby moisture regimes and water tables are controlled directly, in both total amount (i.e., low moisture vs. high moisture) and in variance (i.e., low fluctuations vs. high fluctuations). This would not only provide a controlled way to study causal mechanisms in the relationship between cranefly abundance and soil moisture, but would also allow us to study the possible impacts of changing drought frequencies in peatlands under climate change.

2.5.2 Effects of drainage ditches and drain blocking

Drain blocking had a significant effect on soil moisture in both years, but only increased cranefly abundance significantly in 2010 (Figure 2.4). The likely explanation for the difference between years is that 2009 was wetter than 2010 (see mean soil moisture values in Table 2.2a). Under wet conditions, drainage ditches generate a highly localised moisture reduction next to the drains, but this effect extends further from the drainage ditches under dry climatic conditions and on steeper ground (Coulson *et al*., 1990; Stewart & Lance, 1991). Wilson *et al*. (2010) showed that drain blocking raises water tables and removes a 'dry zone' within 5 m of a drain. Taken together, these findings suggest that dry areas, or areas where soil moisture fluctuates strongly, can be reduced by drain blocking, but that under wetter conditions, the difference in soil moisture between blocked and open drains may be smaller. Reducing or removing dry areas would be an important aspect of climate change adaptation in peatlands, given that dry areas may form foci for peatland erosion and degradation (e.g., Holden *et al*., 2004).

Our results showed a statistically significant 4.5-fold increase in cranefly abundances at blocked drains in 2010. The much weaker 1.3-fold increase at blocked drains and non-significant models (Table 2.4) in 2009 may be a consequence of overall population density being lower in 2009, the possibility of drowning of individuals in the very wettest places prior to the 2009 emergence, or the limited impact of unblocked drains under high rainfall conditions (Coulson, 1962; Meats, 1970; Coulson *et al*., 1990). Although the exact mechanism may be unclear, the results are sufficient to conclude that the magnitude of the benefits of drain blocking is likely to vary between locations and years. As summer conditions are projected to become increasingly dry, the potential importance of blocking drains to maintain cranefly populations could increase substantially under climate change. Indeed, it may be in areas where drains remain unblocked that negative impacts of climate change on craneflies and their avian predators first become visible.

2.5.3 Implications and conclusions

In the British uplands, drain blocking is already taking place. Around €250m has been spent on drain blocking between the late 1980s and 2009, but there is often little monitoring of the subsequent effects (Armstrong *et al*., 2009; Armstrong *et al*., 2010; but see Wilson *et al*., 2010). It may seem self-evident that damming drainage ditches should increase soil moisture levels, but the efficacy of peatland restoration remains relatively uncertain (Ramchunder *et al*., 2009; Wilson *et al*., 2010).

The effects of climate change on northern ecosystems will be first visible in the southern margins; this makes British peatlands a key location for monitoring climate change effects and testing adaptation strategies for other, widely-distributed northern peatlands. Substantial areas of British peatlands are projected to experience drier summers and increased temperatures under climate change, with records from some locations already displaying such trends (Burt & Horton, 2003; Holden *et al*., 2007c). The area climatically suitable for peatlands is likely to contract northwards, with the south Pennines (represented here by the Peak District site) and the North York Moors amongst the most vulnerable to change (Clark *et al*., 2010b). Given, the sensitivity of cranefly populations to soil moisture as shown here, projected increases in summer drought frequency (UKCP09, Murphy *et al*., 2009) could cause cranefly abundances to decrease, with the effects most intense where unblocked drains remain. However, drain blocking may ameliorate negative drought impacts.

Some of the major reasons for blocking drainage ditches in Britain have been to reduce water colouration and dissolved organic carbon concentrations, slow or stop erosion of dried peat surfaces, and promote carbon storage (Wallage *et al*., 2006; Worrall *et al*., 2007; Armstrong *et al*., 2009; Bussell *et al*., 2010). Here, we have demonstrated that cranefly populations should also benefit from this restoration technique, due to increased soil moisture levels. As breeding bird populations that are of conservation interest rely on craneflies for food, benefits of drain blocking may even extend to wider peatland biodiversity (Pearce-Higgins, 2010; Pearce-Higgins *et al*., 2010). Indeed, if drain blocking helps to maintain cranefly populations under increasingly dry conditions, there is significant potential for this ecosystem restoration technique to be an effective climate change adaptation strategy.

Conservation efforts must now explicitly consider climate change adaptation if they are to be successful in the long term (Hannah *et al*., 2002). Whilst uncertainty about the long-term effectiveness of management to increase the resistance of systems to climate change has been expressed by some (Mawdsley *et al*., 2009), our study presents evidence that maintaining soil moisture levels by manipulating the hydrology can be an effective adaptation option in some circumstances. Indeed, for high latitude and upland systems, it may be the only possible option. Others have highlighted concerns about the potential costs of continued conservation investment for species that require long-term management intervention (Scott *et al*., 2010). Climate change is likely to exacerbate such costs, but for peatlands the case for such adaptation management is more robust; maintaining high levels of soil moisture not only maintains biodiversity but also provides climate change mitigation through reduced carbon loss and ecosystem service provision through improved drinking water quality (Wallage *et al*., 2006; Worrall *et al*., 2007; Armstrong *et al*., 2009; Bussell *et al*., 2010). Our study also highlights the importance of large-scale experimentation as a way of developing evidence-based management strategies, which are urgently required in the context of climate change adaptation (Pullin *et al*., 2004; Sutherland *et al*., 2004); past experience may not provide an adequate model for future management.

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Chapter 3

Modelling water tables in British blanket peatlands

3.1 Abstract

Northern peatlands are a major global carbon store but could become sources of atmospheric carbon under climate change. Several models of peatland hydrology and development exist, providing a good background to understanding the processes that drive changes in water table depth (WTD) and carbon storage. However, there is a need to develop models that examine peatland processes that can be driven by the broad-scale climate data that is output by climate models, and which do not need to be parameterised with extensive local data. Here, a development of the MILLENNIA peat cohort model is presented, so that water table behaviour can be predicted on a monthly timescale, using only numerically-derived equations, parameterised using freely-available water table data, and driven using simple monthly climate data. A sensitivity analysis indicated that model predictions of WTD fluctuations and mean WTD were relatively robust to changes in parameter values, but minimum WTD was somewhat sensitive. Model performance was evaluated using data from four British upland blanket bogs. At two sites with intact peat, between half and two thirds of the variation in WTD over time was explained and mean WTD was predicted to within 0.2 cm. At three sites where dipwells monitored blocked drainage ditches, model success decreased: between 36% and 55% of variation in WTD over time was predicted, but mean WTD was still predicted to within 1 – 3 cm. At a site where dipwells monitored open drainage ditches, slightly over half of the variation in WTD was explained, but mean WTD was only predicted to within 6 cm. Hence, the model produces realistic estimates of WTD position and fluctuations at monthly time scales, but drainage appears to degrade performance. The model therefore provides the opportunity to examine effects of climate change on British blanket peatlands.

3.2 Introduction

3.2.1 Peatland hydrology and climate change

Northern peatlands are one of the most important terrestrial carbon stores (Gorham, 1991). The stability of peatlands as a carbon store is threatened by human activity such as peat extraction, drainage and afforestation (Laine *et al*., 2009), and by warmer temperatures and changed precipitation regimes under climate change (e.g., Gorham, 1991; House *et al*., 2010; Frolking *et al*., 2011). Northern peatlands are associated with a cold, wet climate, such that the decay of biological material is slow, forming peat (Bragg & Tallis, 2001). The maintenance of such waterlogged conditions is necessary for continued sequestration of carbon (Belyea & Malmer, 2004) and to ensure that oxidation of peat does not lead to loss of stored carbon (Fenner & Freeman, 2011). Indeed, increased emissions from drier peatlands could accelerate global warming, creating a positive feedback loop (Gorham, 1991; Davidson & Janssens, 2006). The ability to model and predict impacts of climate change on peatlands, mediated by water table position, is therefore of great importance.

Hydrology exerts a dominant control over growth and decay of peat, as well as the ecosystem services provided by peatlands (Holden, 2005b). Water table position influences gas emissions (Strack & Waddington, 2007), plant species composition (Jones *et al*., 1991) and growth (Smolders *et al*., 2003) and peat decomposition (Ise *et al*., 2008), all of which feed back into the hydrology of the peatland. As a result, to predict climate change effects, there is a need to understand peatland hydrology. However, as climate change is likely to increase seasonal differences (Holden *et al*., 2007c), and as ecosystem functions may be affected by conditions at specific times of year (e.g., Charman, 2007; Pearce-Higgins *et al*., 2010), it is important to study hydrological processes on a sub-annual timescale.

Britain contains around 10×10^6 ha of blanket peat, which is approximately 7 – 13% of the world's blanket bog (Ratcliffe & Thompson, 1988). British blanket bogs provide important ecosystem services, such as carbon storage, drinking water provision and supporting important biodiversity (e.g., Thompson *et al*., 1995; Bradley *et al*., 2005; Reed *et al*., 2009). However, as Britain is towards the southern extent of northern peatland occurrence, it may be one of the first locations where peatlands experience warmer temperatures and changed precipitation under climate change (Clark *et al*., 2010b; Gallego-Sala *et al*., 2010).

Given the need to predict and understand the consequences of climate change for peatlands, the development of models linking climate and peatland behaviour is desirable.

3.2.2 Modelling peatland behaviour

Several models of peatland processes have been developed over the past three decades, varying according to their aim, the type of peatland represented and the degree of specific parameterisation required. Models can be split into broad categories based on their primary aim. The first category is models dealing explicitly with peatland hydrology (e.g., Guertin *et al*., 1987; Kennedy & Price, 2004; Weiss *et al*., 2006; Ballard *et al*., 2011). Such models use realistic, physical-based hydrological equations, so provide accurate predictions. However, they often require site-specific parameterisation, so modelled sites must be well-studied. This intensive data requirement could limit application of the models to other sites or time periods, which could limit their use in predicting climate change impacts.

The second category of model examines peatland development (e.g., Clymo, 1984; Hilbert *et al*., 2000; Frolking *et al*., 2001; Bauer, 2004; Baird *et al*., 2012; Morris *et al*., 2012). These aim to understand how peatlands develop and change over time, which is a major consideration for climate change predictions. Models have included realistic features such as fluctuating water tables, plant species composition and 2-D processes, but their more theoretical nature may limit their application to real bogs. Furthermore, models have typically focussed on raised bogs rather than the blanket bogs found in upland Britain.

The third broad category includes models which aim to estimate multiple peatland properties, such as peat depth, carbon storage and gas emissions (e.g., Worrall *et al*., 2009; Frolking *et al*., 2010; Heinemeyer *et al*., 2010; Smith *et al*., 2010a; Smith *et al*., 2010b). Although the nature and intended use of each model varies, they generally provide a holistic approach to modelling peatland systems, allowing them to be used over larger areas and in unobserved time periods. They may also allow human influences such as land management to be taken into account. However, their broadly-applicable nature means that finer-scale processes may not be included, and outputs may not be as realistic as highly-parameterised models of specific processes.

It is clear that models are needed to produce realistic representations of key peatland processes, but without requiring extensive input and parameterisation data; such models would allow widely-applicable projections of peatland behaviour under climate change to be made. Here, to achieve this, the peatland processes model of Heinemeyer *et al*. (2010) is developed to produce monthly water table depth (WTD) predictions; this should allow the model to reproduce sub-annual processes, which are required to produce more realistic behaviour (Frolking *et al*., 2010). To reduce the need for extensive parameterisation data, the model will be developed based on published estimates of runoff production and monthly water table data available from the Environmental Change Network.

By comparing model projections to observed water table data from four British peatlands, the following key questions will be addressed:
1) Can the model predict water table position, as defined by mean, maximum and minimum depth, at different peatlands without requiring specific local parameterisation?
2) Can the model predict a large proportion of the variation in water table depth over time, thus showing that seasonal and climate-driven fluctuations are reproduced?
If both of these conditions are met, it will confirm that the model produces sufficiently realistic projections of water table behaviour to allow it to be used to estimate broad-scale climate change effects for blanket peatlands throughout Britain.

3.3 Methods

3.3.1 The MILLENNIA peat cohort model background

The MILLENNIA peat cohort model (Heinemeyer *et al*., 2010) aims to provide a general development trajectory of peatlands from peat initiation onwards, without the need for extensive, site-specific parameterisation. Therefore, it is based on a combination of published equations, equations developed to fit data, and expert opinion. The model therefore makes broad predictions, rather than highly specific, localised predictions. The conceptual background and results from the initial model formulation have been previously published (Heinemeyer *et al*., 2010), so the following sections will focus on developments of the model and provide extra information about the hydrological component.

The model assumes that peat can be represented as a 1-dimensional column. All processes occur vertically within the column and happen instantaneously. Although others have stated the need to develop models with two or three dimensions (e.g., Baird *et al*., 2012), such models would require substantial extra information for parameterisation. The model starts from the approximate start of peat formation up to 10,000 years ago. Rainfall and temperature drive a dynamic water table, which in turn influences vegetation composition; the driving climate data for this spin-up period are described in Heinemeyer *et al*. (2010). The vegetation is split into above-ground and below-ground material, and into different chemical fractions, as in Bauer (2004). Litter from vegetation is added to an annual cohort of peat, which then undergoes erosion, decay and compaction over time. Carbon in the system can be lost via erosion or as a gas, with the conversion to CO_2 or CH_4 determined by the position of the water table. Therefore, over time, peat columns grow, shrink and emit gases, with these processes driven by the dynamically-varying water table.

3.3.2 The dynamic water table model

The model described in Heinemeyer *et al*. (2010) was based on an annual timestep. Although monthly data could be applied (see Clark *et al*., 2010a), further development was required to more adequately reflect processes on a sub-annual scale. All further descriptions refer to the monthly model, which runs after the model has been spun-up over thousands of model years at an annual timestep to develop peat columns.

Water table variation is driven by input from rainfall, losses from runoff and evapotranspiration and a small, constant drainage out of the system to reflect loss into groundwater. To drive these processes, each modelled peatland is assigned total monthly rainfall (mm) and mean monthly temperature (°C). Each column within the peatland is also assigned values for slope (°), aspect (°) and elevation (m).

Relationships with topography are used to modify weather inputs from weather stations [or from UK Met Office gridded weather data (Perry & Hollis, 2005)] to provide locally-adjusted values for each peat column. Annual rainfall increases with elevation by 2.25 mm m^{-1}. Although this relationship varies from 0 mm m^{-1} to 4.5 mm m^{-1} around the UK (Brunsdon *et al*., 2001), this value represents a compromise to make the relationship widely-applicable. Equation 3.1 describes local rainfall adjustment:

$$R_L = R_O + \frac{2.25}{12} * E \qquad (3.1)$$

Here, R_L = local rainfall, R_O = observed rainfall, and E = relative elevation, i.e., the difference in metres between the modelled location and the elevation that weather data refer to. Therefore, a negative relative elevation decreases local rainfall, while a positive relative elevation increases local rainfall. For the monthly model, the 2.25 mm m^{-1} change is divided by 12, so that when summed over the year, the annual change is 2.25 mm m^{-1}.

Temperature decreases with elevation by 0.006°C m^{-1}, which should be applicable throughout the UK (Lennon & Turner, 1995). Temperature is also adjusted by slope and aspect to account for variation in incident radiation (Bennie *et al.*, 2008). The equation used in the annual model (Heinemeyer *et al.*, 2010) is retained for the monthly model, and is described by Equation 3.2:

$$T_L = T_O - 0.006 * E + \left((\cos(S) * cos(L) + \sin(S) * \sin(L) * \cos(A - 200)) - \cos(L)\right) * 10 \tag{3.2}$$

Here, T_L = local temperature (°C), T_O = observed temperature (°C), E = relative elevation (m), S = local topographic slope (°), L = site latitude (°), A = local aspect (°). The strength of the slope-aspect-temperature relationship varies with latitude to reflect variation in solar angle. The use of cos(aspect-200) means that the maximum temperature occurs at 200° aspect, while the minimum occurs at 20°. On southerly aspects, temperature increases with slope, while on northerly aspects, temperature decreases with slope.

Water input occurs via precipitation; water is lost through evapotranspiration and runoff. Evapotranspiration is calculated using the Thornthwaite equation (Thornthwaite, 1948) in the monthly model. This only requires precipitation and temperature inputs, and can be used for humid and wetland areas (e.g., Dolan *et al.*, 1984). Potential evapotranspiration (PET) estimates are adjusted based on the WTD and vegetation composition to give actual evapotranspiration (AET); AET decreases as WTD becomes deeper (e.g., Brooks, 1992; Brooks *et al.*, 2011). The relationship between the AET:PET ratio and WTD changes between plant functional types (PFTs), and is estimated based on root depths and the shape of relationships presented by Guertin *et al.* (1987) and Nungesser (2003): declines in AET occur sooner and faster in PFTs with shorter roots. For *Sphagnum* and other bryophytes, minimum AET is 50% of PET (Nungesser, 2003); for all other PFTs, minimum AET is 80% of PET (Koerselman & Beltman, 1988). AET:PET relationships are described in Table 3.1. Details on how PFT proportions vary with WTD are available in Heinemeyer *et al.* (2010) so are not described further here.

Table 3.1. Summary of relationships between AET:PET ratio and WTD for different plant functional types used in the model.

Plant functional type	Minimum AET:PET ratio	WTD where AET starts to fall (cm)	WTD when AET reaches minimum (cm)	Shape of relationship
Sphagnum	0.5	0	~40	Approximates shape in Nungesser (2003)
Bryophytes (e.g., *Polytrichum commune*)	0.5	0	~40	Approximates shape in Nungesser (2003)
Herbs (e.g., *Potentilla erecta*)	0.8	0	~12	Linear
Shrubs (e.g., *Calluna vulgaris*)	0.8	5	~19	Linear
Grasses (e.g., *Molinia caerulea*)	0.8	10	~30	Linear
Rushes (e.g., *Juncus squarrosus*)	0.8	10	~38	Linear
Sedges (e.g., *Eriophorum vaginatum*)	0.8	10	~38	Linear

Water inputs and outputs are summed to give a change value. An exponential relationship is assumed between distance to the water table and available pore space, such that available space increases with distance from the water table. Total space is calculated by integrating over the different peat cohorts. By combining the water entering the system with the available space, a new WTD is calculated.

3.3.3 Monthly runoff equations

New runoff equations were developed for the monthly model. The model does not use formal hydrological functions, but instead uses equations that aim only to reproduce dominant water table behaviour. Evans *et al*. (1999) show that runoff varies from 90% to <10% of rainfall, so equations were developed and parameterised to reflect these proportions. Runoff is strongly influenced by the existing water table, so runoff is a function of the previous time step's WTD; based on data presented by Evans *et al*. (1999), runoff was assumed to be related to WTD exponentially, but with runoff higher and more sensitive to WTD when the water table is within 5 cm of the surface. Runoff also increases with slope angle (e.g., Chaplot & Le Bissonnais, 2003 [refers to mineral soils]; Meyles *et al.*, 2003), so a cos function of slope was used to increase runoff. A condition was set such that runoff could never be higher than total precipitation.

The runoff equation used is determined by WTD in the preceding time step. Hence, if the antecedent WTD is deeper than 5 cm, Equation 3.3 is used to calculate runoff:

$$\left(1-\left(\alpha-\beta*(\exp(-0.01*WTD)^{\gamma})\right)-\kappa\cos(\lambda*\mathrm{S})\right)*R_L \qquad (3.3)$$

Here, WTD = previous time step's WTD, S = slope and R_L = local rainfall. See Table 3.2 for parameter descriptions and fitted values. This is based on the equation used in the annual model, and produces an exponential relationship between runoff and WTD; as the water table moves deeper, less rainfall is lost as runoff. After parameterisation (see below), at a slope of 0 the minimum runoff was 7.5% of rainfall, while at a WTD of 5 – 10 cm, runoff ranged from 60% to 50%.

When antecedent WTD is within 5 cm of the surface, runoff is calculated by Equation 3.4:

$$(\delta-(0.01*WTD^2)-\kappa\cos(\lambda*\mathrm{S}))*R_L \qquad (3.4)$$

WTD, S and R_L are as for Equation 3.3; see Table 3.2 for parameter descriptions and fitted values. Here, to reflect the higher, more sensitive runoff, a quadratic function of WTD is used. For the fitted model, runoff when WTD = 5 cm was 65% of rainfall, rising to 90% when WTD = 0 cm.

It was assumed that if water was standing on the surface, almost all rainfall would run off. An exponential relationship was once again used, and is shown in Equation 3.5:

$$\left(\varepsilon-\left(\eta*\left(\exp(0.01*WTD)^{\theta}\right)\right)-\kappa\cos(\lambda*\mathrm{S})\right)*R_L \qquad (3.5)$$

WTD, S and R_L are as for Equation 3.3; other parameters and values used are described in Table 3.2. As runoff data from situations with standing water were not available, the fitted model was set to produce a minimum of 95% runoff, but not to vary strongly with the depth of standing water.

3.3.4 Model parameterisation and sensitivity

Parameter values (Table 3.2) were set by trialling different values and comparing model output to observed data. Values were initially chosen to approximately reproduce the runoff proportions described in Evans *et al*. (1999) when slope = 0°. When suitable values were found, the model was run for an Environmental Change Network (ECN) site at Moor House, Cumbria, for which observed monthly WTD data were freely-available (see below); values were accepted if they predicted WTD fluctuations for 1999 – 2003 well; R^2 from a regression of observed vs. predicted WTD and measures of WTD position (mean, standard deviation, minimum, maximum) were used to judge model performance. As standing water was rarely observed, Equation 5 was parameterised by choosing values that did not cause dramatic water table drops due to runoff being too high, but did not allow standing water to last longer than observed.

Table 3.2. Parameters used in monthly runoff equations and fitted values.

Parameter	Equation	Description	Value
α	3	Defines minimum runoff at slope = 0 (i.e. $1 - \alpha - \kappa$)	0.425
β	3	Strength of WTD effect below surface (adjusts slope of relationship)	0.7
γ	3	Exponent of WTD effect below surface (adjusts curve of relationship)	5
δ	4	Maximum runoff at slope = 0 (i.e. $\delta - \kappa$)	1.4
ε	5	Maximum runoff at slope = 0 (i.e. $\varepsilon - \kappa$)	1.46
η	5	Strength of WTD effect above surface (adjusts slope of relationship)	0.01
θ	5	Exponent of WTD effect above surface (adjusts curve of relationship)	50
κ	3,4,5	Minimum slope effect (i.e. when slope = 0)	0.5
λ	3,4,5	Strength of slope effect (adjusts how quickly runoff increases with slope)	4.5

After parameters were fitted, a simple sensitivity analysis was carried out, where each value was raised and lowered by 10%; see Appendix 1 for sensitivity analysis values and plots of modelled water table depths. The range in R^2 was 0.15, but this was primarily caused by ε being lowered; excluding ε-10%, the range was only 0.06. The range in mean WTD was 2.6 cm; this variation appeared to be caused by ε-10% and κ+10%, and when these were excluded, the range was only 1.5 cm. The most sensitive value was minimum WTD, which had a range of 5.2 cm, but this was again caused by ε-10%; when this was excluded, the range was only 2.3 cm. Maximum WTD appeared to be relatively insensitive, with a range of only 1.6 cm. When the error relative to observed WTD was examined, the mean absolute error was 0.6 cm for mean WTD, 0.5 cm for minimum WTD and 1.9 cm for maximum WTD, indicating relatively robust performance. Qualitatively, there was little effect on model predictions from parameter value variation; only ε-10% caused substantially different behaviour by allowing floods to occur more frequently.

The strength of the slope effect (parameter λ) could not be parameterised using the Moor House data, as data were not available over a range of slopes. To set the value, first, modelled WTD was compared to observed WTD from a steep slope (~15°) at Lake Vyrnwy RSPB Reserve (see below) to see if mean WTD was close to observed; then, modelled peat depth (which is driven by erosion, which in turn is driven by runoff) was compared to observed peat depth data across shallow, moderate and steep slopes at Lake Vyrnwy (A. Heinemeyer, unpublished data). The slope parameterisation was accepted when it broadly reproduced observed patterns. The use of cos(4.5*slope) means that no slopes over 40° can be modelled with this parameterisation.

3.3.5 Evaluating model performance

The model was run for four independent blanket peat-covered sites across England and Wales for which observed WTD data were available. The sites were Moor House, the Goyt Valley, Lake Vyrnwy and Oughtershaw Moss; summaries of datasets are presented in table Table 3.3. Observed water tables were converted to monthly means for use in evaluation.

Sites differed in condition and monitoring method so datasets may vary in suitability for use in evaluation. As the model is parameterised for an intact peatland, it may not represent the hydrology at drained sites well. At Lake Vyrnwy, manual dipwell data were not frequent enough to represent true monthly means, so may not be well-predicted. Oughtershaw Moss data allow effects of peatland drainage to be explicitly examined, but as data span only 18 months, longer-term behaviours cannot be evaluated. Consequently, results should be interpreted in the context of site condition and monitoring method.

To generate model predictions, models were first spun-up to establish peat columns; spin-up periods were based on approximate peat ages and depths from the literature [Lake Vywny ~2500 years (Tallis, 1991), Goyt Valley ~7000 years (Tallis, 1964; Tallis, 1991), Moor House ~9000 years (Heinemeyer *et al*., 2010), Oughtershaw Moss ~7000 years (Holden *et al*., 2011)]. The model was then driven with monthly climate data to make WTD predictions. The monthly model started in 1914, at the start of the UK Met Office 5 km gridded climate data (Perry & Hollis, 2005). All models were driven by these data until 2010, apart from the Moor House run, which was driven by data from a local ECN weather station from 1999 onwards (available from http://data.ecn.ac.uk, last accessed 25.06.12); these data were gap-filled using the UK Met Office gridded data, which were first locally calibrated via regression against the ECN weather station data.

To evaluate model performance, measures of water table position (mean, maximum, minimum and standard deviation) were calculated for modelled and observed data. To examine how well fluctuations were replicated, modelled WTD was regressed against observed WTD. Finally, root mean squared error (RMSE) and maximum absolute error were calculated to examine model accuracy. Moor House data were also used to examine the timing and frequency of predicted droughts by looking at times in which WTD dropped below 5 cm and 10 cm; Evans *et al*. (1999) indicate that the water table stays within 5 cm of the surface 83% of the time, so these values may indicate reasonable thresholds to judge drought by. All analyses were conducted in R v. 2.15 (R Development Core Team, 2012).

Table 3.3. Summary of observed water table datasets used in model evaluation, indicating site location, peatland condition, and monitoring method.

Site	Location	Peatland drainage status	Number and type of dipwells	Duration of dipwell data	Dipwell recording frequency	Data source	Extra information
Moor House	Cumbria (54° 41' N, 2° 22' W)	Intact peat	1 automatic dipwell	January 1999 – December 2010	Hourly	Environmental Change Network	Automatic dipwell readings calibrated against fortnightly manual dipwell readings to correct for systematic bias in automatic dipwell. Further site information in Heinemeyer *et al*. (2010).
Goyt Valley	Peak District (53° 14' N, 1° 58' W)	Drains blocked in 2006	1 automatic dipwell	January 2008 – December 2010	Hourly	United Utilities/Penny Anderson Associates	Dipwell within 1 m of blocked drainage ditch. No manual calibration possible.
Lake Vyrnwy	Mid Wales (52° 47' N, 3° 35' W)	Drains blocked in 2007	24 manual dipwells	November 2007 – November 2010	Fortnightly or monthly	Active Blanket Bog Wales EU LIFE Project/RSPB	Three blocked drains crossed by a single dipwell transect; dipwells at distances of 0.5 – 10 m from the drains. Data from Afon Eiddew catchment used for model evaluation; data from Eunant catchment used to parameterise model's slope parameter. Further information on site and data in Wilson *et al*. (2010).
Oughtershaw Moss	North Yorkshire (54° 13' N, 2° 14' W)	3 areas: one intact, one drained, one blocked in 1999	9 automatic dipwells in each area	January 2005 – June 2006	Every 20 minutes	Prof. Joe Holden and Dr. Zoe Wallage, Leeds University	One transect of 9 dipwells in each area; dipwells at distances of 1 – 34 m from drains in blocked and drained areas. Further information on site and data in Holden *et al*. (2011).

3.4 Results

3.4.1 Results from an intact peatland with automatic dipwell data

The model performed well for Moor House, closely predicting the magnitude and timing of seasonal fluctuations (Figure 3.1). A regression of modelled vs. observed across all months indicated that modelled WTD was a highly significant predictor of observed WTD, and over 56% of variation was explained (Table 3.4). Winter WTD was correctly predicted to be typically at or near the surface, whilst summer WTD dropped to 10 – 15 cm. In 2003, the model replicated the timing and magnitude of a large drop in WTD, but the magnitude of similar fluctuations in 2006 and 2010 was underestimated.

The model predicted mean WTD to within 0.2 cm, and standard deviation to within 0.32 cm, whilst maximum WTD was predicted to within 1.8 cm and minimum WTD was predicted to within 1.2 cm (Table 3.5). Root mean squared error (RMSE) was 2.9 cm and the largest single error was 13.5 cm, which occurred in May 2010.

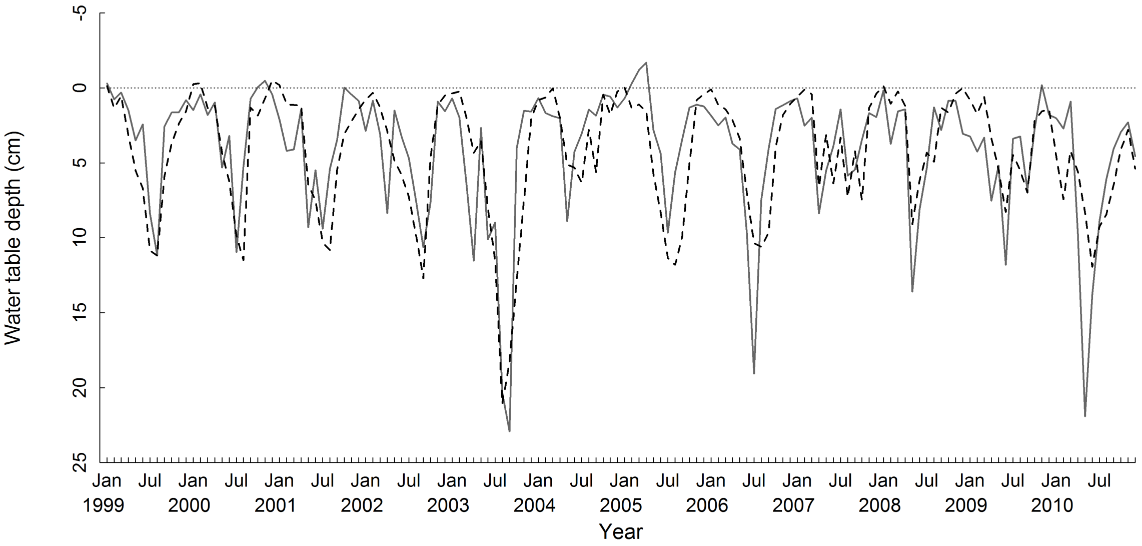

Figure 3.1. Time series of observed (grey, solid line) and modelled (black, dashed line) mean monthly WTD for Moor House. 0 cm indicates the peat surface (dotted line); positive WTD values indicate a water table below the surface; negative values indicate a water table above the surface.

Table 3.4. Results from linear regressions of observed WTD vs. modelled WTD.

	Intercept (± SE)	Slope (± SE)	R^2
Moor House (I)	0.595 ± 0.350, $P = 0.091$	0.813 ± 0.060, $P < 0.001$	0.567
Goyt Valley (B)	3.207 ± 1.074, $P = 0.005$	0.590 ± 0.133, $P < 0.001$	0.362
Lake Vyrnwy (B)	-0.726 ± 0.630, $P = 0.258$	0.545 ± 0.107, $P < 0.001$	0.474
Oughtershaw Moss (I)	2.474 ± 0.804, $P = 0.007$	0.581 ± 0.106, $P < 0.001$	0.653
Oughtershaw Moss (D)	8.256 ± 0.956, $P < 0.001$	0.576 ± 0.126, $P < 0.001$	0.565
Oughtershaw Moss (B)	6.036 ± 0.762, $P < 0.001$	0.472 ± 0.106, $P < 0.001$	0.554

Table 3.5. Mean, maximum and minimum monthly WTD values for observed data and for MILLENNIA model predictions. 'I' refers to intact peat; 'B' refers to peat with blocked drainage ditches; 'D' refers to peat with open drainage ditches.

	Mean WTD ± S.D. (cm)		Max WTD (cm)		Min WTD (cm)	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
Moor House (I)	4.1 ± 4.33	4.3 ± 4.01	22.9	21.1	-1.7	-0.5
Goyt Valley (B)	6.8 ± 5.36	6.0 ± 5.46	19.4	20.4	-0.3	-0.7
Lake Vyrnwy (B)	1.8 ± 2.90	4.4 ± 3.46	8.7	13.5	-2.7	-0.7
Oughtershaw (I)	5.9 ± 3.58	5.8 ± 4.98	14.2	18.6	2.0	1.3
Oughtershaw (D)	11.6 ± 3.78	5.9 ± 4.93	19.2	18.5	5.9	1.3
Oughtershaw (B)	8.6 ± 3.05	5.5 ± 4.81	15.3	17.9	4.7	1.0

Model ability to predict drought characteristics was tested using Moor House data, as this was the longest dataset. Over 144 months, 41 were observed with WTD > 5 cm (28.5% of time), whilst the model predicted 55 (38.2% of time); 12 months were observed with WTD > 10 cm (8.3% of time), compared to 15 months (10.4% of time) modelled. The distribution of these months between years matched relatively well for WTD > 5 cm, but for WTD > 10 cm the model underestimated drought frequency in 2008–10 (Figure 3.2).

The mean first and last months of WTD > 5 cm were 4.9 (late April) and 8.1 (early August) respectively for observed data, and 5.0 (start of May) and 9.3 (early-mid September) respectively for modelled data. For WTD > 10 cm, mean first and last months were 6.4 (mid June) and 7.1 (early July) respectively for observed data, and 7.3 (early-mid July) and 8.1 (early August) respectively for modelled data.

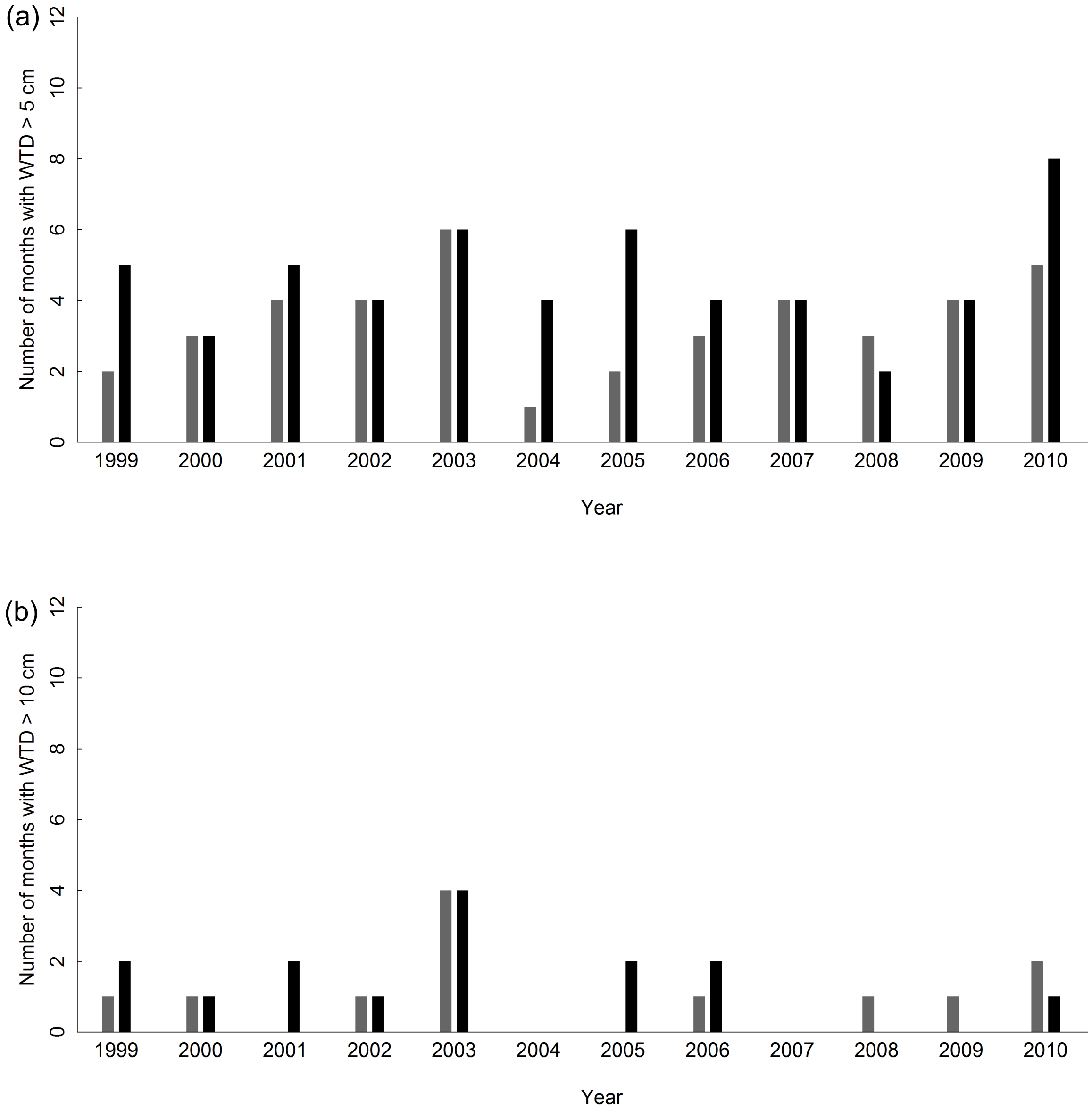

Figure 3.2. Frequency of months with a) WTD > 5 cm and b) WTD > 10 cm at Moor House, for observed (grey) and modelled (black) data.

3.4.2 *Results from a peatland with blocked drains and automatic dipwell data*

For the Goyt Valley dataset, WTD fluctuations were less well predicted (Figure 3.3). Modelled WTD described only around a third of observed variation, but remained a highly significant predictor of observed WTD (Table 3.4). In 2007–08 and 2008–09, winter water tables were deeper than predicted, remaining 5 – 10 cm below the peat surface. Conversely, in summer and autumn 2009, observed WTD did not show the sharp drop predicted. Predictions throughout 2010 matched fluctuations better, with the timing and magnitude of the summer water table fall well predicted.

The difference between modelled and observed mean WTD was only 0.8 cm, and the difference in standard deviation was 0.1 cm (Table 3.5). Modelled maximum WTD was 1 cm greater than observed, and minimum WTD was predicted to within 0.4 cm. The biggest single difference was 11.6 cm in August 2010, although a difference of 11.0 cm occurred in September 2009. RMSE was 4.8 cm, nearly 2 cm greater than at Moor House.

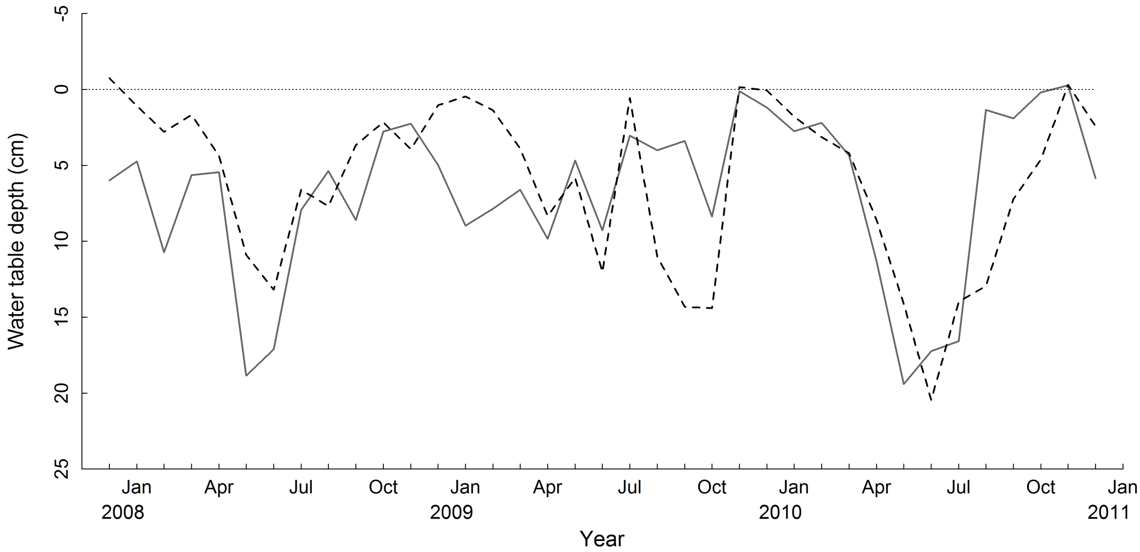

Figure 3.3. Time series of observed (grey, solid line) and modelled (black, dashed line) mean monthly WTD for the Goyt Valley. Dotted line indicates peat surface. Y-axis as for Figure 3.1.

3.4.3 *Results from a peatland with blocked drains and manual dipwell data*

At Lake Vyrnwy, dipwells monitored peat with blocked drainage ditches, and data were recorded manually, so monthly means may not accurately describe the true monthly WTD. To represent this, Figure 3.4 presents each month's mean WTD as a separate point with error bars showing the standard deviation, rather than as a continuous trace over time.

Observed fluctuations were reasonably well represented by the model (Figure 3.4). Modelled WTD was a highly significant predictor of observed WTD, and over 47% of variation was explained (Table 3.4). The timing and magnitude of water table falls each spring and summer were well predicted, particularly larger fluctuations in 2008 and 2010. However, wetter periods were not as well predicted, often showing a deeper WTD than observed; predictions were, however, typically within one standard deviation, and observed means for this dataset must be viewed with caution.

Mean predicted WTD was 2.6 cm greater than observed, and the predicted standard deviation was 0.56 cm greater (Table 3.5). Maximum predicted WTD was 4.8 cm deeper than observed, while minimum predicted WTD was 2 cm shallower, although as observed values were not true monthly means, these comparisons are less useful diagnostically. The biggest single difference between observed and predicted was 9.8 cm, in July 2010. Mean model performance was better than for the Goyt Valley, with a RMSE of 3.9 cm.

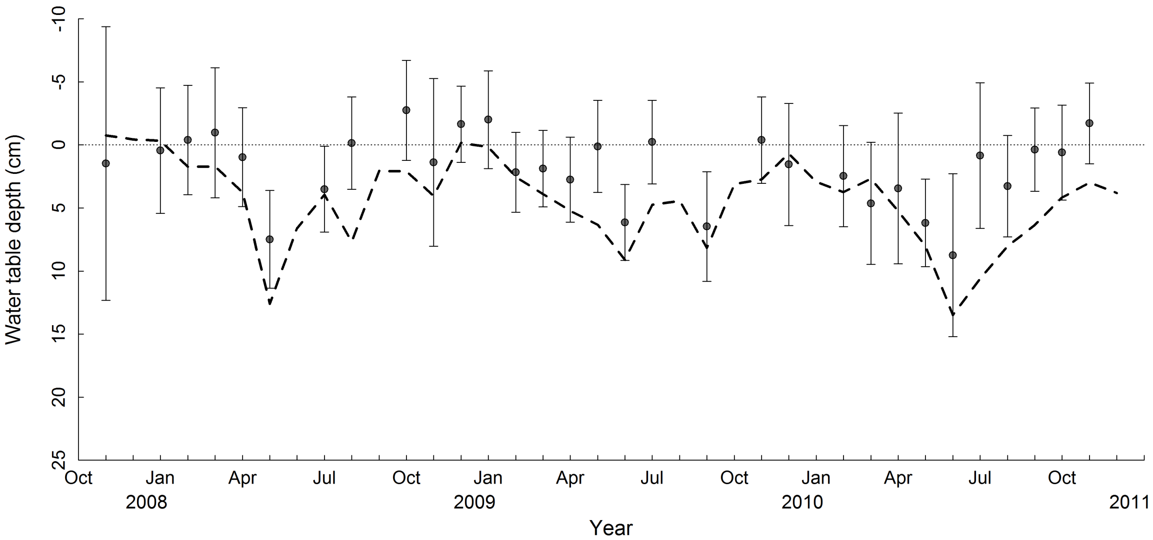

Figure 3.4. Time series of observed WTD (grey points) for Lake Vyrnwy and modelled mean monthly WTD (black, dashed line). Error bars show ± standard deviation of observed WTD. Dotted line indicates peat surface. Y-axis as for Figure 3.1.

3.4.4 Results from a peatland with intact, blocked and drained areas and automatic dipwell data

Modelled WTD was a highly significant predictor of observed WTD at all areas of Oughtershaw Moss (Table 3.4). Regression slopes were similar between areas; the intercept was smallest for the intact area and largest for the drained area (Table 3.4). Almost two thirds of variation was explained at the intact area, but even at the drained and blocked areas over 50% of variation was explained (Table 3.4). At the intact area, the timing and magnitude of the summer WTD fall was well predicted, but subsequent re-wetting occurred slower in the model (Figure 3.5a). At drained and blocked areas, the model predicted shallower WTDs and larger summer declines than observed (Figure 3.5b and Figure 3.5c).

WTD position was best predicted at the intact area, with a difference of only 0.1 cm in mean WTD, compared to 5.7 cm at the drained area and 3.1 cm at the blocked area (Table 3.5). Standard deviations were predicted moderately well, with differences between modelled and observed of 1.40 cm, 1.15 cm and 1.76 cm at intact, drained and blocked areas respectively. The model over-predicted maximum WTD at the intact area (4.4 cm deeper) and blocked area (2.6 cm deeper), but under-predicted the maximum at the drained area (0.7 cm shallower). Minimum WTD was better predicted at the intact area (0.7 cm shallower), but the drained (4.6 cm shallower) and blocked (3.7 cm shallower) areas did not show the same improvement. At the intact area, the largest observed difference was 5.3 cm in August 2005, whilst the RMSE was 2.9 cm, the same as that from Moor House. Larger differences were observed at the drained area, with a maximum difference of 11.6 cm in March 2006, and a RMSE of 6.6 cm, the largest of all areas. Blocked area performance fell between intact and drained, with a maximum difference of 7.7 cm in February 2005 and a RMSE of 4.5 cm, which is similar to values from the other two blocked sites.

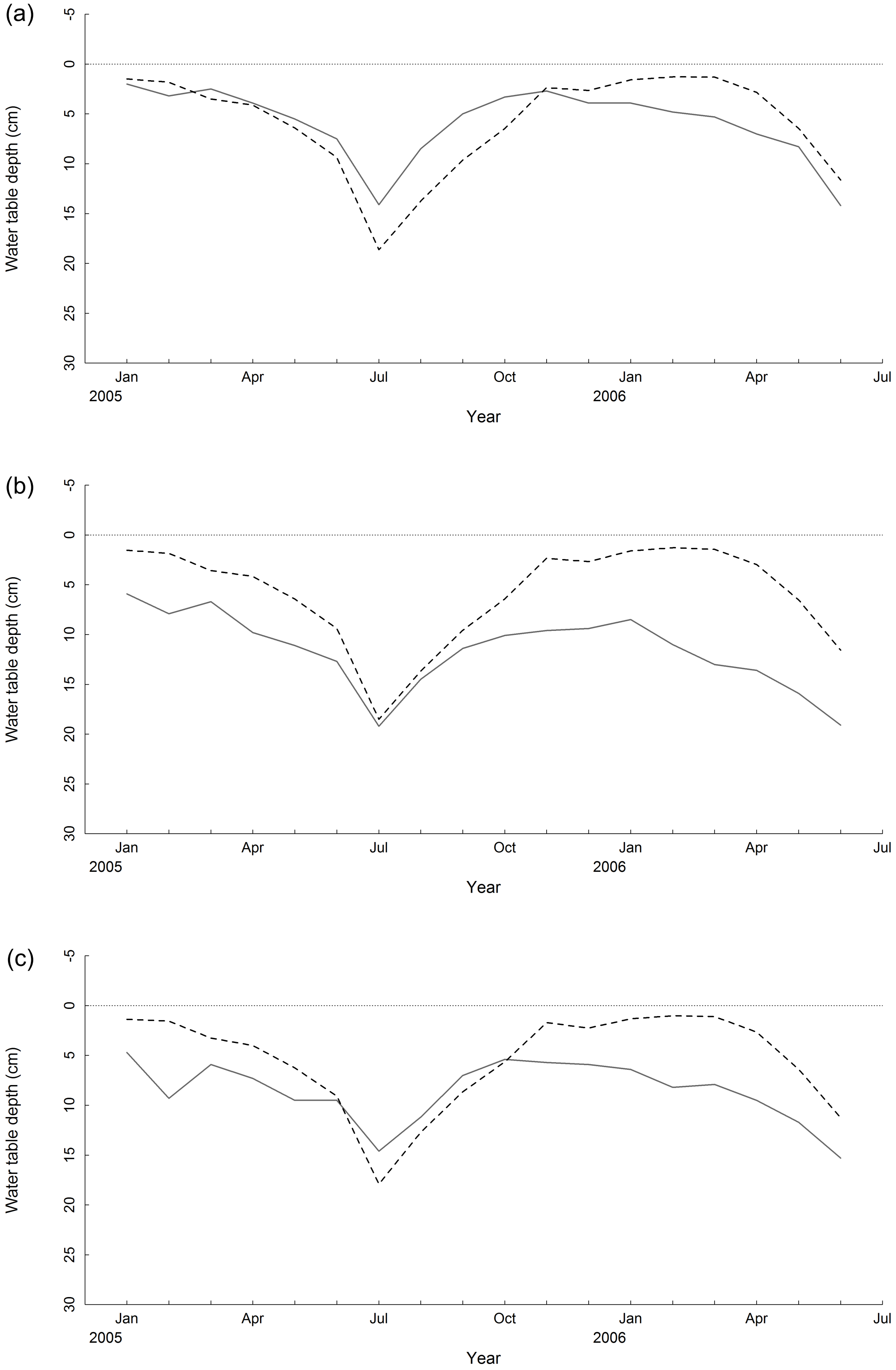

Figure 3.5. Time series of observed (grey, solid line) and modelled (black, dashed line) mean monthly WTD for Oughtershaw Moss, for a) intact peat, b) drained peat and c) peat with blocked drains. Dotted line indicates peat surface. Y-axis as for Figure 3.1.

3.5 Discussion

A development of the MILLENNIA peat cohort model has been presented, which predicts mean monthly WTDs using simple climatic and topographic input data. The aim of MILLENNIA is to make projections of peat accumulation and gas emissions for upland peatlands in the UK (Heinemeyer *et al*., 2010). As the water table drives major processes within the model, it is important that it predicts broadly realistic WTD behaviours. Monthly predictions are useful, as there may be important dynamics within peatland systems that are missed by annual models (Frolking *et al*., 2010). This could be particularly relevant when looking at water table behaviour under climate change, as patterns of seasonality in rainfall are likely to become more intense (Holden *et al*., 2007c). Understanding these sub-annual patterns could be vital to understanding possible impacts of climate change on biodiversity and carbon storage, which may be influenced by only a few months of each year (e.g., Charman, 2007; Pearce-Higgins *et al*., 2010).

Model results should not be expected to match reality perfectly: the model makes many simplifying assumptions and accepts little site-specific parameterisation. However, evaluation of two key properties, water table position and water table fluctuations, suggested that the model performed well: at intact peatlands, mean WTD was predicted to within 0.2 cm, and over 50% of variation in observed WTD was predicted. At sites subject to artificial drainage, model performance decreased, although aspects of WTD behaviour were still well replicated. It therefore appears that the model performs as intended, reproducing dominant water table behaviours in a realistic manner.

3.5.1 Model fitting

Model equations were developed and parameterised based on published data and simple monthly WTDs for Moor House NNR. This is a different approach from other peatland hydrology models, which may use extensive site-specific data (e.g., Kennedy & Price, 2004; Ballard *et al*., 2011). Here though, the intention was to reproduce broadly realistic WTD patterns so that projections can be made for new sites and future climate scenarios. If the model had aimed to reproduce every fluctuation, this would have led to overfitting, which creates problems when generalising results for both hydrological (e.g., Abebe & Price, 2003) and ecological (e.g., Guisan & Thuiller, 2005; Merckx *et al*., 2011) models. Therefore, parameter values were set to produce runoff proportions similar to those reported by Evans *et al*. (1999), and to produce reasonable representations of WTD position and fluctuations in observed data.

A simple sensitivity analysis was carried out (see Appendix 1). Model performance was most sensitive to reductions in runoff when WTD < 0 cm (parameter ε). This was one of the hardest parameters to fit, because observed data had very few months in which the water table was above the surface, so this behaviour could not be thoroughly examined. Other than this, the model appeared reasonably robust in predicting WTD fluctuations and mean WTD, with relatively small ranges and absolute errors found in the sensitivity analysis. Encouragingly, the difference between modelled and observed values when using the fitted parameter values were always smaller than or equal to the mean absolute error; whilst some parameterisations produced better results in individual performance measures, the fitted model performed reasonably well across all measures, suggesting it is a good general parameterisation. Variation between sites can mean that generally-parameterised hydrological models are not very robust (Peel & Blöschl, 2011), but in the absence of more long-term datasets, particularly for restored peatlands (Holden *et al*., 2011), wider uncertainty cannot be appropriately assessed. However, good model performance (see below) for sites and time periods not involved in model fitting suggested that the aim of producing realistic water table behaviour was achieved.

3.5.2 Model performance

Model performance was best for sites with intact peat and automatic dipwell data. At Moor House, over half of WTD variation over twelve years was predicted, and mean, maximum and minimum WTDs matched observed data closely. The model performed similarly well for the intact area of Oughtershaw Moss, but with nearly two thirds of WTD variation predicted. Where dipwells monitored drained and restored peatlands, model performance decreased, but predictions remained reasonably strong. Fluctuations were predicted moderately well for an area with blocked drains at Lake Vyrnwy, but WTD position was only predicted to within several centimetres. Fluctuations were predicted less well in peat with blocked drains at the Goyt Valley, but WTD position was relatively well predicted. The drained and blocked areas at Oughtershaw Moss had over 50% of variation explained, with WTD position predicted worst where active drainage remained.

Areas where the model performed well and poorly may give some indication of its strengths and limitations; for this, comparisons with Moor House and the intact area of

Oughtershaw Moss are most valuable, as the evaluation was based on automatic dipwell data (thus true monthly means) and intact peat (thus not displaying drainage effects). Mean WTD is a key determinant of many peatland ecosystem properties (Rydin & Jeglum, 2006), and the very strong model performance in predicting mean WTD should mean that longer-term trends are well predicted. Further, as WTD was measured on steeper slopes at Oughtershaw Moss than at Moor House (~5° c.f. ~2°), but mean WTD was well predicted at both, the model's slope effect appears to be reasonably realistic. However, floods and droughts can affect peatland biodiversity and functions (e.g., Coulson, 1962; Fenner & Freeman, 2011), so the larger errors in maxima and minima suggest that greater caution should be attached to predictions of these events; the Moor House time series shows that the timing and magnitude of large drops in WTD can be predicted well, but not always. Overall, fluctuations were well predicted; the Oughtershaw Moss data provided a totally independent test, as they were not used in model calibration, but the model produced the highest R^2 for this site. Therefore, the model appears to predict seasonal water table behaviour well, which was a key aim of developing the monthly version.

The model compares favourably with other peatland WTD models. Kennedy and Price's (2004) model of mined Canadian bogs showed a difference between modelled and observed annual mean WTD of around 5 cm, and a difference in standard deviation of 0.2 – 0.3 cm. The model of Finnish bogs by Weiss *et al*. (2006) showed a mean error across a year of 2.6 – 3.3 cm, with the maximum differences observed 11 – 13 cm. The hydrological model of Ballard *et al*. (2011) produced RMSE values of 2.7 – 16.3 cm when modelling a drained British peatland on a 10 minute timescale. Therefore, values reported here (e.g., Moor House: difference between means 0.2 cm; difference between standard deviations 0.32 cm; maximum error 13.5 cm; RMSE 2.9 cm) are of a similar magnitude to those reported for other models.

As increased drought frequency is a specific concern associated with climate change, the model's ability to predict drought was tested using the Moor House dataset. The model predicted the total amount of time spent with WTD deeper than 5 cm and 10 cm reasonably well, but the exact timing of droughts did not always match. This could be linked to the use of monthly climate values to drive the model, which spread weather effects across a whole month, creating less rapid WTD fluctuations than may be caused by intense weather events. Alternatively, model equations may not allow rapid-enough WTD falls and rises, although this could not be tested without other long-term datasets from intact peatlands.

3.5.3 Drainage effects

A major driver of differing performance between sites was the presence of artificial drainage. Drainage substantially alters peatland hydrology (e.g., Holden *et al*., 2004), producing a lower, more variable water table (Wilson *et al*., 2010; Holden *et al*., 2011). In many areas, drainage ditches are now being blocked to restore peatlands for various reasons, such as improving water quality (Worrall *et al*., 2007; Armstrong *et al*., 2010) and reducing erosion (Armstrong *et al*., 2009). Biodiversity benefits may also be achieved (Chapter 2; Ramchunder *et al*., 2012). A major driver behind blocking drains is the assumption that it will raise water tables and ultimately return the peatland to a more natural hydrological state.

At sites where dipwells monitored drain blocking programmes, model performance degraded. After drain blocking, local hydrology may not return to a ‘natural’ state, instead reaching an intermediate state between intact and drained (Wilson *et al*., 2010; Holden *et al*., 2011). Mean WTD may become more like intact areas, but WTD fluctuations may remain very different (Ketcheson & Price, 2011), with reduced seasonality due to changes to water flow routes (Holden *et al*., 2011). Evaluation of model performance showed aspects of these observations. At blocked and drained sites, mean WTD was predicted to be nearer the surface than observed and seasonal fluctuations were larger than observed. It is unclear how long it may take for hydrology to recover, but effects of drainage are visible five to six years after blocking occurs (Holden *et al*., 2011). There may also be longer-lasting physical and chemical impacts that continue to affect hydrology even after drain blocking (Holden *et al*., 2004; Holden, 2005b). Therefore, the ability of the model to predict WTD fluctuations may be somewhat impaired even after drain blocking, but WTD position is still reasonably well predicted, as shown at the Goyt Valley and Oughtershaw Moss.

3.5.4 Spatial and temporal variation

The broad nature of the model excludes fine-scale spatial and temporal heterogeneity, so discrepancies with observations will always occur. Vegetation composition can affect water tables due to differing evapotranspiration rates (Koerselman & Beltman, 1988); as the model uses only broad plant functional types, vegetation cover may not match reality. Human influences on vegetation and WTD such as burning, pollution and grazing (Bragg

& Tallis, 2001; Holden *et al*., 2007c; Ramchunder *et al*., 2009), are excluded. Microtopography influences peatland water tables (Hayward & Clymo, 1982; Kellner & Halldin, 2002), but the coarse scale used here cannot account for such variation. The model also cannot replicate different water transport methods, with processes such as pipe flow and macropore flow (Holden & Burt, 2003b; Holden & Burt, 2003a) excluded due to the 1-D nature of the model. Therefore, it is highly encouraging that even lacking such features, dominant WTD behaviours are well replicated.

The nature of WTD monitoring may mean that some evaluation results artificially appeared less favourable. At the Goyt Valley, an automatic dipwell was used, so WTDs represented true monthly means, and were accordingly well predicted. However, as only one dipwell was used, local drainage, vegetation and microtopography effects would strongly influence observations, contributing to poor representation of fluctuations. Conversely, at Lake Vyrnwy, 24 dipwells were sampled manually, so local influences on WTD would be minimised, leading to improved prediction of fluctuations. However, monthly sampling meant that WTDs did not represent true monthly means, contributing to larger prediction errors in WTD position. The use of multiple automatic dipwells at Oughtershaw Moss meant that fine-scale spatial and temporal effects were minimised, allowing a fairer evaluation of model performance and contributing to higher R^2 values. To effectively monitor peatland restoration, it may be necessary to have frequent WTD measurements from multiple dipwells (Holden *et al*., 2011); such datasets are also necessary to thoroughly evaluate models of peatland hydrology.

3.5.5 Implications and conclusions

Northern peatlands provide multiple ecosystem services, such as carbon storage, water provision and supporting biodiversity (Whitfield *et al*., 2011). All of these are underpinned by the high water tables associated with peatlands. As the climate changes, higher temperatures and changed precipitation regimes will almost certainly affect peatland water tables, in turn affecting the ecosystem services provided by peatlands. To model the behaviour of peatlands under climate change, we must be able to relate peatland hydrology to climatic variables in a realistic manner. Here, a model has been presented that allows broad-scale peatland hydrology to be predicted using only widely-available climate data and requiring little local parameterisation.

Understanding how well predictions match reality is a key part of interpreting model output. Here, model behaviour was tested against datasets from four British blanket peatlands. However, the evaluation was somewhat limited by the varying monitoring methods and drainage statuses of the different sites. Longer-term datasets, with multiple dipwells and frequent recording, are required to improve calibration and evaluation of models of peatland processes. It is therefore encouraging that the model performed best at sites with the best evaluation datasets.

There is a need to develop hydrological models which can be widely applied without requiring extensive field data to parameterise complex hydrological functions. The attempt presented here performs well for intact peatlands, and still performs reasonably for restored and drained peatlands, although drainage does appear to reduce model performance. Even though the model makes many simplifying assumptions, overall it appears to be able to produce realistic monthly predictions of peatland hydrology across Britain, and could be used to examine long-term trends driven by climate change.

3.6 Acknowledgements

The MILLENNIA peat cohort model was originally developed by Dr. Andreas Heinemeyer and coded by Simon Croft; further coding for the monthly model was carried out by Dr. Chris West. Moor House WTD data were provided by the ECN. Goyt Valley WTD data were kindly provided by Penny Anderson Associates and United Utilities. Lake Vyrnwy WTD data were kindly provided by the Active Blanket Bogs Wales EU LIFE project and RSPB. Oughtershaw Moss data were kindly provided by Prof. Joseph Holden and Dr. Zoe Wallage at Leeds University.

Chapter 4

Modelling the abundance of upland craneflies under climate change

4.1 Abstract

Under climate change, increased temperatures and changed rainfall patterns could increase the risk of droughts in upland peatlands, which require high water tables to maintain ecosystem functions. Craneflies (Diptera: Tipulidae), which are a major component of upland peatland invertebrate communities, could be particularly threatened by drier conditions due to high mortality under desiccation. If cranefly populations decline, there could be substantial impacts on breeding birds that feed on them. Further, impacts of artificial drainage could intensify under climate change, so must also be considered in conservation plans. Using a climate-driven model of peatland water tables along with field-derived relationships between craneflies and moisture, climate and drainage impacts on cranefly populations were explored for three British upland peatlands. Under the current climate, drainage was projected to reduce mean abundances by at least 3.9 – 5.5%, even though drains were assumed to affect only 6 – 9% of each modelled area. Climate change was projected to drive highly significant declines in cranefly abundance by causing summer water tables to fall. Without drainage, reductions in mean abundance of 20 – 37% were projected by 2050–80; if the whole landscape was drained, declines of 29 – 41% were projected. Spring water tables were not projected to fall significantly under climate change, so when abundance was linked to spring soil moisture, mean abundance declined only 0 – 2% by 2050–80. However, spring moisture is likely to have limited influence on cranefly abundance, so it is concluded that climate-driven declines are a real threat to cranefly populations. Blocking peatland drains appears to be a ‘no lose’ conservation strategy, increasing populations in the present and slowing climate-driven declines. However, even with drain blocking, cranefly populations could still decline, so it may be necessary to find other ways to preserve high water tables if large cranefly populations are to be maintained.

4.2 Introduction

4.2.1 Conserving biodiversity in a changing climate

One of the most pressing threats to global biodiversity is anthropogenic climate change (Fischlin *et al*., 2007; Pereira *et al*., 2010), which could drive extinctions as species shift ranges to track suitable climates (Thomas *et al*., 2004; Parmesan, 2006; Chen *et al*., 2011). Conservation plans must therefore acknowledge shifting patterns of biodiversity over the coming century (e.g., Pressey *et al*., 2007; Groves *et al*., 2012). However, northerly-distributed species are particularly threatened, as there is little suitable climate space into which they can move (Hill *et al*., 2002; Julliard *et al*., 2004; Jetz *et al*., 2007; Renwick *et al*., 2012). High-altitude species are also sensitive to climate change, because they will be disproportionately affected by habitat shifts (Pounds *et al*., 1999; Sekercioglu *et al*., 2008; Dirnböck *et al*., 2011). Consequently, aiding natural migration, which is a widely-prescribed approach to conservation under climate change (Heller & Zavaleta, 2009), may not aid these species, meaning that understanding threats and adaptation options within current ranges is very important.

To aid conservation planning under climate change, statistical associations between species distributions and climate may be used, although these models may not accurately reflect extinction risk (Pearson & Dawson, 2003; Heikkinen *et al*., 2006; Araújo & New, 2007). Process-based models, including interactions, dispersal and physiological tolerances provide improved understanding of climate change responses, but require more data and complex models (Brooker *et al*., 2007; Morin & Thuiller, 2009). A ‘middle-way’ may be to use statistical associations, but to drive these with process-based models of known drivers of abundance. Such models could be useful for northern and upland species. Soil moisture is a major determinant of the abundance of some species in northern ecosystems (e.g., Chapter 2; Coulson, 1962; Briones *et al*., 1997; Hodkinson *et al*., 1998), and this can be mechanistically modelled (Chapter 3). Further, food webs become simpler at higher altitudes (Usher & Gardner, 1988) and upland invertebrate communities are dominated by relatively few species (Coulson & Butterfield, 1985), so keystone species could be identified to be the focus of modelling. This approach would allow climate change risks and conservation options to be examined for northern and upland communities.

4.2.2 Upland biodiversity under climate change

The British uplands support a unique bird assemblage, a unique mixture of invertebrate assemblages and regionally-important vegetation communities (Thompson *et al*., 1995). The cool, wet climate reduces the risk of desiccation for soil invertebrates, so Nematoda, Enchytraeidae, Acari, Collembola and Tipulidae together make up over 90% of blanket bog invertebrate biomass (Coulson & Whittaker, 1978). Craneflies (Diptera: Tipulidae) are a particularly important component of this fauna. Larval craneflies are present in upland soils throughout the year, and on blanket bogs the synchronised spring emergence of adults represents a huge input of biomass to the above-ground ecosystem; over 80% of above-ground invertebrates during this time are adult craneflies (Coulson & Whittaker, 1978).

The high abundance and biomass of craneflies makes them an important food source for breeding birds. Larval craneflies are present in over 50% of moorland bird diets and adults are present in over 20% (Buchanan *et al*., 2006a). They also constitute large proportions of adult or chick diets for species such as Dunlin, Whimbrel, Golden Plover and Meadow Pipit (Pearce-Higgins, 2010). For these species, breeding success, behaviour and habitat choice may be influenced by cranefly availability (e.g., Coulson & Whittaker, 1978; Park *et al*., 2001; Pearce-Higgins & Yalden, 2003a; Pearce-Higgins & Yalden, 2004), and therefore by environmental drivers of cranefly abundance (Buchanan *et al*., 2006a). Consequently, craneflies could be seen as keystone invertebrates in upland peatlands.

Cranefly eggs and larvae are highly sensitive to soil moisture variation, with desiccation a major risk (Coulson, 1962; Meats, 1967b; Meats, 1968). Indeed, moisture availability may be the dominant influence on larval survival (Pritchard, 1983), and contributes to spatial and temporal trends in abundance (e.g., Chapter 2; Milne *et al*., 1965; McCracken *et al*., 1995). In lowland species, droughts have caused population crashes of over 90% (Milne *et al*., 1965). In upland peatlands, populations may only survive dry years in wet flushes, with several years required to recolonise the landscape (Coulson, 1962). Hence, cranefly populations could be modelled based on the relationship with soil moisture alone.

Climate change could lead to warmer, drier summers in the uplands (Holden *et al*., 2007c), particularly in southerly areas (Gallego-Sala *et al*., 2010). This could increase drought risk during the period in which craneflies are most susceptible to desiccation (Coulson, 1962). A previous model showed that cranefly populations could decline due to rising August temperatures, in turn driving local Golden Plover extinctions (Pearce-Higgins *et al*., 2010).

Increasing cranefly populations could prolong the time to extinction, but large increases would be required (Pearce-Higgins, 2011b). These models give a first indication of climate change risks for craneflies and upland birds. However, August temperature is assumed to act as a surrogate for soil moisture; modelling moisture more explicitly would complement these findings by combining temperature and precipitation changes, improving biological realism, and linking more closely to peatland restoration and conservation actions.

Climate change impacts on upland biodiversity could be exacerbated by land management. Peatland drainage has caused widespread drying and degradation (e.g., Holden *et al*., 2004; Holden *et al*., 2007c; Ramchunder *et al*., 2009), with effects stronger during drier months and in drier regions (Stewart & Lance, 1983; Coulson *et al*., 1990). We would therefore expect drainage to become more damaging as summers become drier. This could intensify declines in cranefly abundance, so would be an important conservation consideration.

Here, an analysis is presented based on the combination of a mechanistic model of peatland water tables (Chapter 3) and field data on soil moisture and cranefly abundance (Chapter 2). To evaluate the ability of the hydrological model to describe variation in soil moisture, the hypothesis will be tested that modelled water table depth is a significant predictor of observed moisture. As observations were taken separately from blocked and open drains, the hypothesis will be tested separately for each. As both spring and summer water tables could affect moisture patterns and cranefly abundance, the hypothesis will also be tested separately for each season. The resulting regression equations will be used to convert modelled water table depth to estimated moisture; a further regression equation derived from field data will convert moisture to expected cranefly abundance. After this conversion process, the model will be further evaluated by testing the hypothesis that modelled and observed abundance are positively and significantly correlated.

The model will then be run for different combinations of slope, aspect and elevation so that landscape-scale projections can be made for three studied peatlands. The model will be driven by observed climate data from the 20th Century and projected climate data for the 21st Century to test the following hypotheses:
1) Climate change will cause cranefly abundance to fall due to drier conditions.
2) Climate-driven declines will be of a smaller magnitude if peatland drains are blocked.
These analyses should help to examine climate change impacts on peatland ecosystems and assess the ability of drain blocking to aid climate change adaptation for key invertebrates.

4.3 Methods

4.3.1 Establishing links between cranefly abundance and soil moisture

The link between cranefly abundance and soil moisture was established by conducting field sampling over two years and across three sites. Full descriptions of sites and methods are given in Chapter 2. These study sites were retained for the current modelling analysis, as all are associated with conservation or grouse shooting, so would benefit from maintaining large cranefly populations, and all are towards the southern margins of blanket bog occurrence in Britain. Data were collected by sampling emerging adult cranefly abundance and soil moisture in spring. The main analyses occurred at the individual trap level, but as each trap only covered 0.115 m^2, here, individual trap data were aggregated into one value for each sampling location (hereafter, 'sampling location' refers to the area containing four individual traps). This was done because moisture model projections represent broad-scale water table depths (WTDs), and because spatial projections are limited to the relatively coarse scale of digital elevation models (DEMs). At each sampling location, the area sampled was 0.46 m^2, spread over 40 – 50 m^2 of ground, making the spatial scale comparable to DEM scales. Abundances were therefore summed across all four traps at each sampling location, and the mean soil moisture value was calculated, giving 128 locations for analysis.

4.3.2 Predicting water table depths as a function of climate

Soil moisture is strongly influenced by water table depth (Weiss *et al*., 2006). Therefore, WTD may first be modelled as a function of climate and then converted to soil moisture. To model WTD, the MILLENNIA model was used; a full description of the model is given in Heinemeyer *et al*. (2010) and Chapter 3. In Chapter 3 it was shown that the model produces broadly-realistic, widely-applicable WTD projections, which are driven only by simple monthly climate data. Therefore, the model could be used to drive projections of WTD under climate change.

The model requires inputs of slope, aspect and elevation for each point to be modelled. These were derived from NEXTMap DEMs at a 10 m × 10 m scale (Intermap Technologies. NEXTMap Britain: Digital terrain mapping of the UK. NERC Earth Observation Data Centre, 2007, accessed 04/04/2011. Available from http://badc.nerc.ac.uk). DEMs were converted to slope and aspect using Spatial Analyst functions in ArcMap 9.3 (ESRI; Redlands, California, USA). To reduce the number of model runs required to describe a whole landscape, topographic variables were rounded into bins of 50 m for elevation, 10° for aspect and 1° for slope; bin sizes were chosen to allow the relationship between WTD and each variable to be adequately described.

The model is driven by monthly temperature and precipitation data. Observed data were acquired from UK Met Office gridded datasets (Perry & Hollis, 2005). These cover 1914–2010 and describe weather at a 5 km scale. As climate data grid squares did not perfectly overlap sampling sites, representative squares had to be chosen. For Lake Vyrnwy and Bransdale Moor, the 5 km square containing most sampling locations was used to represent site climate. For Wood Moss, sampling locations were on the south west margin of a large area of deep peat, but fell at the edge of a weather data grid square with low elevation and no other deep peat; to ensure that weather data were relevant to the sampling site, and to ensure that landscape-scale projections could be made, weather data from the grid square immediately to the north east were used. These squares will hereafter be referred to by regions (i.e., mid Wales, Peak District, and North York Moors). Monthly precipitation values were taken directly from the gridded dataset; mean monthly temperature was calculated as the mean of maximum and minimum monthly temperatures.

Projected climate data for the 21st Century were acquired using the UKCP09 weather generator (Jones *et al.*, 2009). This produces stochastic sequences of weather data based on 30-year climatic means on a 5 km^2 scale (Jones *et al.*, 2009). The weather generator was run for each 30-year climate period (2010–39, 2020–49, 2030–59, 2040–69, 2050–79, 2060–89 and 2070–99), and for three SRES scenarios: A1FI (high emissions), A1B (medium emissions) and B1 (low emissions). Data were aggregated to total monthly precipitation and mean monthly temperature. 100 random realisations were produced from each run, so data within each climate period were sorted in order of mean spring and summer rainfall, and the 50th driest run was selected to approximately represent the median. As climate periods overlapped, the middle 10 years from each were combined into one sequence of 70 years; running all available years would have represented 70 real years with 210 model years. Therefore, by driving the model with these future climate data, projections could be made for 2010-80.

4.3.3 Converting predicted WTD to soil moisture

In Chapter 2, spring soil moisture and emerging cranefly abundance were sampled. Cranefly abundance is affected by moisture, and moisture is affected by WTD; it was decided that this causality should be preserved when making projections. Therefore, to link modelled WTD to cranefly abundance, it was first necessary to link WTD projections to soil moisture.

Although spring moisture could influence cranefly abundance, summer moisture is more likely to drive abundance directly via larval mortality (e.g., Rennie, 1917; Coulson, 1962; Milne *et al*., 1965; Pearce-Higgins, 2010). Further, the relationship derived in Chapter 2 may actually reflect relative wetness, with summer water tables responsible for determining spatial patterns of wetness (e.g., Charman, 2007). Therefore, two mean WTDs were calculated for each sampling location: spring in the observation year (April, May, June; when adult craneflies emerge), and summer in the year before observations (July, August, September; when egg and early larval stages are present). Mean WTDs were regressed against observed soil moisture to validate the model's ability to predict variation in soil moisture. Regressions used data from all sites and both years together, to make the relationship broadly-applicable. Analyses were carried out in R v2.15 (R Development Core Team, 2012). To account for hydrological differences between blocked and open drains (e.g., Holden *et al*., 2011) separate regressions were carried out for each.

Equations derived from regressions of observed moisture against modelled WTD could be used to convert modelled WTD to soil moisture. As a comparison to regressions, published conversion equations were also tried. Methods of Granberg *et al*. (1999), Kettridge and Baird (2008) and Weiss *et al*. (2006) were tried. Results indicated that modelled WTD was a highly significant predictor of observed moisture, and equations from regressions produced the most suitable mean and range when compared to observed values (see section 4.4.1). Hence, modelled WTD was converted to soil moisture using equations derived from regressions. As the equations could fit values outside of the range of possible moisture values, bounds of 1 and 0.15 were set, based on field observations.

4.3.4 Converting soil moisture to cranefly abundance

To convert projections to cranefly abundance, a relationship derived directly from field data was used. Cranefly abundance was modelled as a function of soil moisture, using data from both study years and all study sites. Using the ‘vcd’ R package (Meyer *et al.*, 2012), it was found that abundance data were significantly different from Poisson, but not from negative binomial. Therefore, the model was created using ‘glm.nb’ in the ‘MASS’ R package (Venables & Ripley, 2002), which fits generalised linear models (GLMs) with log link and negative binomial error. Soil moisture was found to be a significant predictor of cranefly abundance at the ‘sampling location’ scale (see section 4.4.1), allowing the regression equation to be used to convert projected moisture to expected cranefly abundance.

4.3.5 Producing projections

The model was run for each of the three study sites. Model runs were completed for all topographic value combinations in each 5 km grid square. Mean spring and summer WTDs were calculated as described above. Each grid cell was assigned WTD values from the run corresponding to its topography, thus creating a spatial representation of model projections. As MILLENNIA cannot differentiate between peat and mineral soil, areas for which model projections would not apply were removed. First, using Ordnance Survey MasterMap data (© Crown Copyright/database right 2012. An Ordnance Survey/EDINA supplied Service: License 100018355), areas not falling into the “rough grassland” or “heath” habitat classifications were removed, as these were the only two habitat types that would reflect underlying peat. Next, as the peatlands of interest occur at high altitudes, any remaining land below 250 m a.s.l. was removed.

Conversion equations derived from regressions (see section 4.4.1) were used to convert WTD to moisture and then to cranefly abundance. Separate conversions for blocked drains and open drains were each used across the whole square to represent a landscape without drainage and a totally drained landscape respectively; hereafter, these will be referred to as ‘blocked’ and ‘open’ conversions. To give a more realistic estimate of drainage effects, drain location maps were used to apply the open conversion to all cells within 20 m of a drain [approximately the distance over which effects are detected (Wilson *et al.*, 2010)], and the blocked conversion to all remaining cells; hereafter, this is referred to as the ‘drained’ conversion. Finally, projections were converted to abundance m^{-2}. The whole modelling process, showing how the different aspects and data sources are brought together, is described as a flow chart in Figure 4.1.

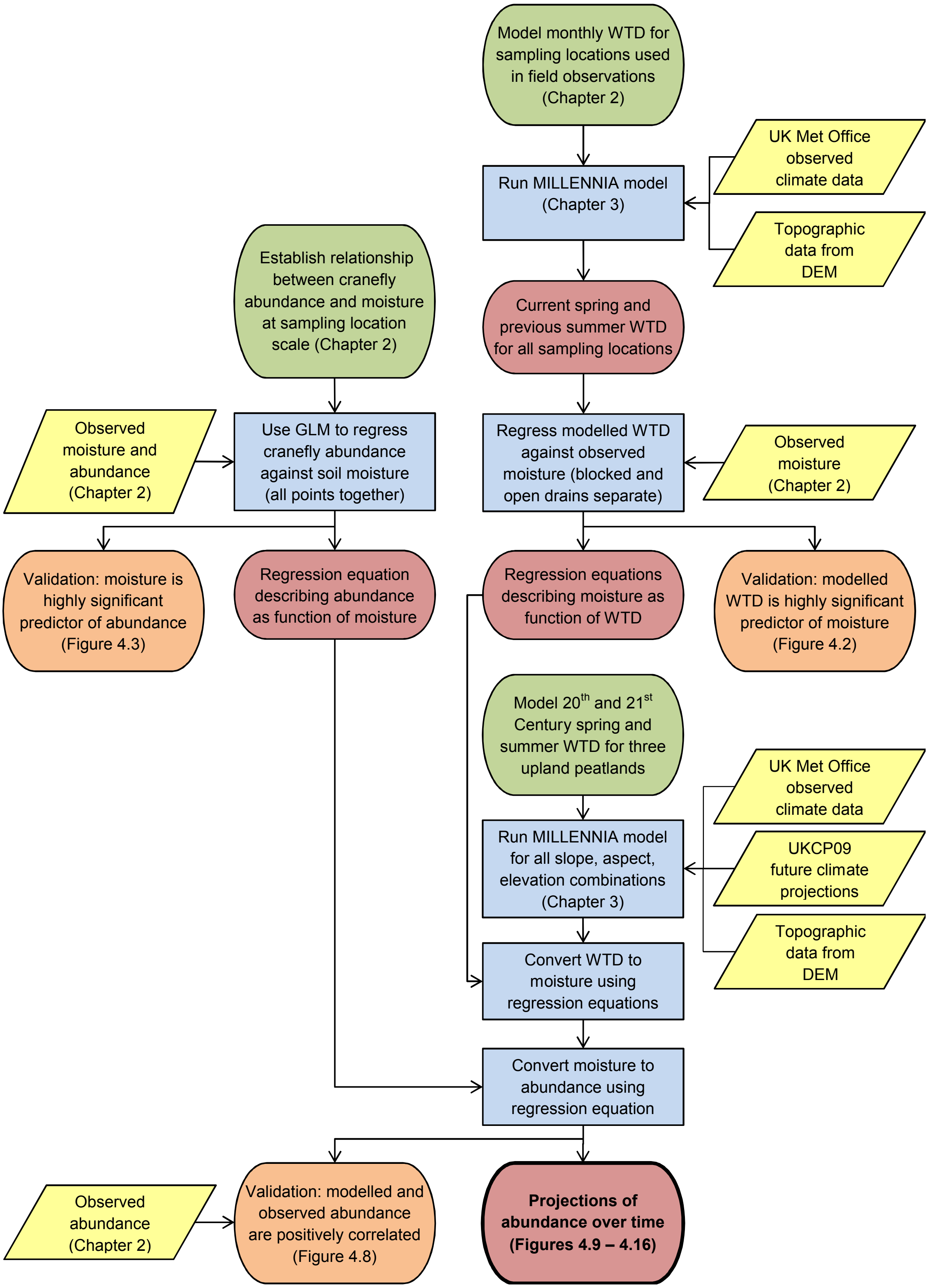

Figure 4.1. Flow chart describing whole modelling process. Green boxes show initial aims; blue boxes show key processes; yellow boxes show input data; orange boxes show model validations; red boxes show key outputs. Relevant chapter and figure references are included to show where results or extra information can be found.

To examine model behaviour, projections for field observation years (2009 and 2010) were made. This allowed examination of overall patterns of projected site wetness and cranefly abundance. Specific projections were also made for each sampling location, so that projected abundance could be correlated against observed abundance; this allowed assessment of whether abundance projections were realistic.

To examine change over time, mean abundance was calculated for each year, and then aggregated to decadal means; mean abundance was then regressed against decade. This was done because individual years of future climate data represent random realisations, but dominant climatic shifts occur between decades. Shapiro-Wilk tests indicated that summer WTD-driven model residuals were not significantly different from Normal. However, spring-driven residuals were significantly different from Normal for the mid Wales medium and high scenarios and for the Peak District low and high scenarios; transformations could not make the residuals normally distributed. Therefore, *P*-values from spring-driven models should be regarded cautiously. To examine abundance changes spatially, projections were converted to 30-year means for 1961–90, 2021–50 and 2051–80, to represent baseline, mid-century and late-century periods respectively. Images were created using image.plot in the 'fields' R package (Furrer *et al.*, 2012).

4.4 Results

4.4.1 Model validation: deriving conversions

Observed soil moisture was regressed against modelled WTD for the previous summer and current spring to validate model performance and generate conversion equations (Figure 4.2). Modelled WTD was a significant predictor of observed spring soil moisture, for both blocked and open drains, and for both spring and summer WTD:

Summer, blocked: $\text{moisture} = 1.040 - 0.021 \times \text{WTD}$, $P < 0.001$, $R^2 = 0.195$
Summer, open: $\text{moisture} = 0.938 - 0.033 \times \text{WTD}$, $P < 0.001$, $R^2 = 0.228$

Spring, blocked: $\text{moisture} = 1.038 - 0.015 \times \text{WTD}$, $P = 0.004$, $R^2 = 0.127$
Spring, open: $\text{moisture} = 0.922 - 0.022 \times \text{WTD}$, $P = 0.003$, $R^2 = 0.136$

All coefficients were negative, showing that deeper WTD corresponded to lower moisture. ‘Open’ intercepts were smaller and the slopes were steeper than those from ‘blocked’ regressions, so soil moisture would be lower and would decrease faster as WTD dropped. Summer WTD predicted around 20% of variation in moisture, while spring WTD predicted around 13%, suggesting that summer WTD was a better predictor of spatial moisture patterns. If separate slopes and intercepts were fitted for blocked and open in the same regression, spring R^2 rose to 0.362, while summer R^2 rose to 0.425.

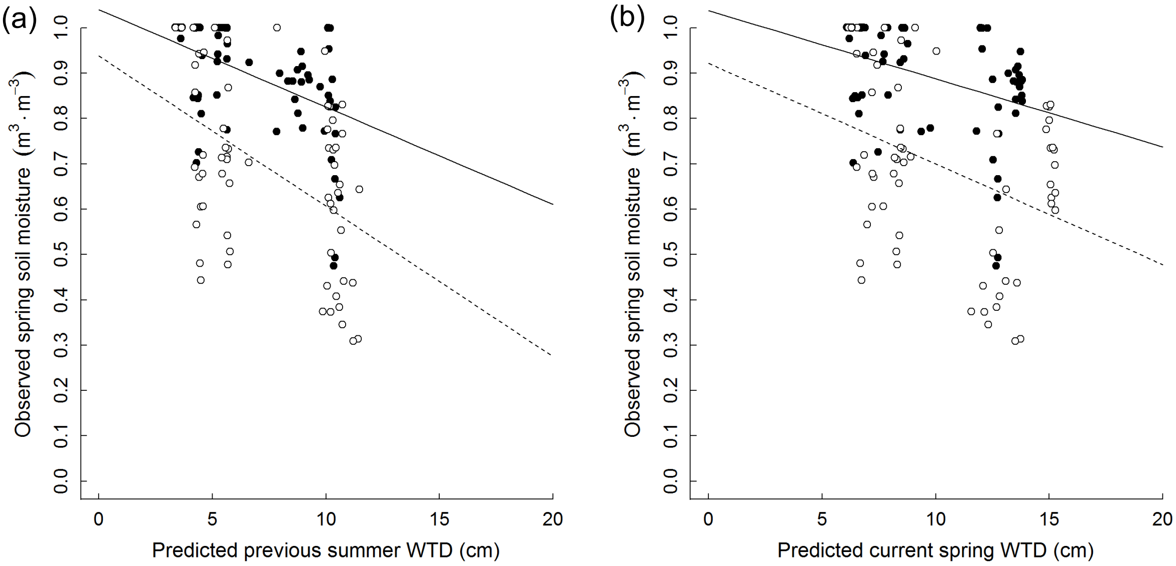

Figure 4.2. Plots of modelled water table depth against observed soil moisture and associated regression lines for blocked (●, solid line) and open (○, dashed line) drainage ditches, for a) summer WTD (mean of July, August and September of year before observation) and b) spring WTD (mean of April, May and June of observation year).

Converted soil moisture values from regressions were compared to values from published conversion relationships to ensure that the most appropriate method was selected (Table 4.1). Kettridge & Baird and Granberg conversions gave lower mean and maximum values than observed; the Weiss conversion gave mean and maximum values closer to those observed, but the range was smaller. Regression-based conversions provided the closest match to the observed mean and a larger range than the Weiss conversion. Values produced by the different conversions were highly correlated (Spearman’s rho > 0.9 for all comparisons), so the primary difference between the methods was the range of values produced. Hence, equations derived from regressions provided the best method of converting modelled WTD to soil moisture.

Table 4.1. Mean, minimum and maximum values from different methods of converting modelled WTD to soil moisture. ‘Blocked’ and ‘open’ regressions used only one conversion for all sampling locations; ‘combined’ regressions used the conversion appropriate to the blocked/drained condition of the sampling location.

	Mean ($m^3.m^{-3}$)	Min ($m^3.m^{-3}$)	Max ($m^3.m^{-3}$)
Kettridge and Baird	0.436	0.316	0.574
Granberg	0.426	0.234	0.655
Weiss	0.851	0.773	0.926
Summer blocked regression	0.885	0.794	0.968
Summer open regression	0.698	0.558	0.827
Summer regression (combined)	0.790	0.558	0.965
Spring blocked regression	0.886	0.809	0.947
Spring open regression	0.697	0.583	0.787
Spring regression (combined)	0.790	0.583	0.947
Observed	0.790	0.309	1.001

A GLM with negative binomial error and log link showed that, at the sampling location scale, observed soil moisture was a significant predictor of observed cranefly abundance (intercept = -0.461, slope = 3.507, $P < 0.001$; Figure 4.3). Therefore, when transformed back from the log link scale [i.e., exp(-0.461 + 3.507*moisture)], this equation could be used to convert projected soil moisture to expected cranefly abundance.

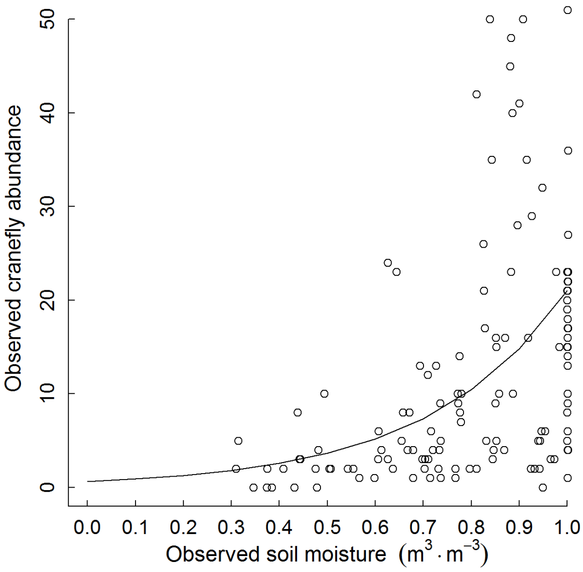

Figure 4.3. Plot of observed cranefly abundance against soil moisture at the ‘sampling location’ scale. Data used were from both sampling years and all sites. Solid line describes expected values from negative binomial GLM with log link.

4.4.2 Model validation: projections for observed years

Projections of WTD (Figure 4.4) and cranefly abundance (Figure 4.5 – Figure 4.7) were produced for years in which field observations occurred. The model predicted mid Wales to be the wettest site, and as a result to have the highest cranefly abundance (indicated by darker colours on maps). Steep slopes were predicted to be driest (indicated by lighter colours) and to have the lowest cranefly abundances. Projections also show spatial heterogeneity in abundance, but such areas may not correspond to real areas of high or low abundance due to the lack of true 2-D structure in the hydrological model.

Projections based on 'blocked' or 'open' conversions differed dramatically (Figure 4.5 and Figure 4.6), with open conversions producing low abundances across large parts of the landscape (Figure 4.6). When real drain locations were used (Figure 4.7), abundances were lower around drains, but the surrounding landscape maintained high abundances. Mean WTD and abundance for each modelled square are presented in Table 4.2. For the Peak District and North York Moors, where predicted WTD was lower, the difference between blocked and open conversions was more pronounced, due to the steeper slope of the open conversions; this is likely to reflect an interaction between drainage and climate, whereby drainage impacts are stronger in drier conditions. Comparatively, differences produced by using spring or summer WTD to drive abundance projections were relatively small; summer WTD produced slightly lower means with larger standard deviations, but the differences were much smaller than those between blocked and open conversions.

Comparison of abundance between blocked results, which assume no active drainage, and drained results, which apply the open conversion to all cells within 20 m of drains, gives some measure of potential drainage impacts. When driven by summer WTD, for mid Wales 2009, drained abundance was 4.3% lower than blocked; in 2010, it was 4.6% lower; for the Peak District, drained abundance was 5.5% lower; and for the North York Moors, it was 3.9% lower. When driven by spring WTD, drained abundance was 4.2% lower for mid Wales 2009, 4.4% lower for mid Wales 2010, 5.1% lower for the Peak District, and 3.4% lower for the North York Moors. Although these reductions seem small, the area within 20 m of a drain in mid Wales is only 9.2% of the square, in the Peak District it is 9.5%, and in the North York Moors is it 6.4%. Hence, even though only 6–9% of each 5 km square is within 20 m of a drain, the entire square's abundance is lowered by around 3–6%.

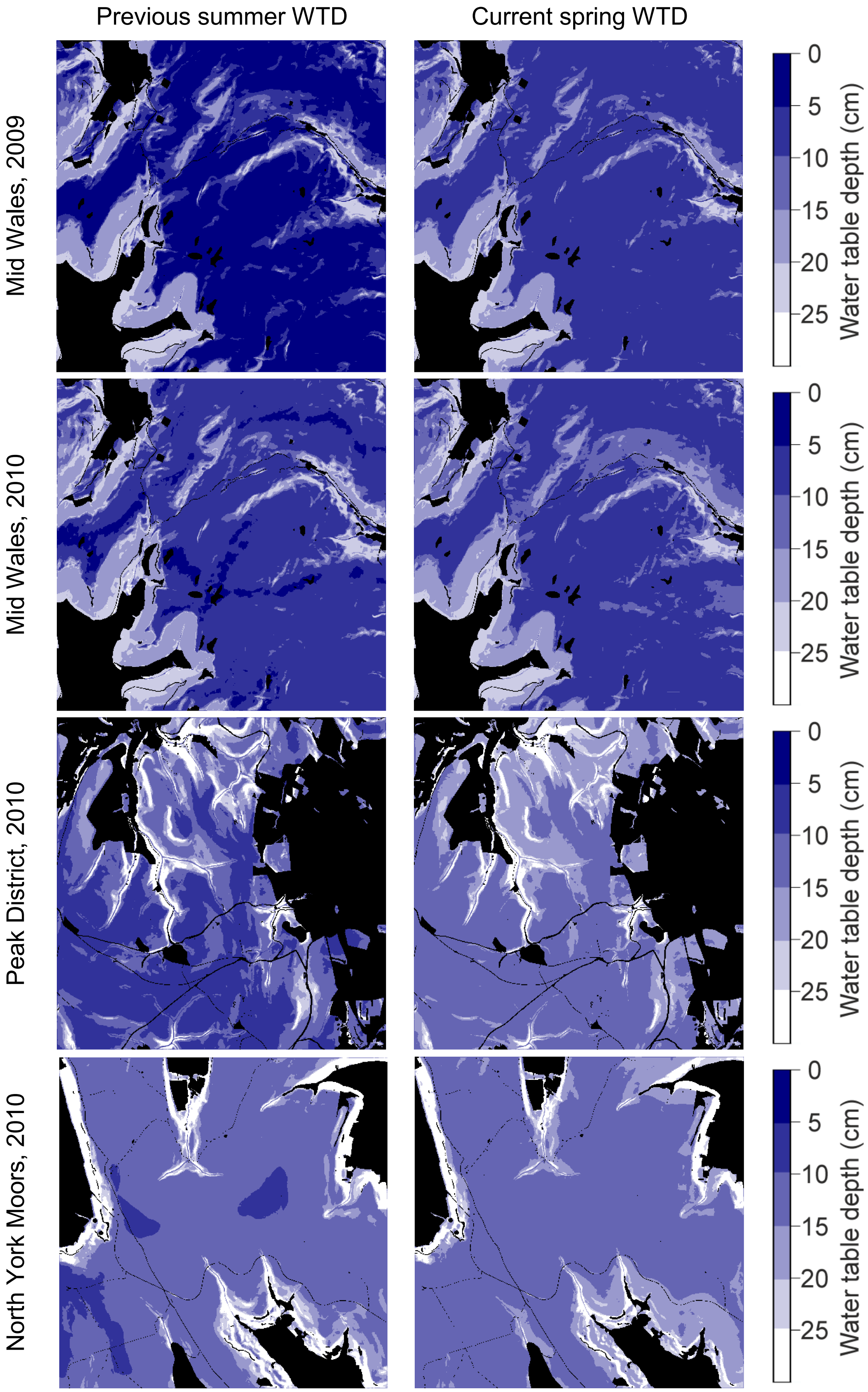

Figure 4.4. Predicted WTD for modelled sites in observation years. Previous summer WTD is the mean of July, August and September WTD in the year before observation. Current spring WTD is the mean of April, May and June WTD of the year of observation. Darker blue indicates shallower WTD; lighter blue and white indicate deeper WTD. Black indicates areas of low altitude or inappropriate habitat types.

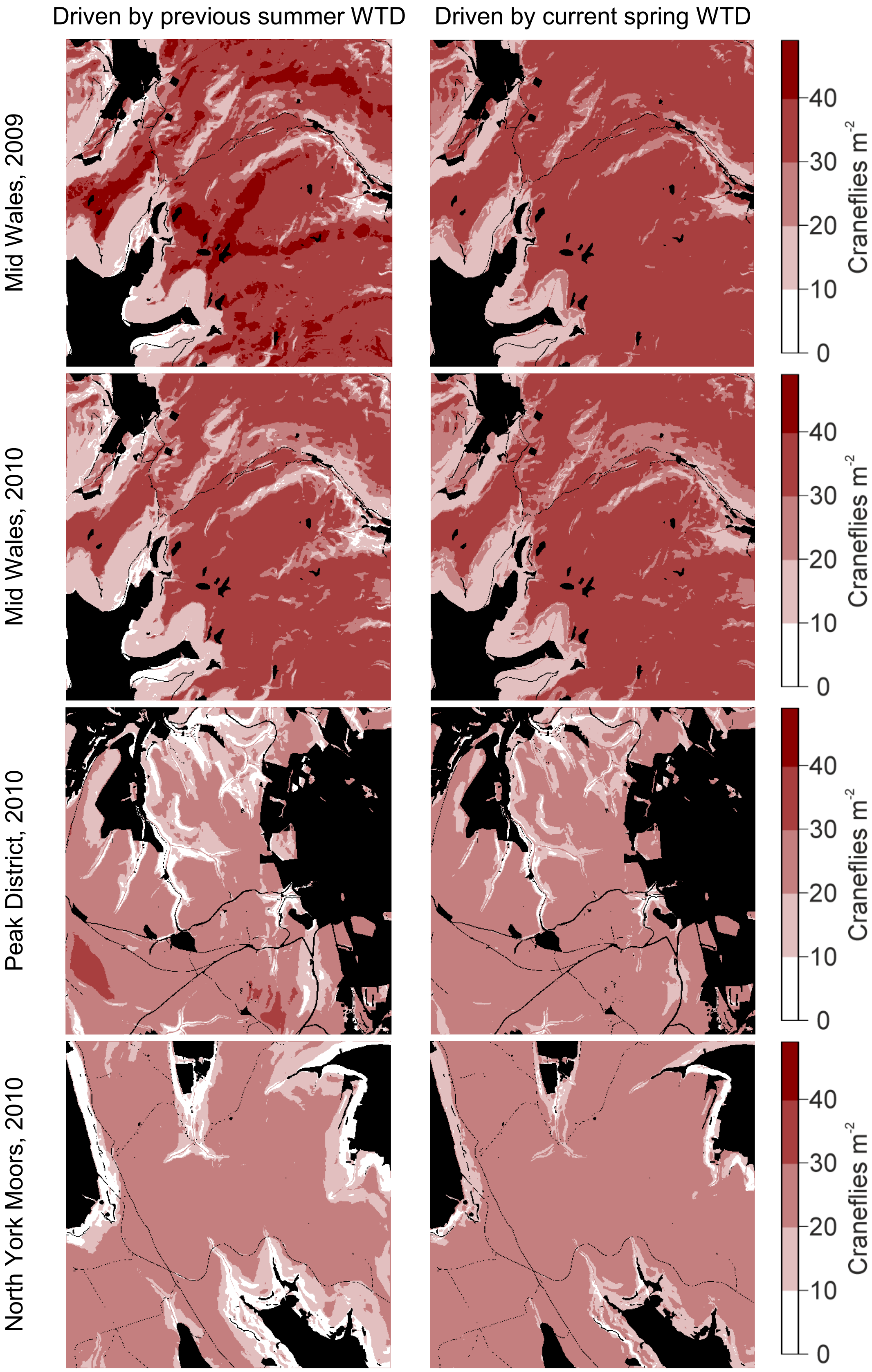

Figure 4.5. Predicted cranefly abundance in observation years based on ‘blocked’ soil moisture conversions. Spring and summer definitions as for Figure 4.4. Darker red indicates areas of higher cranefly abundance; lighter pinks and white indicate areas of lower cranefly abundance. Black indicates areas of low altitude or inappropriate habitat types.

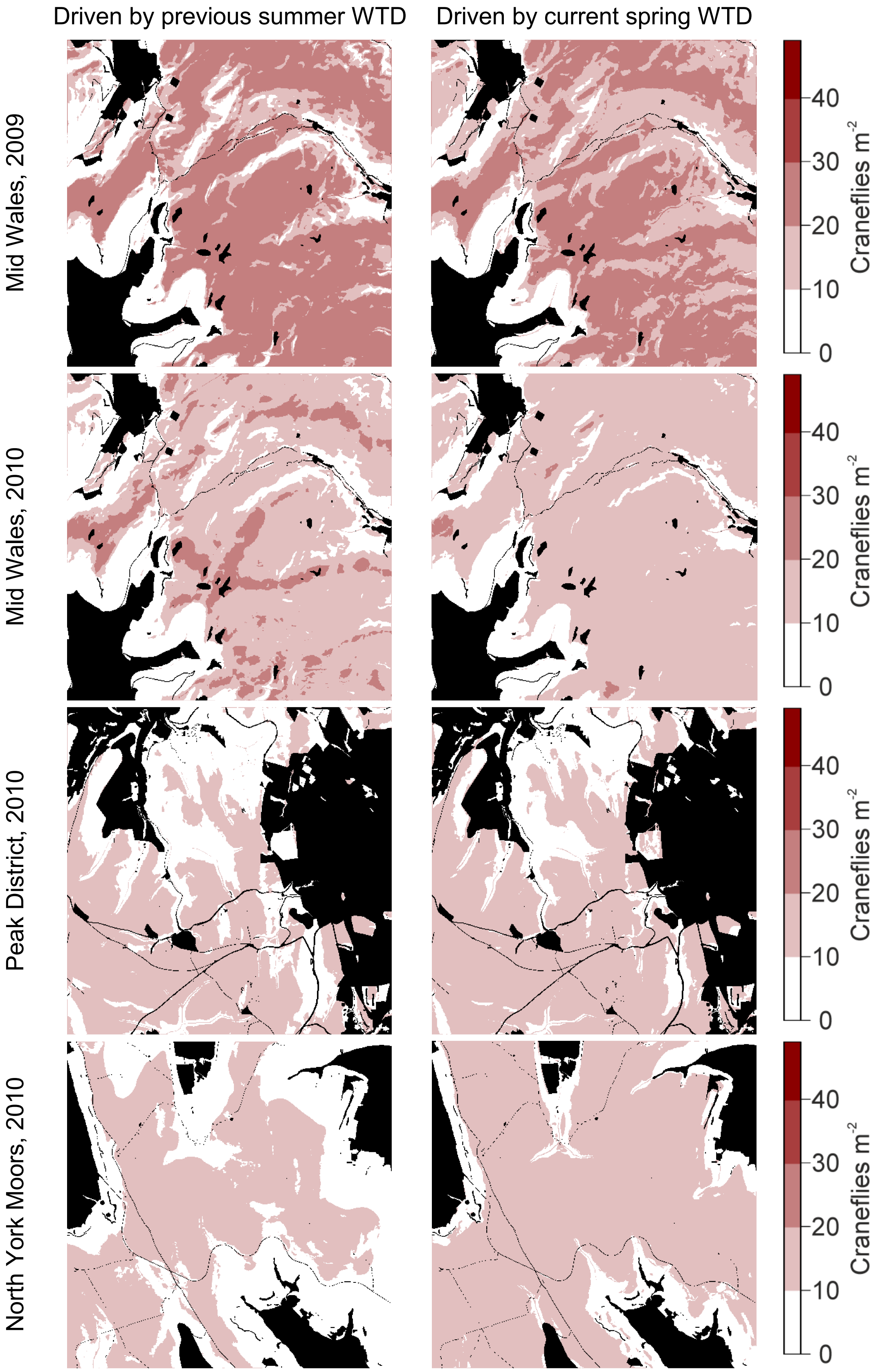

Figure 4.6. Predicted cranefly abundance in observation years based on 'open' soil moisture conversions. Interpretation as for Figure 4.5.

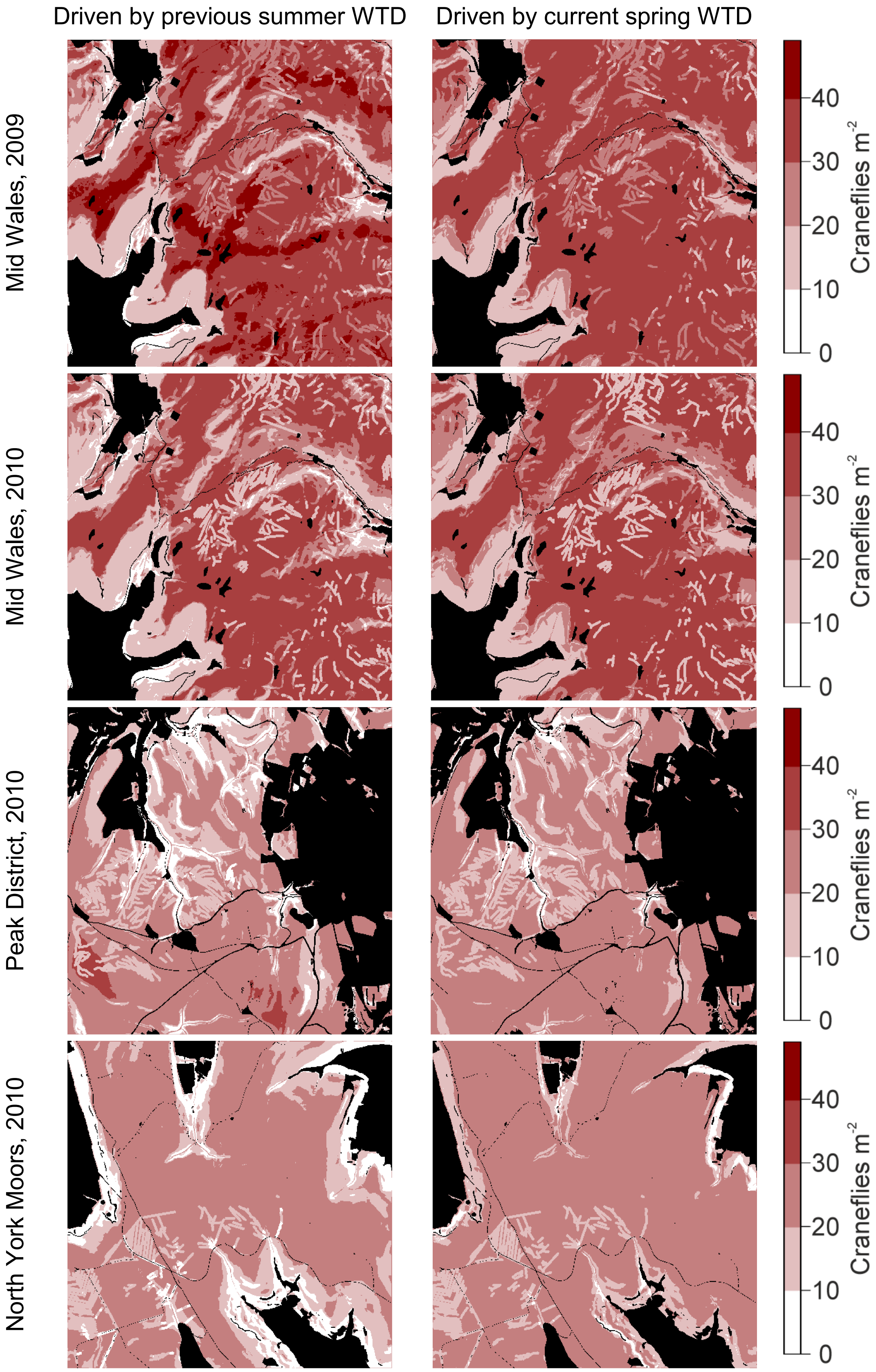

Figure 4.7. Predicted cranefly abundance in observation years based on ‘drained’ soil moisture conversions, i.e., applying ‘open’ conversions to cells within 20 m of drainage ditches, and ‘blocked’ conversions to all other cells. Interpretation as for Figure 4.5.

Table 4.2. Mean values (± standard deviation) of modelled WTD and cranefly abundance for years in which field observations were made. 'Blocked' values refer to a conversion based on the WTD-moisture relationship at blocked drains; 'open' values refer to a conversion based on the relationship at open drains; 'drained' values refer to the use of the open conversion at real drain locations and the blocked conversion elsewhere.

		Mid Wales, 2009	Mid Wales, 2010	Peak District, 2010	North York Moors, 2010
Summer WTD	Predicted WTD (cm)	8.36 (± 6.208)	9.66 (± 5.802)	13.04 (± 6.794)	14.11 (± 6.435)
	Blocked abundance (craneflies.m^{-2})	30.72 (± 10.764)	27.59 (± 9.315)	21.67 (± 7.094)	19.82 (± 6.071)
	Drained abundance (craneflies.m^{-2})	29.41 (± 10.788)	26.32 (± 9.405)	20.48 (± 7.241)	19.05 (± 6.368)
	Open abundance (craneflies.m^{-2})	16.90 (± 7.822)	14.26 (± 6.446)	9.89 (± 4.047)	8.63 (± 3.006)
Spring WTD	Predicted WTD (cm)	9.90 (± 4.926)	11.34 (± 4.501)	16.12 (± 5.218)	15.14 (± 4.609)
	Blocked abundance (craneflies.m^{-2})	32.00 (± 6.985)	29.52 (± 6.056)	23.05 (± 4.616)	24.14 (± 4.438)
	Drained abundance (craneflies.m^{-2})	30.65 (± 7.522)	28.23 (± 6.704)	21.88 (± 5.385)	23.31 (± 5.128)
	Open abundance (craneflies.m^{-2})	17.14 (± 5.088)	15.18 (± 4.292)	10.54 (± 2.756)	11.25 (± 2.728)

Cranefly abundance was predicted for each sampling location used in the field. Predicted values were compared to observed values using Spearman rank correlations (Table 4.3; Figure 4.8). As blocked and open conversions produced values which were ranked identically, correlation coefficients were also identical; blocked and open correlations are therefore presented together. In most cases, projections and observations were positively and significantly correlated. Using the appropriate conversion (i.e., blocked or open) for each sampling location typically produced stronger correlations than using one conversion across all points. The only site this did not hold for was mid Wales in 2009; this is likely to be because there was relatively little difference between blocked and open drains that year (see Chapter 2). Across all sites, summer-driven abundance showed the highest correlation with observed abundance, although this varied between individual sites. Projections for the Peak District were lower than observations (Figure 4.8). This may be because local influences on cranefly abundance may not be accounted for. However, across all sites, the positive correlations suggest that broad spatial patterns are reasonably well reproduced.

Table 4.3. Spearman's rank correlation coefficients and associated *P*-values comparing observed and modelled cranefly abundance. Results significant at $P < 0.05$ are highlighted in bold. 'Combined' refers to using the appropriate blocked or open conversion for the point, rather than one conversion across all sampling locations.

	Summer-driven, blocked or open	Summer-driven, combined	Spring-driven, blocked or open	Spring-driven, combined
Mid Wales, 2009	**ρ = 0.522, *P* < 0.001**	**ρ = 0.383, *P* = 0.010**	**ρ = 0.359, *P* = 0.017**	ρ = 0.296, *P* = 0.051
Mid Wales, 2010	**ρ = 0.454, *P* = 0.015**	**ρ = 0.618, *P* < 0.001**	ρ = 0.099, *P* = 0.615	**ρ = 0.549, *P* = 0.002**
Peak District, 2010	**ρ = 0.767, *P* < 0.001**	**ρ = 0.815, *P* < 0.001**	**ρ = 0.866, *P* < 0.001**	**ρ = 0.866, *P* < 0.001**
North York Moors, 2010	ρ = 0.060, *P* = 0.762	**ρ = 0.398, *P* = 0.036**	ρ = -0.003, *P* = 0.988	**ρ = 0.416, *P* = 0.028**
All sites and years	**ρ = 0.196, *P* = 0.027**	**ρ = 0.489, *P*<0.001**	ρ = 0.008, *P* = 0.925	**ρ = 0.410, *P* < 0.001**

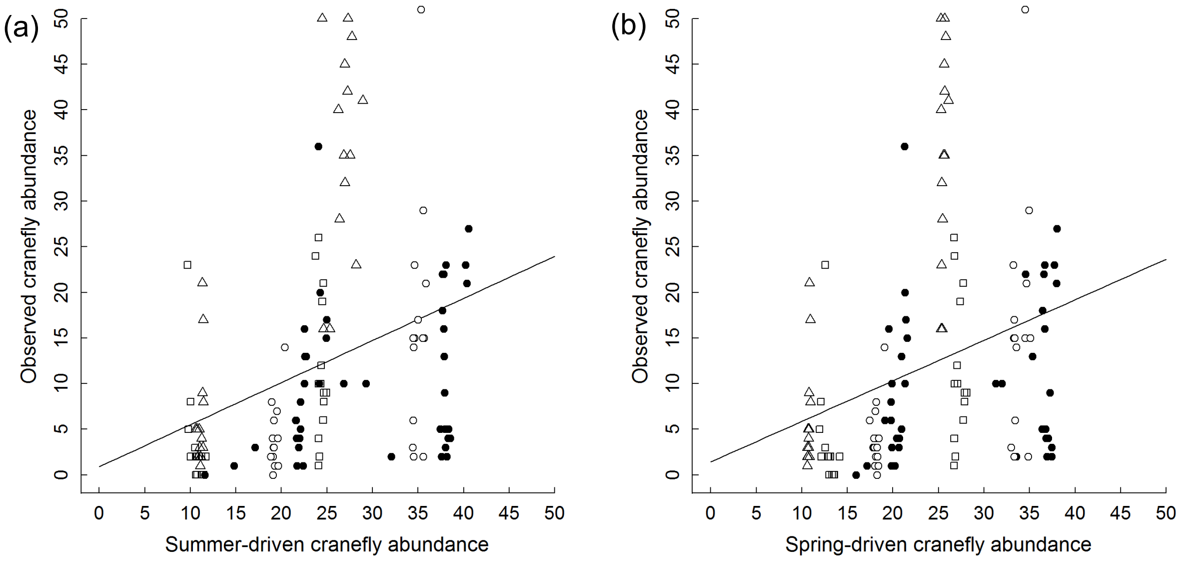

Figure 4.8. Predicted cranefly abundance plotted against observed cranefly abundance for a) summer WTD-driven projections, and b) spring WTD-driven projections. Lines show linear regressions of observed against predicted across all points. ● = mid Wales 2009, ○ = mid Wales 2010, △ = Peak District, □ = North York Moors.

4.4.3 Model projections: future trends driven by summer water tables

To understand how climate change may affect cranefly abundance, mean abundance was regressed against decade for 1920–2080; Figure 4.9 shows the change over time for each site and SRES scenario, driven by summer WTD. Projections indicated that falling summer water tables could cause cranefly abundance to decline substantially across all sites; all regression coefficients were negative and significantly different from zero (Table 4.4). All SRES scenarios showed broadly similar declines, and declines occurred regardless of whether the whole landscape was subject to the 'blocked' or 'open' conversion.

Table 4.4. Coefficients and associated *P*-values from linear regressions of projected mean cranefly abundance against decade, for projections driven by summer WTD. Column headings refer to SRES scenario of climate data driving the model.

		Low (B1)	Medium (A1B)	High (A1FI)
Mid Wales	Blocked	-0.055, $P = 0.001$	-0.056, $P < 0.001$	-0.066, $P < 0.001$
	Open	-0.038, $P = 0.001$	-0.039, $P < 0.001$	-0.044, $P < 0.001$
	Drained	-0.054, $P = 0.001$	-0.054, $P < 0.001$	-0.064, $P < 0.001$
Peak District	Blocked	-0.042, $P = 0.044$	-0.072, $P < 0.001$	-0.062, $P = 0.004$
	Open	-0.027, $P = 0.027$	-0.039, $P < 0.001$	-0.034, $P = 0.003$
	Drained	-0.041, $P = 0.042$	-0.069, $P < 0.001$	-0.059, $P = 0.004$
North York Moors	Blocked	-0.064, $P < 0.001$	-0.075, $P < 0.001$	-0.079, $P < 0.001$
	Open	-0.037, $P < 0.001$	-0.041, $P < 0.001$	-0.043, $P < 0.001$
	Drained	-0.063, $P < 0.001$	-0.073, $P < 0.001$	-0.076, $P < 0.001$

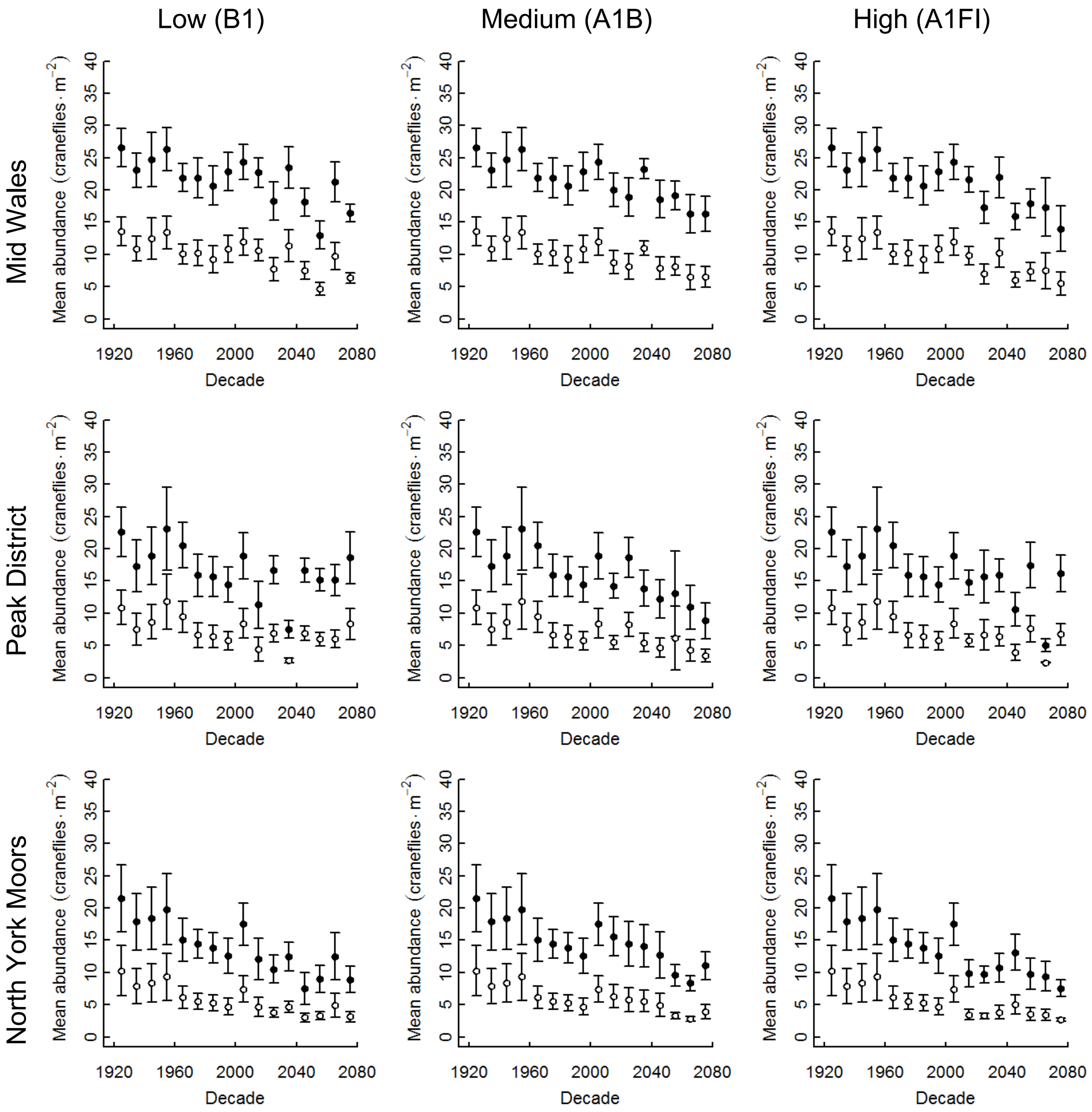

Figure 4.9. Decadal means of projected cranefly abundance plotted against time, driven by summer WTD, for the blocked conversion applied to the whole square (●) and the open conversion applied to the whole square (○). 'Drained' results are omitted for clarity, as they are very similar to 'blocked' results. Error bars are ± 2 standard errors.

To explore spatial changes, mean abundances for 30-year periods were calculated and mapped, representing baseline, mid-century and late-century periods (Figure 4.10 – Figure 4.12). As patterns were very similar between SRES scenarios, only results for the medium (A1B) scenario are presented. Areas of high abundance were projected to disappear altogether if the whole landscape was drained; by 2051–80 in the Peak District, no cells produced abundances greater than 10 craneflies m^{-2}, indicating substantial landscape-wide declines. In the North York Moors, the open conversion produced no cells with abundances >10 craneflies m^{-2} in any time period. When the blocked conversion was used, pockets of moderate abundance remained in flatter, wetter areas until the late 21st Century (Figure 4.10 – Figure 4.12), but abundance still declined in the wider landscape. When real drain locations were used, drains produced localised areas with abundance <10 craneflies m^{-2} even at mid Wales, which otherwise retained moderate abundances.

To estimate the scale of climate-driven declines, mean abundance from 1961–90 was compared to the A1B scenario in 2051–80. Based on the blocked conversion, mid Wales showed a decline of 19.7%, the Peak District showed a decline of 37.1%, and the North York Moors showed a decline of 33.1%. For projections based on the open conversion, mid Wales abundance declined by 28.5%, Peak District abundance declined by 38.6% and North York Moors abundance declined by 40.8%.

To examine ‘realistic’ drainage effects under climate change, blocked and drained conversions were compared for 2051–80. Drained abundance was 5.2% lower at mid Wales, 6.3% lower at the Peak District, and 4.9% lower at the North York Moors; these are larger than the values calculated for 2009 and 2010 (see Section 4.4.2). Hence, the scale and rate of declines was larger when the landscape was subject to drainage, and the impacts of drainage increased under drier conditions.

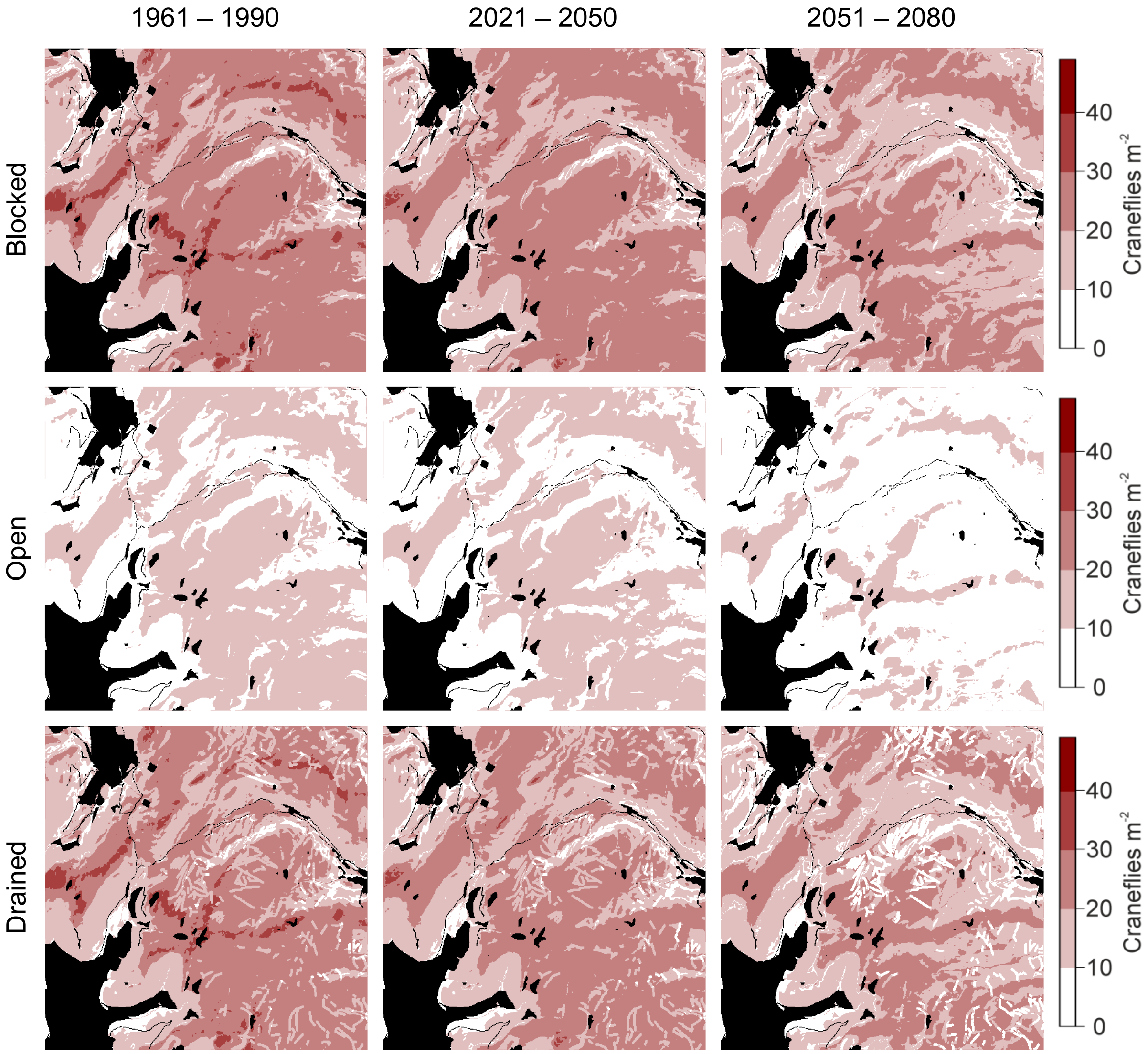

Figure 4.10. Spatial projections of cranefly abundance for mid Wales under the A1B SRES scenario, driven by summer WTD. Rows refer to different methods of converting between predicted WTD and moisture; blocked = blocked conversion applied to whole square, open = open conversion applied to whole square, drained = open conversion applied to cells within 20 m of real drain locations and blocked conversion applied to all other cells. Columns refer to periods for which the mean values were calculated. Darker red indicates higher cranefly abundance; lighter pinks and white indicate lower cranefly abundance. Black indicates areas of low altitude or inappropriate habitat types.

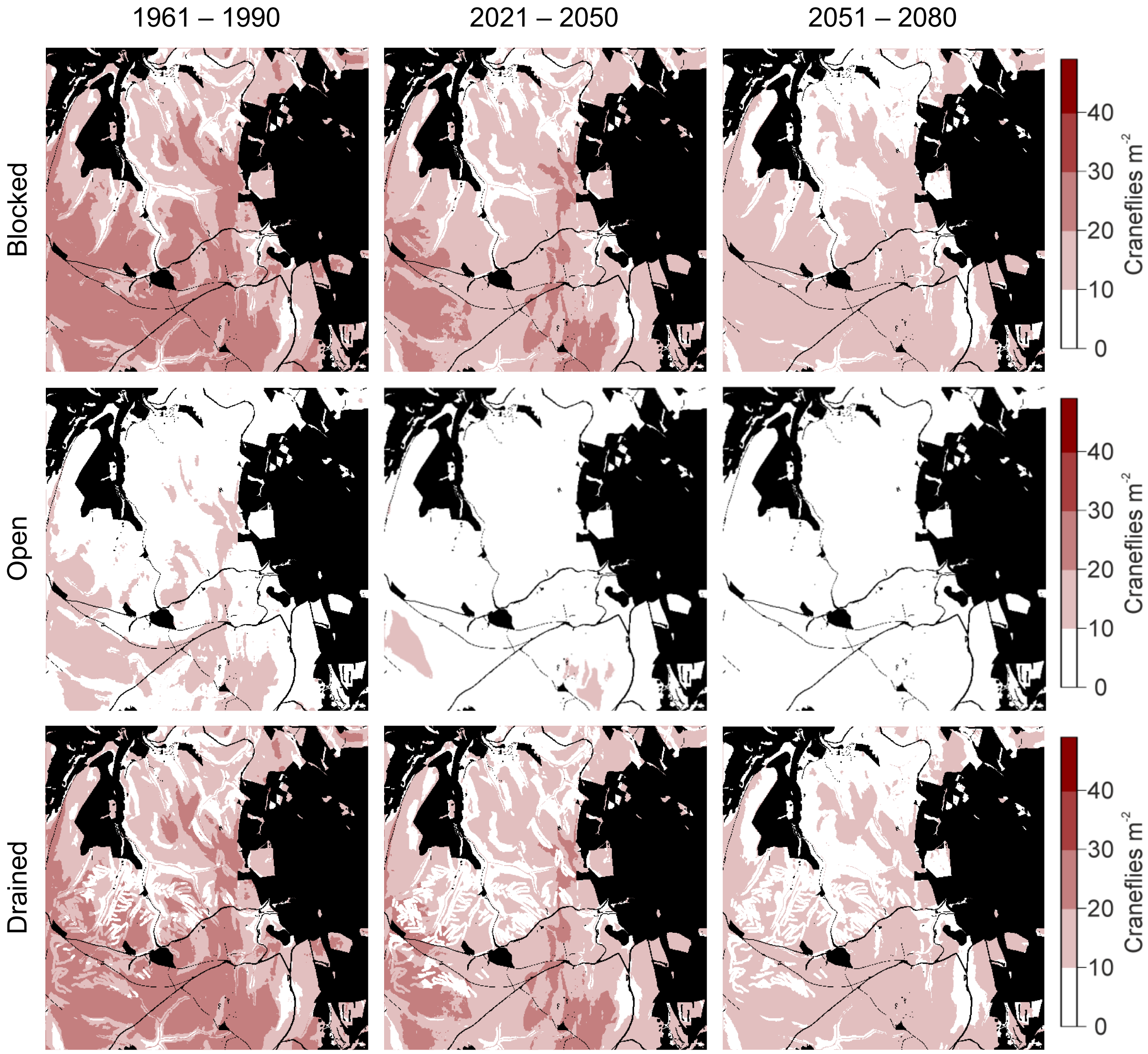

Figure 4.11. Spatial projections of cranefly abundance for the Peak District under the A1B SRES scenario, driven by summer WTD. Interpretation as for Figure 4.10.

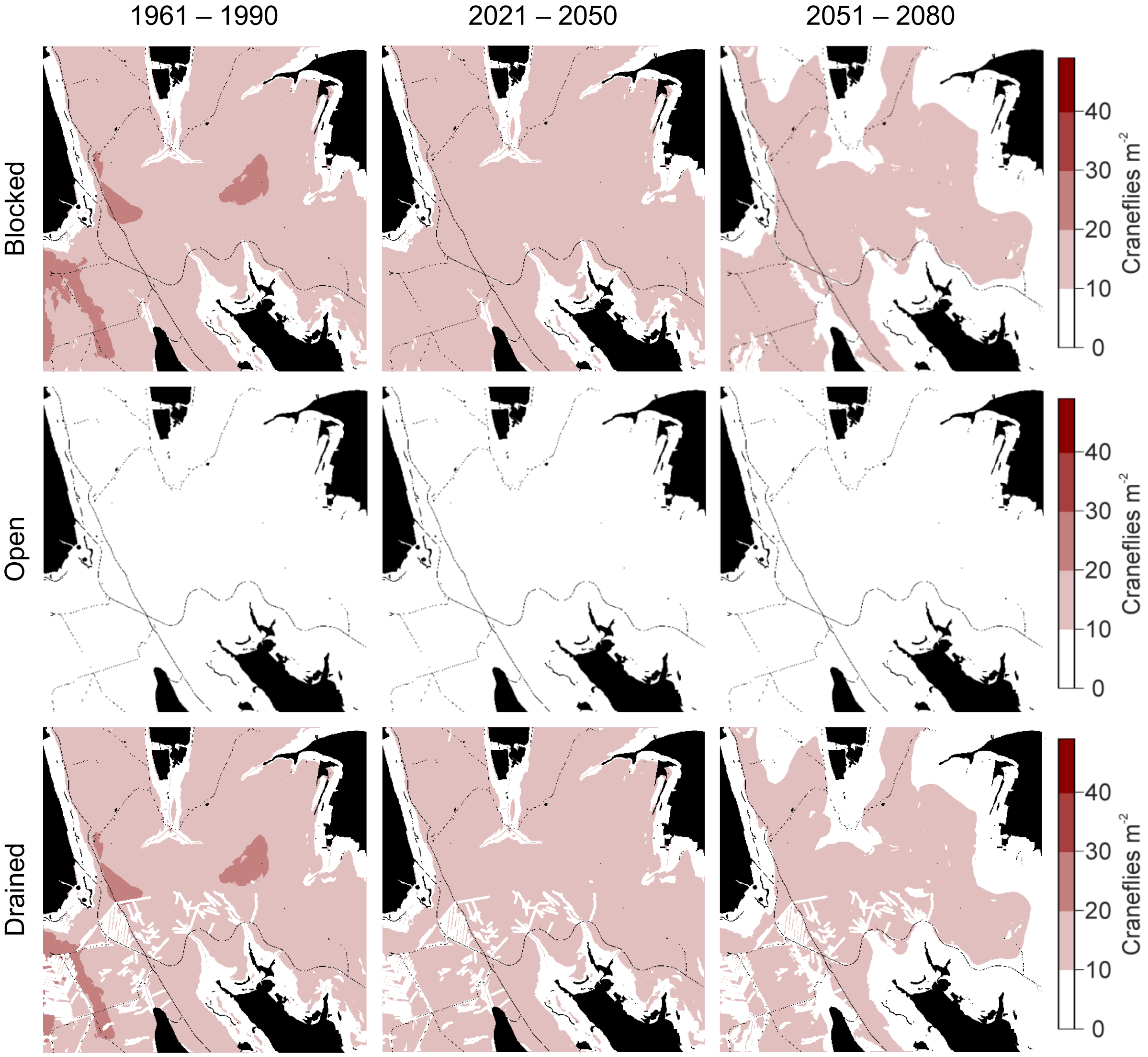

Figure 4.12. Spatial projections of cranefly abundance for the North York Moors under the A1B SRES scenario, driven by summer WTD. Interpretation as for Figure 4.10.

4.4.4 Model projections: future trends driven by spring water tables

When driven by spring WTD, no declines in cranefly abundance were predicted at any site (Figure 4.13). No regression coefficients were significantly different from 0 (Table 4.5). Spatial projections indicated that the distribution of areas producing high abundances and low abundances across the landscape should remain nearly identical across the 21st Century (Figure 4.14 – Figure 4.16). Results for the Peak District suggested that some periods may even produce slightly higher abundances (e.g., 2060s in high scenario, Figure 4.13).

Table 4.5. Coefficients and associated *P*-values from linear regressions of projected mean cranefly abundance against decade for projections driven by spring WTD. Column headings refer to SRES scenario of climate data driving the model.

		Low (B1)	Medium (A1B)	High (A1FI)
Mid Wales	Blocked	-0.004, $P = 0.122$	-0.002, $P = 0.646$	-0.009, $P = 0.106$
	Open	-0.003, $P = 0.160$	-0.001, $P = 0.693$	-0.007, $P = 0.114$
	Drained	-0.004, $P = 0.123$	-0.002, $P = 0.647$	-0.009, $P = 0.106$
Peak District	Blocked	0.002, $P = 0.728$	0.003, $P = 0.660$	0.005, $P = 0.586$
	Open	0.001, $P = 0.730$	0.002, $P = 0.703$	0.004, $P = 0.567$
	Drained	0.002, $P = 0.723$	0.003, $P = 0.653$	0.005, $P = 0.583$
North York Moors	Blocked	0.003, $P = 0.514$	-0.001, $P = 0.824$	-0.010, $P = 0.225$
	Open	0.003, $P = 0.492$	-0.001, $P = 0.864$	-0.007, $P = 0.241$
	Drained	0.003, $P = 0.514$	-0.001, $P = 0.823$	-0.010, $P = 0.224$

To assess the scale of changes, mean abundance in 1961–90 was compared to the A1B scenario in 2051–80. Using the blocked conversion, mid Wales showed a decline of 1.4%, the Peak District showed a decline of 0.1%, and the North York Moors showed a decline of 0.3%. Using the open conversion, mid Wales abundance declined by 2.0%, and both Peak District and North York Moors abundance declined by 0.3%. To estimate 'realistic' drainage effects, blocked and drained conversions were compared for 2051–80. 'Drained' abundance was 4.1% lower at mid Wales, 4.3% lower at the Peak District, and 3.1% lower at the North York Moors; these reductions are smaller than those calculated for 2009 and 2010 (see Section 4.4.2). Therefore, if cranefly abundance were driven by spring WTD, climate change would not cause substantial declines, with drainage impacts alone much greater than climate change impacts, and drainage effects not becoming stronger over time.

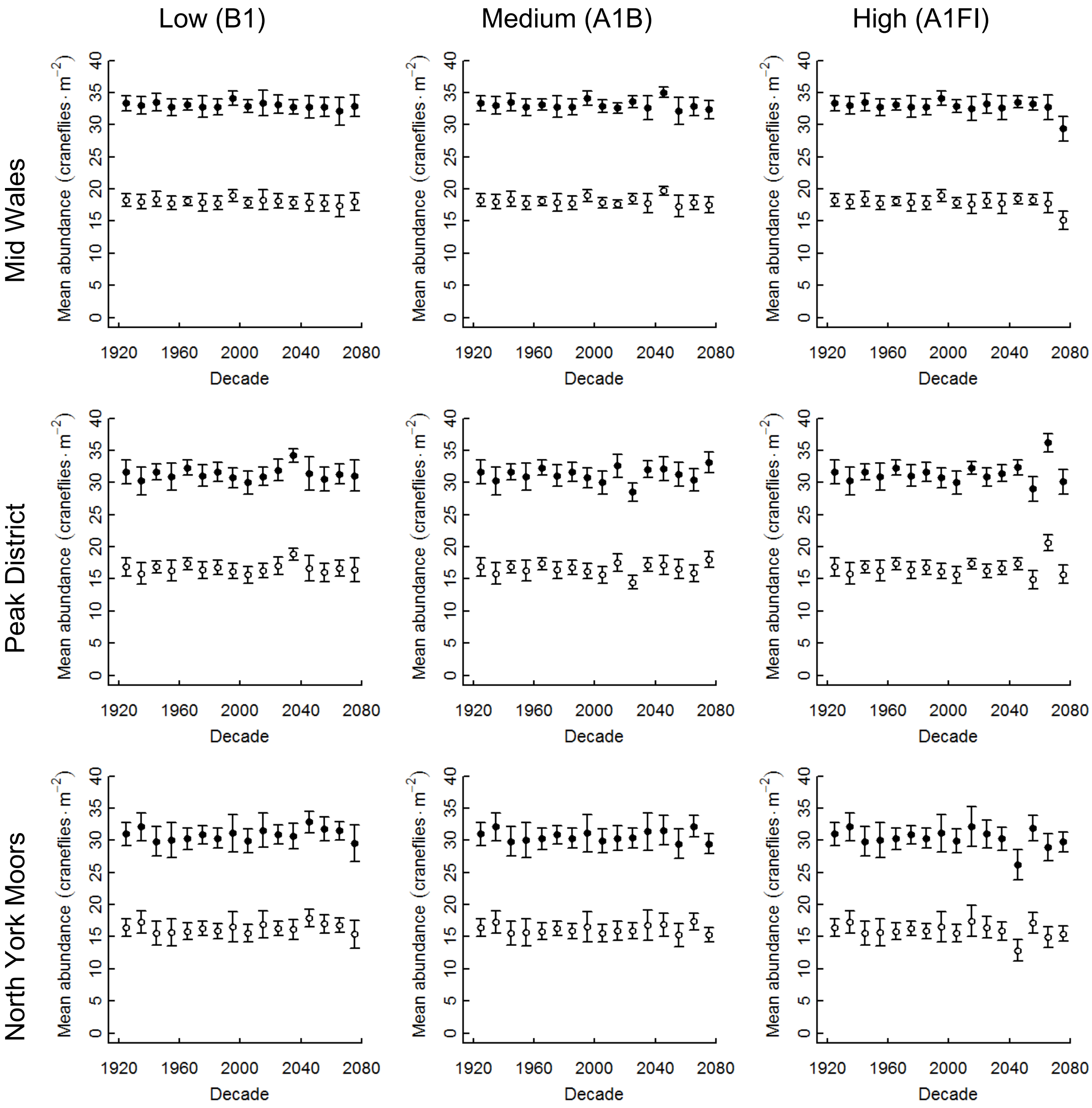

Figure 4.13. Decadal means of projected cranefly abundance plotted against time, driven by spring WTD, for the blocked conversion applied to the whole square (●) and the open conversion applied to the whole square (○). ‘Drained’ results are omitted for clarity, as they are very similar to ‘blocked’ results. Error bars are ± 2 standard errors.

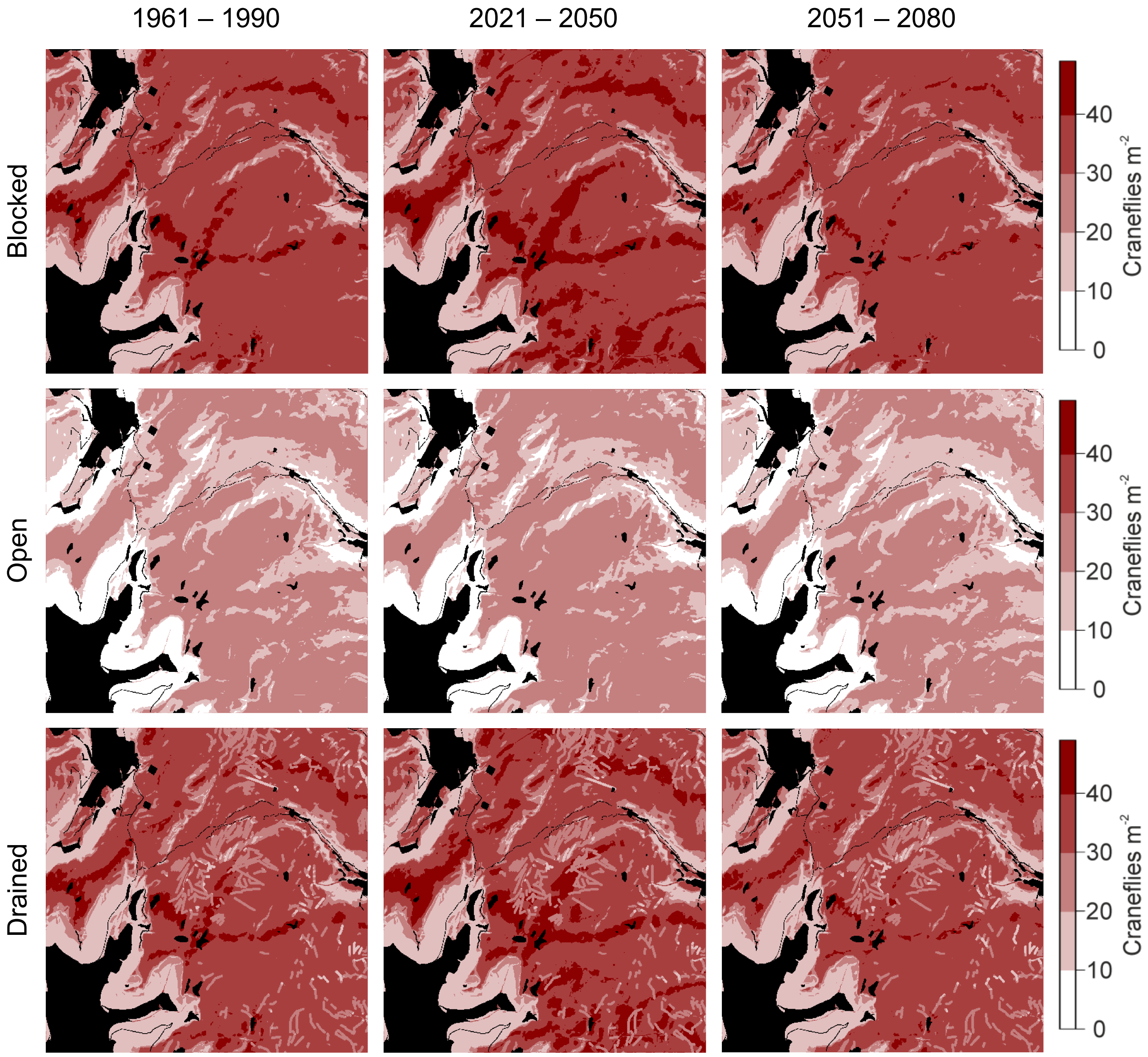

Figure 4.14. Spatial projections of cranefly abundance for mid Wales under the A1B SRES scenario, driven by spring WTD. Rows refer to different methods of converting between predicted WTD and moisture; blocked = blocked conversion applied to whole square, open = open conversion applied to whole square, drained = open conversion applied to cells within 20 m of real drain locations and blocked conversion applied to all other cells. Columns refer to periods for which the mean values were calculated. Darker red indicates higher cranefly abundance; lighter pinks and white indicate lower cranefly abundance. Black indicates areas of low altitude or inappropriate habitat types.

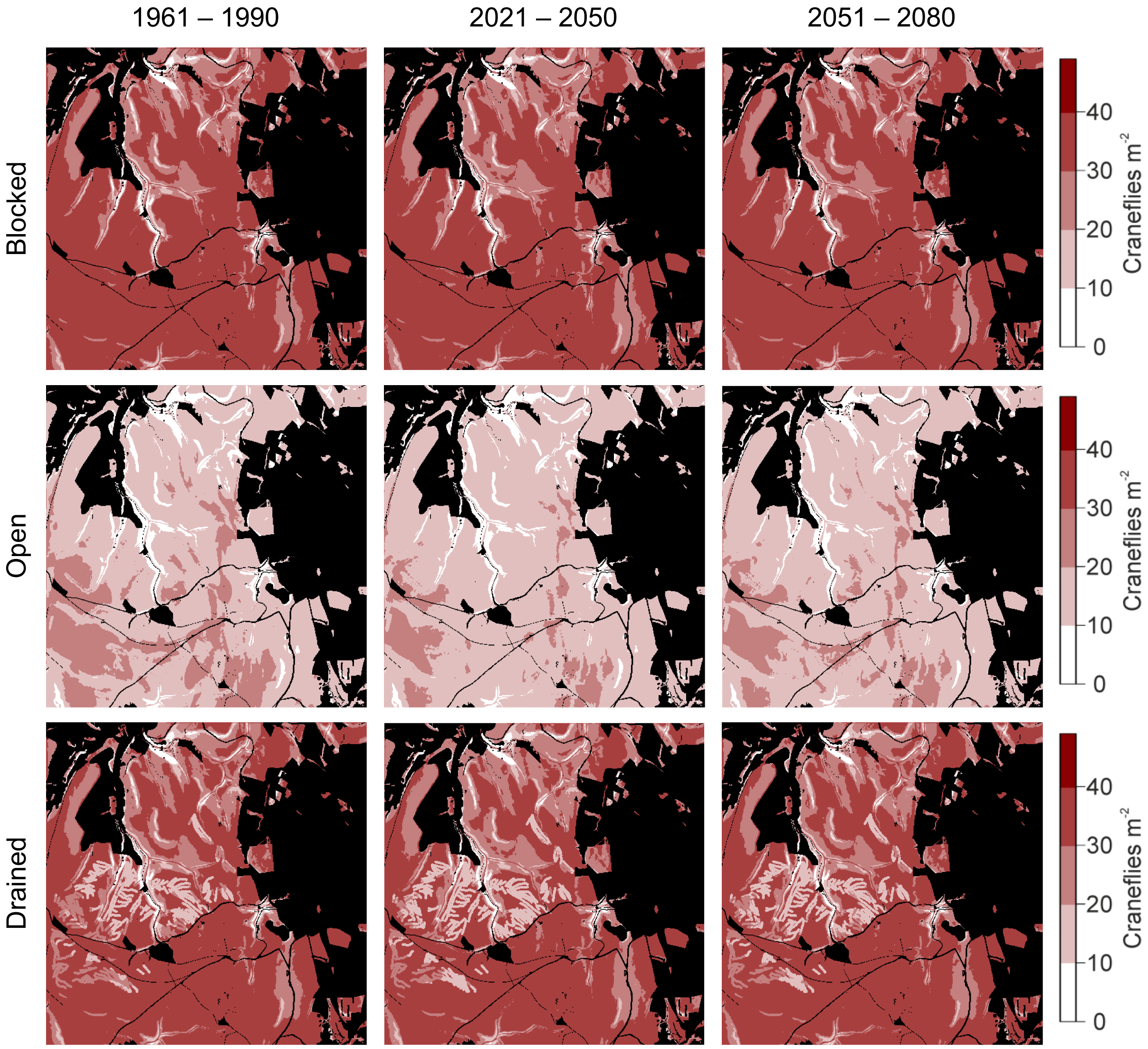

Figure 4.15. Spatial projections of cranefly abundance for the Peak District under the A1B SRES scenario, driven by spring WTD. Interpretation as for Figure 4.14.

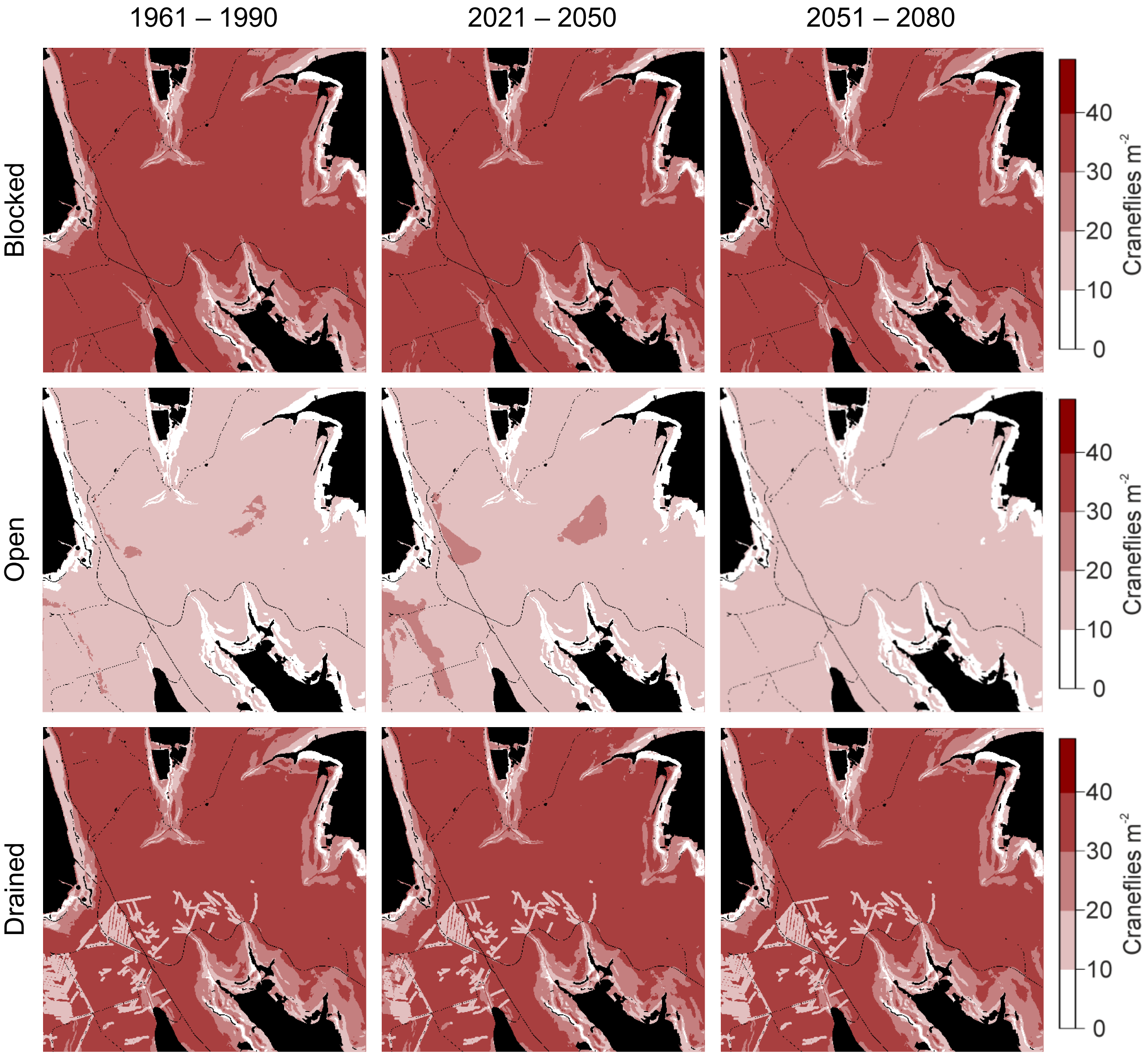

Figure 4.16. Spatial projections of cranefly abundance for the North York Moors under the A1B SRES scenario, driven by spring WTD. Interpretation as for Figure 4.14.

4.5 Discussion

An analysis has been presented of cranefly abundance trends driven by climate change, combining empirically-derived relationships with a mechanistic model of peatland hydrology. This approach provides a more direct means of driving projections than previous models, which have relied on statistical associations with surrogate climate variables. Hypotheses related to model validation were all met: modelled water table depth was a highly significant predictor of observed soil moisture from both blocked and open drains, with summer water tables predicting more variation in moisture; and modelled cranefly abundance was positively and significantly correlated with observed abundance within and across modelled landscapes. Therefore, model results generally reflected real patterns. However, projections should be seen to represent dominant, broad-scale patterns and trends rather than specific projections of realised abundance for individual locations.

Both hypotheses related to climate change and drainage effects were met when summer water tables drove abundance projections: significant declines in cranefly abundance were driven by falling water tables, and declines were of a larger magnitude when the landscape was subject to drainage than when all drains were blocked. However, when spring water tables drove abundance projections, neither hypothesis was met: abundance did not significantly decline over time and drainage did not lead to greater declines. These results can help us to understand likely impacts of climate change and peatland drainage for key upland soil invertebrates; such information could be important in attempts to conserve wider upland biodiversity.

4.5.1 Evaluating the model approach

Several assumptions were made in modelling, and the effects of these must be evaluated before results can be interpreted. Perhaps the most important assumption is that projected WTD can be linked to cranefly abundance using two regressions. First, projected WTD was regressed against observed soil moisture. The subsequent conversion to cranefly abundance was based on a regression with observed soil moisture, so to generate realistic abundance estimates, modelled soil moisture values needed to be in the observed range. Using empirical conversions produced means or ranges that were too small (see Section 4.4.1), but the regression-based conversion produced more appropriate values. Although summer moisture observations were not available for use in a direct conversion with modelled WTD, the regression approach allowed modelled summer WTD to be linked to observed moisture. Summer WTD influences annual moisture patterns (Charman, 2007), and here, the higher R^2 values from summer WTD regressions (see Section 4.4.1) suggested that it may indeed have a stronger influence on spatial moisture patterns. Nevertheless, converted moisture should be seen primarily as an intermediate modelling stage. This approach also maintained the chain of causality in the system, from WTD to moisture to craneflies, meaning that the model's logic is more satisfactory.

A related assumption is that soil moisture is linked to WTD by a linear relationship. Empirical conversion methods (Granberg *et al.*, 1999; Weiss *et al.*, 2006; Kettridge & Baird, 2008) generally use exponential or power-law relationships. Experimental results, upon which several conversions are based, also show nonlinear relationships (Hayward & Clymo, 1982). However, these results relate to *Sphagnum* cores, so the relationship may differ from peat made of mixed vegetation types, or of more decomposed peat. Indeed, field measurements from Sweden (Kellner & Halldin, 2002) and Canada (Price, 1997) suggest a predominantly linear relationship. The model also assumes that the WTD-moisture relationship will be maintained under climate change, whereas changes to peat structure on drying (Holden, 2005a) could affect the relationship. However, without further study of the link between WTD and soil moisture, such matters cannot be predicted or modelled. Therefore, given the uncertainty in the form of the relationship, the highly significant linear relationship seems adequate.

A further assumption is that WTD can drive separate moisture conversions to reflect drainage effects. Preferably, WTD would be lowered by drainage, with a single moisture conversion applied thereafter. However, drainage effects are not simple. Some authors report effects to be limited to drain edges (Coulson *et al.*, 1990; Stewart & Lance, 1991), whilst others report effects over greater distances (Wilson *et al.*, 2010; Holden *et al.*, 2011). Drains also affect WTD fluctuations (Holden *et al.*, 2011; Ketcheson & Price, 2011), which could influence soil moisture. Hence, a single WTD reduction would be hard to parameterise, and could not reproduce all drainage effects. As observed moisture was recorded from both blocked and open drains, it integrates multiple effects, thus providing a practical way of modelling drainage impacts.

In MILLENNIA, peat is represented as a 1-D column. It was therefore necessary to assume that a landscape can be represented by multiple non-interacting columns. Consequently, 2-D processes such as accumulation of water in depressions, slope position effects and drainage from ridges (e.g., Kellner & Halldin, 2002; Holden, 2005b) are not represented. Spatial representations may therefore not correspond to real locations of wet or dry areas. However, on the scales modelled, the wet and dry areas should balance out, with ridges flanked by hollows, and dry upper slopes balancing wet lower slopes. Therefore, landscape-level wetness should not be strongly affected, with spatial representations instead reflecting the degree of topographic heterogeneity within the landscape.

Abundance projections were generated using a deterministic equation that did not account for variation in the relationship between abundance and moisture. The ‘wedge-shaped’ relationship in Figure 4.3 shows considerable variation in abundance at higher moisture levels; this may be related to factors such as vegetation cover, predation, egg-laying behaviour, or just stochasticity (e.g., Coulson, 1962; Freeman, 1967). However, data were not available to explore these possibilities in field observations, and most of these processes could not be directly modelled. It is therefore worth re-stating that modelled abundance represents an expected value; other processes could increase or decrease realised abundance, but expected values should be sufficient for examining broad-scale patterns and trends.

Finally, there is no time-dependence in cranefly projections. The relationship between abundance and soil moisture was derived spatially, so temporal effects could not be parameterised. Also, cranefly abundance is calculated independently every year, so cycles of retreating during dry periods and subsequent recolonisation (Coulson, 1962) cannot be replicated. Further information on population-level responses to temporally-varying moisture would be required for a time-dependent model. However, the absence of time-dependence makes modelled populations more resilient, as large population declines would not impact subsequent abundance, so estimates of declines may be somewhat conservative.

4.5.2 Matching model results to observations

Projections of cranefly abundance were significantly and positively correlated with observations across all sites and within most sites. The significant correlations for both observation years in mid Wales, along with the lower moisture in 2010, suggested that some temporal patterns may also be replicated, but longer time series would be required to test this. Overall, results were encouraging, as the model produced projections that adequately represented overall spatial patterns.

The greatest discrepancy between modelled and observed abundance was found at the Peak District, where modelled abundance was lower than observed. This may be because higher temperatures in the Peak District climate data caused more evapotranspiration, thus producing deeper WTDs and lower abundances; the model does not account for cloudiness, so could overestimate evaporative losses. Alternatively, land management and vegetation impacts, which are not modelled, could influence results. The Peak District site was *Eriophorum*-dominated, which would favour higher abundances (e.g., Pearce-Higgins & Yalden, 2004), but vegetation cover was not considered in conversions. The area where high abundances were observed was subject to restoration through drain blocking, and pools had developed near dams; these may have caused local soil moisture and cranefly abundance to be artificially high. As discussed above, model projections should not be expected to exactly reproduce realised abundance. However, given the absence of such processes, it is encouraging that there were still significant, positive correlations between observed and modelled abundance within and between sites.

4.5.3 Current drainage effects

Drainage was projected to reduce cranefly abundance. Applying the ‘open’ conversion to the whole landscape gave an unrealistically high estimate of drainage effects, but could be seen to represent the maximum possible drainage effect. However, the more realistic ‘drained’ results may underestimate drainage effects. The distance over which drains affect moisture is uncertain, with various authors reporting different extents (e.g., Coulson *et al*., 1990; Stewart & Lance, 1991; Wilson *et al*., 2010; Holden *et al*., 2011); the value of 20 m chosen here represents just one possibility. Topography, climate and drain condition influence drain efficiency, so impacts of drainage will vary within and between landscapes (Coulson *et al*., 1990; Holden *et al*., 2004; Holden *et al*., 2006). Further, the lack of 2-D hydrology excludes processes such as interception by drains, which dries areas down slope (Holden *et al*., 2006). Hence, although the projected 3.4 – 5.5% abundance decreases may appear small, this is likely to be towards the lower end of real effects. This value must also be viewed in context of drain density; drains covered only 6 – 9% of each square, so for a relatively small element of the landscape, they produced a relatively large effect.

4.5.4 Future climate and drainage effects

Projections driven by summer WTD showed dramatic population declines under climate change. Declines of 20 – 41% were projected by 2080; this supports results of Pearce-Higgins *et al.* (2010), who projected declines in Golden Plover populations of 27 – 100% by 2100, caused by August temperature-driven declines in craneflies. There was little difference between SRES scenarios, implying that cranefly populations may be locked into climate-driven declines, regardless of global climate change mitigation strategies. Drain blocking did not stop population declines, but did reduce the scale of declines, with population reductions of 20 – 37% in a 'blocked' landscape, but 29 – 41% in an 'open' landscape. Blocking could therefore prevent extinctions: if the whole landscape was drained, very low abundances would be widespread by the mid-21st Century, and results using real drain locations suggested that drains would act as centres of abundance declines. If drains were blocked, however, moderate abundances could be maintained until the late 21st Century. Further, population reductions caused by drainage could increase from 3.9 – 5.5% under recent climatic conditions to 4.9 – 6.3% by the late 21st Century, supporting the suggestion that drainage impacts could become stronger under climate change.

Spring soil moisture could also influence cranefly abundance (Horobin, 1971 cited in Pritchard, 1983). Results indicated that if this were the primary driver of abundance, cranefly populations would not decline. The lack of WTD declines is probably driven by wetter winters: single storms can re-saturate peat and winter rainfall recharges water tables each year (Evans & Warburton, 2007). Winter rainfall is projected to increase under climate change (Holden *et al.*, 2007c), so the capacity for water tables to recharge could also increase. Therefore, for any upland biodiversity dependent on high soil moisture in spring, drainage effects would be more important than climate-driven moisture changes, and blocking drains would provide benefits both now and throughout the 21st Century. Further, maintaining water in peatlands throughout spring could slow summer water table falls, reducing the scale of droughts and increasing ecosystem resilience.

Summer moisture is likely to be the dominant driver of cranefly abundance, as it affects the sensitive period of the cranefly life cycle. Lab experiments (e.g., Meats, 1967b) and field experiments (Milne *et al.*, 1965) on mineral soil species show that eggs and early instar larvae are most at risk of desiccation. This is also likely in peatland species (Coulson, 1962), which have early larval instars during summer. This could explain the statistical association between cranefly abundance and August temperature (Pearce-Higgins *et al.*, 2010). Therefore, it is more likely that climate change will drive population declines than it is that populations will remain stable. Conservation efforts should focus on ensuring adequate moisture remains in peatlands throughout the sensitive summer period.

Climate and drainage effects were stronger in the Peak District and North York Moors than in mid Wales. This supports previous work indicating that drainage impacts are greater in drier locations (Coulson *et al*., 1990) and that peatlands in the South Pennines and North York Moors are more threatened by climate change than those in wetter areas (Clark *et al*., 2010b). Therefore, conservation strategies must consider that these areas may experience the worst climate-driven declines, but could also benefit the most from drain blocking.

4.5.5 Implications and conclusions

Both drainage and climate change could cause upland cranefly populations to decline, which would harm birds that rely on craneflies for food. To effectively plan conservation strategies for bird populations, craneflies must also be considered. Drier summers could drive substantial declines in cranefly abundance, with 20 – 41% decreases by the late 21st Century. Further, under climate change the impact of drainage on cranefly populations could increase, and open drains could be the focus of population declines. Climate change should not cause moisture declines in spring, but drainage would still have a substantial effect on soil moisture. Therefore, blocking drains appears to be a 'no lose' strategy, providing both immediate and longer-term benefits. However, as macropore development, natural piping and peat cracking all increase under drainage (e.g., Holden *et al*., 2004; Holden, 2005a; Holden *et al*., 2006), and are not necessarily removed after restoration, studies of long-term effects are required before the benefits can be fully understood.

Further study of the moisture sensitivity of two key cranefly species, *Tipula subnodicornis* and *Molophilus ater*, would allow more accurate, time-dependent models to be parameterised and would substantially aid conservation planning. Of particular importance are the effects of varying drought lengths, the effects of increasing magnitudes of moisture fluctuations, and whether mortality increases gradually with drought or whether a threshold exists. Some of these have been examined for mineral soil species on an individual basis (Meats, 1967b; Meats, 1968), but understanding population-level responses in peatland species is also important.

The model presented here gives a first impression of likely trends, but if specific landscape-level conservation plans are required, models incorporating more real processes would be beneficial. The most important developments would be to add explicit spatial structure to moisture models (e.g., Baird *et al*., 2012) and time-dependence to cranefly projections. Such projections would allow conservation actions to be focussed on the most amenable parts of landscapes and on the most sensitive times of year.

The trends identified by this model warrant further exploration and consideration in conservation planning. Although summer moisture changes could drive cranefly population declines, the relationship between abundance and moisture provides hope that land could be managed to maintain large populations; if soil moisture levels could be raised, perhaps through the use of bunds or mulches (e.g., Price *et al*., 2003), population declines could be reduced. Under current conditions, blocking drains seems to be beneficial, and could become more beneficial still under climate change. If moisture management for craneflies were combined with other management actions (e.g., Pearce-Higgins, 2011b), the resilience of upland bird populations could increase. By combining information gained from field observations and predictive models, we may be able to effectively manage peatlands for conservation of biodiversity as the climate changes.

4.6 Acknowledgements

Drain location maps were kindly provided by the EU LIFE Project/RSPB, United Utilities, and the North York Moors National Park Authority.

Chapter 5

Relationships between abundance of a keystone peatland invertebrate and upland breeding bird distributions

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5.1 Abstract

The UK upland breeding bird assemblage contains a unique mix of species and some large, regionally-important populations. However, some species, primarily waders, are declining, driven by land management changes. Climate change could also impact upland birds, as drier conditions could drive declines in cranefly (Diptera: Tipulidae) populations, a key food source for some species. To effectively conserve upland breeding bird populations under climate change and changing land management regimes, it would be beneficial to understand proximate drivers of bird distributions at large scales. Here, a peatland hydrology model and an empirically-derived cranefly abundance relationship are used to generate cranefly abundance projections for two years in which large-scale surveys of breeding birds in the Peak District National Park occurred. For Golden Plover, a species known to be influenced by cranefly availability, cranefly abundance significantly predicted bird abundance in both survey years (1990, 32.3% model deviance explained; 2004, 24.7% deviance explained), and also colonisations (5.3% deviance explained) and extinctions (14.9% deviance explained) between survey years. Cranefly abundance explained more variation than most habitat-based explanatory variables: only peat cover (1990, 44.7%; 2004, 41.5%) explained more variation in both years, whilst cotton grass (1990, 23.8%; 2004, 32.3%) and enclosed grassland (1990, 22.7%; 2004, 25.6%) explained more in one year. Thirteen other species were then modelled: cranefly abundance was a positive, significant predictor of Red Grouse and Dunlin abundance. Across all species, the proportion of variation explained by cranefly abundance was significantly and positively correlated with the proportion of craneflies in the adult diet (Pearson's r = 0.72 – 0.79); positive, but non-significant, correlations were found for the pullus diet (Pearson's r = 0.45 – 0.59). Conserving upland breeding birds under climate change may therefore require management to increase soil moisture and thus maintain high cranefly abundances.

5.2 Introduction

The avian fauna of the UK uplands consists of a unique mix of species, with oceanic, boreal and northern species co-occurring (Thompson *et al*., 1995; Pearce-Higgins *et al*., 2009a). Some of these species occur in exceptionally high concentrations, with the uplands supporting 7.5% of the European Golden Plover population, 40% of the European Eurasian Curlew population and 17% of the European Meadow Pipit population (Pearce-Higgins *et al*., 2009a). Regionally-important populations of predatory species such as Golden Eagle, Peregrine, Merlin and Hen Harrier also occur (Thompson *et al*., 1995). However, recent estimates suggest that populations of many species are declining (Pearce-Higgins *et al*., 2009a; Pearce-Higgins, 2010). Widespread declines have been observed in species such as Lapwing, Dunlin and Curlew (Sim *et al*., 2005). Other species, such as Golden Plover, show spatially-variable population trends, with declines in some areas but not in others (Sim *et al*., 2005). Conversely, some species, notably Raven and Stonechat, appear to be increasing (Sim *et al*., 2005).

Arguably the strongest driver of change in upland breeding bird abundance is land management. Agricultural intensification has long been suggested to affect bird populations, and improvement of upland grasslands has been linked to wader declines (Baines, 1988; Bibby, 1988). Intensive grazing can reduce invertebrate food supplies (Dennis *et al*., 2008), and may increase predation (Fuller & Gough, 1999). However, the evidence for this having widespread impacts is weak (Pearce-Higgins & Grant, 2006). Afforestation may reduce bird densities and increase rates of decline (Buchanan *et al*., 2003; Hancock *et al*., 2009; Amar *et al*., 2011), although the mechanism driving these patterns remains unclear. In some areas, increasing predation pressure may drive population declines via reduced breeding success (Grant *et al*., 1999). Finally, declining grouse moor management has led to the loss of vegetation mosaics and increased predation, negatively impacting ground-nesting waders, but reducing the threat of illegal persecution for raptors (Pearce-Higgins *et al*., 2009a). Hence, multiple drivers influence upland bird populations, but species respond differently to the different pressures (Pearce-Higgins & Grant, 2006; Amar *et al*., 2011).

Climate change is likely to become increasingly important as a driver of bird population trends (Jetz *et al*., 2007). This may be particularly pertinent for UK upland birds, as many are at the southern extent of their ranges (Pearce-Higgins *et al*., 2009a). Climate change may have a number of impacts on bird populations, often involving complex interactions (Mustin *et al*., 2007). Higher temperatures may increase over-winter survival or productivity, but may also reduce availability of key prey species (Pearce-Higgins, 2010; Pearce-Higgins *et al*., 2010; Pearce-Higgins, 2011a). Further, the timing of peak prey availability may shift, causing a phenological mismatch (Pearce-Higgins *et al*., 2005; Tulp & Schekkerman, 2008). There are already international examples of birds at their southern range margin declining due to climatic effects on food resources (Waite & Strickland, 2006), and examples of UK upland birds whose decline may be linked to climate change (Beale *et al*., 2006a). If we wish to retain large populations of northerly-distributed birds within the UK, more conservation effort will be required as the climate changes (Renwick *et al*., 2012).

To effectively conserve bird populations, it is necessary to gain a thorough understanding of factors influencing their distribution and abundance. A key influence is food supply, which affects abundance through productivity and survival. In Song Sparrows, higher food availability increases clutch size and chick survival (Arcese & Smith, 1988). In the Red-eyed Vireo, lower abundance of key invertebrate prey causes delayed breeding, which in turn can reduce female productivity (Marshall *et al*., 2002). Great Skuas show higher adult mortality when food availability is lower during the breeding season (Ratcliffe *et al*., 2002); similarly, in Black-legged Kittiwakes, low food availability during breeding increases stress hormone concentrations and is associated with lower survival and fecundity (Kitaysky *et al*., 2010).

For upland bird species, habitat quality, predator abundance and anthropogenic disturbance influence distributions (Haworth & Thompson, 1990), but food availability may be the most important influence (Ratcliffe, 1977). Food availability influences habitat selection, foraging site selection and the time spent on high moorland (Coulson & Butterfield, 1985; Whittingham *et al*., 2001; Douglas *et al*., 2008). Further, in high altitude upland ecosystems, food chain lengths may decrease (Usher & Gardner, 1988) and relatively few species dominate the invertebrate fauna (Coulson, 1988), so bird populations may be strongly influenced by the availability of key invertebrate prey species. Therefore, understanding links between upland bird distributions and invertebrate food supply will prove valuable for conservation efforts.

5.2.1 The importance of craneflies to upland birds

Craneflies (Diptera: Tipulidae) are a major component of the upland peatland invertebrate fauna (Coulson & Butterfield, 1985), and thus provide an important food resource for birds. They are found in over 20% of adult moorland bird diets, and in over 50% of chick diets, with both adults and larvae taken (Buchanan *et al*., 2006a). They make particularly large contributions to the adult diet of Dotterel, Golden Plover, Dunlin, Whimbrel, Curlew and Snow Bunting, and the pullus diet of Red Grouse, Golden Plover, Dunlin, Meadow Pipit, Wheatear and Snow Bunting (Pearce-Higgins, 2010). Variation in cranefly abundance can therefore cause population-level responses in birds. Red Grouse chicks display higher growth and survival rates in areas with higher cranefly availability (Park *et al*., 2001). Meadow pipits appear to time their first brood to maximise access to the spring peak of adult craneflies (Coulson & Whittaker, 1978), and may select nesting sites to access high densities of larvae (Douglas *et al*., 2008). Dotterel may also select nest sites based on availability of cranefly prey (Galbraith *et al*., 1993) and are in better condition whilst incubating in areas with more craneflies (Holt *et al*., 2002).

Links between Golden Plover populations and craneflies appear to be particularly strong. Both chicks and adults favour habitats with high cranefly abundance or biomass, and chick growth and survival rates are positively correlated with cranefly abundance (Whittingham *et al*., 2001; Pearce-Higgins & Yalden, 2003a; Pearce-Higgins & Yalden, 2004). As a result, annual fluctuations of Golden Plover populations appear to be driven by changes in adult cranefly abundance (Pearce-Higgins *et al*., 2010). Projected declines in cranefly abundance as a result of climatic warming could cause southern range-margin Golden Plover populations to be threatened with extinction (Pearce-Higgins *et al*. 2010).

5.2.2 Modelling drivers of upland bird abundance

There is a good understanding of the habitat requirements of upland birds, and an increasing knowledge of the different factors driving their abundance (e.g., Pearce-Higgins & Grant, 2006; Amar *et al*., 2011). Such information is being used to inform conservation policy and actions (e.g., Defra, 2011), but the ability to inform management would be improved if we were better able to describe variation in the resources required by birds across large areas and, further, how management influences these resources. Measures of land-cover are often used as surrogates, but there may be little quantitative information about variation in the actual resources of interest, or how they may be influenced by conservation actions.

Here, an attempt is presented to link large-scale spatial and temporal patterns of upland bird abundance to estimates of cranefly abundance, using data from repeated large-scale surveys of breeding birds in the Peak District National Park. The modelling process presented in Chapter 4 will be used to estimate adult cranefly abundance throughout the bird survey region. Model projections will be used to test the hypotheses that:
1) On a regional scale, bird abundance is positively associated with cranefly abundance;
2) Changes in bird distributions between survey periods are associated with cranefly abundance.
Other influences, such as vegetation cover and land management, will also be used to model bird abundance, so that the explanatory power of different drivers can be compared. These analyses will focus on Golden Plover, as it is a species of conservation interest and links with craneflies are well-studied. Relationships with other bird species will then be modelled to test the hypothesis that cranefly abundance should predict more variation in species that rely more heavily on craneflies.

5.3 Methods

5.3.1 Bird abundance data

Bird abundance data from two large-scale surveys of upland breeding birds in South Pennine moorlands were acquired: the first survey, from 1990, was carried out by English Nature (Brown & Shepherd, 1991), and the second survey, from 2004, was conducted by Moors for the Future (Carr & Middleton, 2004). The 2004 survey was designed to repeat the 1990 survey methods to provide updated information on breeding bird distributions and abundances. Data were collected for 1 km^2 grid squares, with survey routes designed to cover a large amount of each square (Carr & Middleton, 2004). Surveyed areas covered the Dark Peak, Eastern Moors and South-West Peak, although the 1990 survey also included sites further north (Carr & Middleton, 2004). For the current analysis, sites were restricted to those that were surveyed in both years; consequently, 557 squares were available for analysis (Fig. 1).

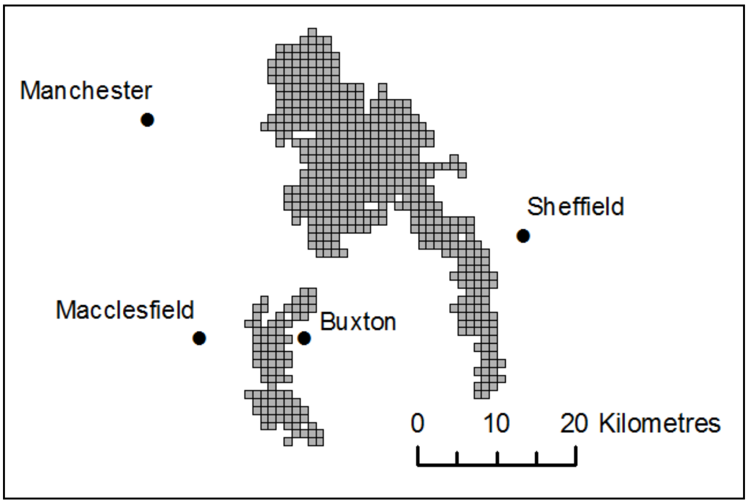


Figure 5.1. Sketch map of 1 km^2 survey locations used in bird analyses.

Two visits were made to each square during the survey period, the first between early April and mid May, and the second between mid May and late June (Carr & Middleton, 2004). Bird counts and estimated locations were recorded. Records were processed such that the values analysed represented the maximum number of individuals of each species observed across the two visits. In 2004, data were collected on 39 species (Carr & Middleton, 2004), but for the current analysis, species were restricted to those analysed by Pearce-Higgins *et al*. (2006), who excluded all raptors, waterfowl and corvids, and all other species not typically associated with open moorland, leaving 14 species: Curlew (*Numenius arquata*), Dunlin (*Calidris alpina*), Golden Plover (*Pluvialis apricaria*), Lapwing (*Vanellus vanellus*), Meadow Pipit (*Anthus pratensis*), Red Grouse (*Lagopus lagopus scotius*), Reed Bunting (*Emberiza schoeniclus*), Ring Ouzel (*Turdus torquatus*), Skylark (*Alauda arvensis*), Snipe (*Gallinago gallinago*), Stonechat (*Saxicola torquata*), Wheatear (*Oenanthe oenanthe*), Whinchat (*Saxicola rubetra*) and Wren (*Troglodytes troglodytes*).

Habitat variables that could influence bird distributions were calculated by Pearce-Higgins *et al*. (2006) from maps and satellite images. Variables fell into four categories. Vegetation data described proportional cover of heather, cotton grass, grasses and non-heather shrubs within each square. Physical environment data described the distance to the nearest stream and peat cover. Fragmentation data described the proportions of woodland and enclosed farmland within a 1 km buffer around each square. Land use data described a disturbance index for each square and the proportion of each square that was burned for grouse moor management. See Pearce-Higgins *et al*. (2006) for a description of methods used to calculate variables.

Data regarding the proportion of craneflies in bird diets were taken from Pearce-Higgins (2010). This analysis used a literature review to collect data on the composition of insectivorous northern and upland bird species' diets, and then modelled expected dietary compositions to account for differences in sampling method, summary method and location. Standardised dietary compositions were estimated separately for adult and pullus life stages. Here, the proportion of craneflies in the diet was extracted for species present in the survey data. Data for adult diets were available for 9 species: Curlew, Dunlin, Golden Plover, Meadow Pipit, Red Grouse, Skylark, Snipe, Wheatear and Whinchat. Data for pullus diets were available for 10 species: Curlew, Dunlin, Golden Plover, Meadow Pipit, Red Grouse, Ring Ouzel, Skylark, Stonechat, Wheatear and Whinchat.

5.3.2 Generating projections of cranefly abundance

To examine whether cranefly abundance drives bird distributions, large-scale spatial projections of cranefly abundance were made. The MILLENNIA model, as described in Heinemeyer *et al.* (2010) and Chapter 3, was used to produce projections of monthly water table depths (WTDs). The model takes topographic and climatic inputs to drive equations describing processes in peat, and does not require site-specific parameterisation. Model output can then be converted to estimated cranefly abundance by applying conversions based on relationships with field data (Chapter 4). Broad-scale patterns of WTD and cranefly abundance are replicated well by the model (see Chapters 3 and 4); as the bird data cover a large area and are on a 1 km^2 scale, only broad-scale patterns are required, meaning that model outputs are suitable for this purpose.

To drive the model, elevation data were derived from NEXTMap DEMs at a 10 m × 10 m scale (Intermap Technologies. NEXTMap Britain: Digital terrain mapping of the UK. NERC Earth Observation Data Centre, 2007, accessed 14/11/2011. Available from http://badc.nerc.ac.uk). Elevation data were converted to slope and aspect using Spatial Analyst functions in ArcMap 9.3 (ESRI; Redlands, California, USA). One model run was required for each combination of slope, aspect and elevation in each grid square. To reduce the number of runs for such a large landscape, topographic variables were rounded into bins of 50m for elevation, 15° for aspect, 2° for slopes $\leq 20°$, and 5° for slopes $>20°$. These are larger bins than used in Chapter 4, but as the scale of this analysis was so much greater

(45 5 km squares for the Peak District, c.f. 3 for Chapter 4), it was decided that finer detail would be less important and reducing model run time would be more important.

To drive the model, observed climate data were taken from UK Met Office gridded observation data sets (Perry & Hollis, 2005), which provide spatially-interpolated weather data for 1914–2010 at a 5 km scale. Monthly precipitation values were taken directly from the dataset; mean monthly temperature was calculated as the mean of maximum and minimum monthly temperatures. The spin-up period for the model was set to 6000 years, based on the peat ages given by Tallis (1991). Although there is clearly variation in peat age throughout the region, data were not available for each grid square, so a typical age was taken to represent the whole region; as the spin-up duration primarily affects modelled peat depth, this should have little effect on WTD projections.

Summer WTD projections (July, August and September) were extracted for 1988, 1989, 2002 and 2003 for each 5 km square. These years were chosen because abundance of adult craneflies emerging in spring of year *t* is influenced by summer soil moisture in year *t-1*. However, Pearce-Higgins *et al*. (2010) showed that Golden Plover abundance in year *t* may also be influenced by adult cranefly abundance in year *t-1*, which would be driven by summer moisture in year *t-2*. Hence, summer moisture in 1988, 1989, 2002 and 2003 would influence adult cranefly populations in 1989, 1990, 2003 and 2004, which in turn could influence bird populations in 1990 and 2004. Only summer WTD was used because, as shown in Chapter 4, summer WTD explained more variation in observed soil moisture than did spring WTD, and because summer moisture is likely to be a major driver of larval survival (Coulson, 1962; Pritchard, 1983).

Mean summer WTD was calculated for each year. Projections were then spatially distributed by applying values from the appropriate model run to each 10 m × 10 m grid cell based on its combination of topographic values. To stop projections being applied to inappropriate habitats, Ordnance Survey MasterMap data (© Crown Copyright/database right 2012, an Ordnance Survey/EDINA supplied service: License 100018355) were used to remove areas not defined as ‘heath’ or ‘rough grassland’, and DEM data were used to remove areas below 250 m a.s.l. To ensure that this did not artificially favour bird species associated with heath and rough grassland, a further set of projections was created that were not filtered by habitat type, although as the hydrology model is not built for mineral soils, these values should be interpreted with caution.

Mean WTDs were converted to an index of expected cranefly abundance by applying conversion equations derived from regressions using field data (see Chapter 4). Projections were not converted to craneflies m^{-2}, as only the relative abundance was required for these analyses; projections should therefore be seen only as an abundance index. As the status of drainage in each square was unknown, only 'blocked' moisture conversions were applied, as this should better represent a natural peatland system. Furthermore, the 'blocked' and 'open' conversions produced values that were very highly correlated (Spearman's $\rho > 0.93$), so would have provided the same information on relative moisture patterns.

Mean modelled cranefly abundances for 1989, 1990, 2003 and 2004 were extracted for each 1 km bird survey square using Spatial Analyst functions in ArcMap 9.3 (ESRI; Redlands, California, USA). These data were used to test the association between bird abundance and cranefly abundance. As the relationship between Golden Plover and craneflies is well-studied, and as Golden Plover populations are of conservation concern in the South Pennines, most analyses focussed on Golden Plover abundance. To gain a broader understanding about the role of craneflies in upland bird diets, analyses were also carried out using data on all available bird species.

Analyses were carried out in R v. 2.15 (R Development Core Team, 2012). Data from both survey years were analysed separately, as correlations between the two years were low to moderate for all species (mean Spearman's $\rho = 0.262$; see Appendix 2). As some squares may have been unsuitable for reasons not accounted for by available data, analyses were carried out once on data from all squares, and again on data excluding squares without any individuals in either survey ('empty' squares). To specify error structure for generalised linear models (GLMs), the distribution of bird abundance data was tested using the 'goodfit' function of the 'vcd' R package (Meyer *et al*., 2012). Almost all species were significantly different from the Poisson distribution. Nine species were not significantly different from the negative binomial distribution in each survey year; the species that were significantly different changed between years. Negative binomial error was therefore specified for all models, as it was most widely representative. GLMs with log link function and negative binomial error were fitted using the 'glm.nb' function in the 'MASS' R package (Venables & Ripley, 2002). The proportion of the GLM deviance explained by each model was calculated as (null deviance - residual deviance)/null deviance.

GLMs were constructed describing Golden Plover abundance in each survey year as a function of cranefly abundance in year *t* and year *t-1*. Models were then created using other habitat variables. Spearman rank tests indicated that several habitat variables were moderately or highly correlated (see Appendix 2). The high degree of correlation meant that multivariate models would be inappropriate. As there was no prior justification to pick one variable over another, GLMs with single predictors were run for each habitat variable, and the proportion of deviance explained was calculated for each.

Changes between time periods in Golden Plover abundance were also modelled. Survey squares were first split into four categories based on Golden Plover abundance: 'empty' squares had no Golden Plovers in either 1990 or 2004 (236 squares); 'colonised' squares had no Golden Plovers in 1990, but at least one in 2004 (54 squares); 'occupied' squares had Golden Plovers in both years (185 squares); and 'extinct' squares had at least one Golden Plover in 1990, but none in 2004 (82 squares). To examine colonisation and extinction, GLMs with binomial error and logit link function were constructed, with habitat variables as predictors. Colonisation GLMs compared 'empty' squares (coded as 0) to 'colonised' squares (coded as 1); extinction GLMs compared 'occupied' squares (0) to 'extinct' squares (1). To examine abundance change, only 'occupied' squares were used. Change in abundance was calculated as $\log(1 + (N_{04} - N_{90})/N_{90})$; these values were used as response variables in GLMs with Gaussian error and identity link function. An individual model was constructed for each predictor variable. Kruskal-Wallis tests were used to test differences in cranefly abundance between the different categories of squares, with pair-wise differences examined using *post hoc* Wilcoxon rank-sum tests.

Finally, GLMs with negative binomial error and log link, describing bird abundance as a function of cranefly abundance, were constructed for the 13 other species. Models were run once using projections filtered by habitat, then again using unfiltered projections. The proportion of deviance explained was calculated for each model. To account for negative relationships (i.e., bird abundance being higher in areas with fewer craneflies), the proportion of deviance was assigned the slope of the coefficient; these values were then correlated against the proportion of craneflies in the diet. As there were few data points, parametric analyses were preferred. Before analysis, data were arcsine square root transformed; proportions of deviance explained had 0.3 added to place all values in the range 0 – 1 before transformation. Shapiro-Wilk tests confirmed that transformed data were not significantly different from Normal, so Pearson correlations were used.

5.4 Results

5.4.1 Predicting Golden Plover abundance

Golden Plover abundance from 1990 and 2004 was compared to projected adult cranefly abundance for year *t* and year *t-1* (Figure 5.2); relationships are not shown for data excluding 'empty squares' due to the high similarity with data including all squares. The relationship was modelled using GLMs with log link function and negative binomial error; results are presented in Table 5.1.

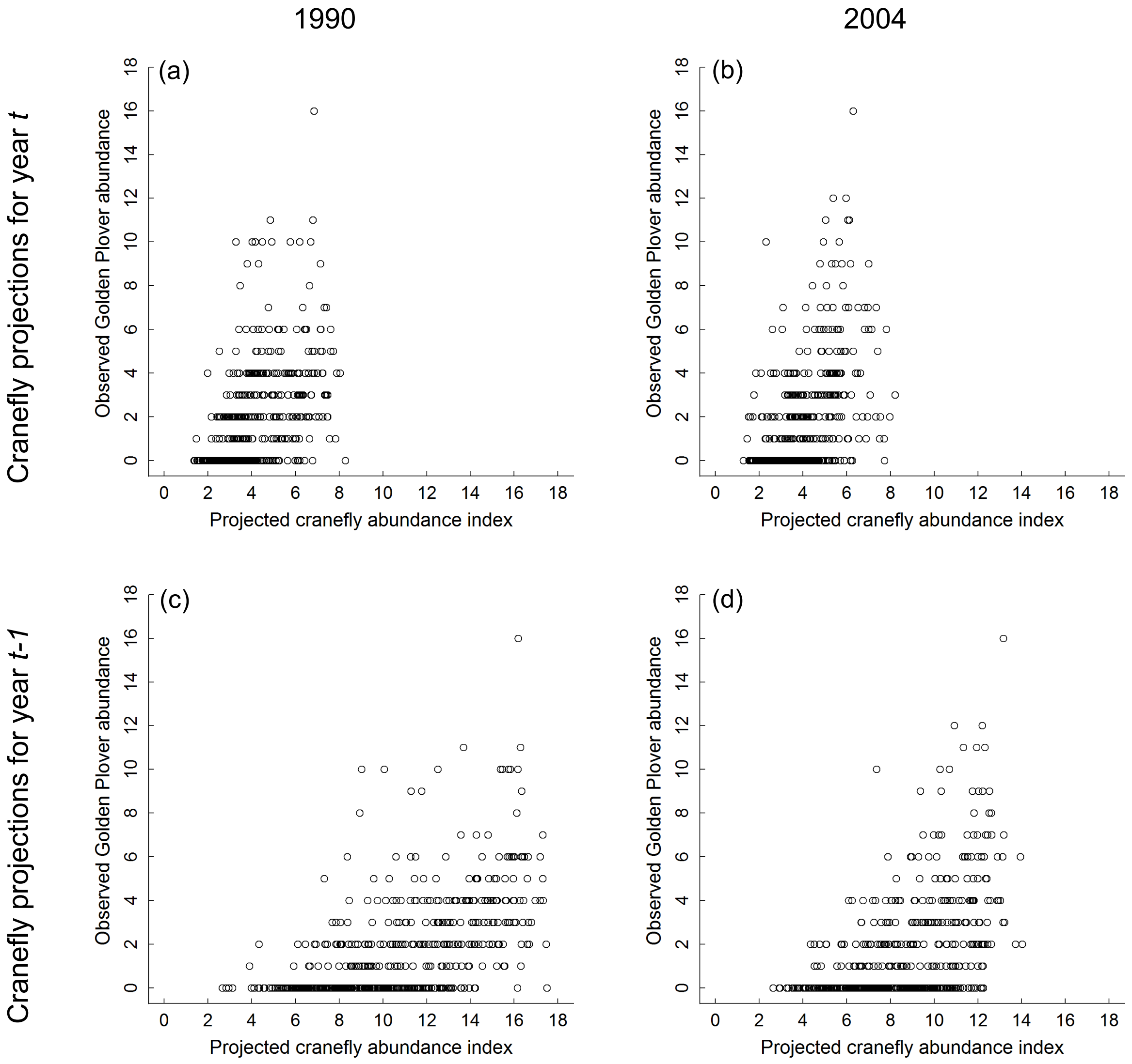


Figure 5.2. Plots of projected adult cranefly abundance against observed Golden Plover abundance for a) 1990 observations, 1990 cranefly abundance, b) 2004 observations, 2004 cranefly abundance, c) 1990 observations, 1989 cranefly abundance, and d) 2004 observations, 2003 cranefly abundance. Data shown are from all survey squares.

Table 5.1. Coefficients, *P*-values and proportion of deviance explained from GLMs describing Golden Plover abundance as a function of projected cranefly abundance. GLMs used negative binomial error and log link function.

	1990 birds, 1989 craneflies	1990 birds, 1990 craneflies	2004 birds, 2003 craneflies	2004 birds, 2004 craneflies
All squares	0.275, $P < 0.001$, dev. expl. = 0.323	0.542, $P < 0.001$, dev. expl = 0.259	0.371, $P < 0.001$, dev. expl. = 0.247	0.577, $P < 0.001$, dev. expl. = 0.217
No empty squares	0.135, $P < 0.001$, dev. expl. = 0.192	0.215, $P < 0.001$, dev. expl. = 0.119	0.205, $P < 0.001$, dev. expl. = 0.155	0.288, $P < 0.001$, dev. expl. = 0.122

Projected cranefly abundance was a highly significant predictor of Golden Plover abundance, both with all squares included and with empty squares removed (Table 5.1). Figure 5.2 suggests that there was little difference in the relationship between the two survey years. Models including all squares had more deviance explained; this may suggest that model performance increased when predicting occurrence and abundance together. More deviance was explained by cranefly abundance in year *t-1* than in year *t*; this implies that WTD in summer 1988 and 2002 drove cranefly abundance in 1989 and 2003, which in turn influenced Golden Plover abundance in 1990 and 2004.

GLMs using other potential drivers of Golden Plover abundance were constructed; results are presented in Table 5.2. Due to correlations between predictor variables (Appendix 2), individual GLMs were constructed for each. Most variables were significant predictors of Golden Plover abundance, with only controlled burning, grass cover and heather cover showing non-significant results. Peat cover explained the most deviance, with 44.7% in 1990 and 41.5% in 2004 when all squares were used; these reduced to 21.4% and 17.8% respectively with empty squares excluded. Cotton grass cover explained 23.8% of deviance in 1990 and 32.3% in 2004 when all squares were used, and 11.8% and 22.6% respectively with empty squares excluded. Enclosed grassland explained 22.7% of deviance in 1990 and 25.6% in 2004 when all squares were used, but these reduced substantially to 7.2% and 9.3% respectively with empty squares excluded. Comparatively, deviance explained by cranefly abundance was 32.3% in 1990 and 24.7% in 2004 when all squares were used, and 19.2% and 15.5% respectively with empty squares excluded. Therefore, only peat cover was a better predictor than cranefly abundance in both years. Those variables performing similarly to or better than cranefly abundance were also those that displayed moderate to high correlations with cranefly abundance (Appendix 2).

Table 5.2. Coefficients and proportions of deviance explained from GLMs of Golden Plover abundance with habitat variables as predictors. GLMs had negative binomial error and log link. Individual models were fitted for each predictor variable due to correlations between predictors. Significance of coefficients is indicated as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. Results significant at $P < 0.05$ are highlighted in bold.

		1990, all squares	2004, all squares	1990, no empty squares	2004, no empty squares
Vegetation	Mean veg. height (cm)	**-0.193***, dev. expl. = 0.206**	**-0.227***, dev. expl. = 0.207**	**-0.077***, dev. expl. = 0.086**	**-0.092***, dev. expl. = 0.071**
	Cotton grass (%)	**9.161***, dev. expl. = 0.238**	**10.846***, dev. expl. = 0.323**	**3.603***, dev. expl. = 0.118**	**5.786***, dev. expl. = 0.226**
	Grass (%)	-0.694, dev. expl. = 0.004	-0.351, dev. expl. = 0.001	**-0.838**, dev. expl. = 0.020**	-0.516, dev. expl. = 0.005
	Heather (%)	0.752, dev. expl. = 0.006	-0.316, dev. expl. = 0.001	-0.240, dev. expl. = 0.002	**-1.248***, dev. expl. = 0.035**
	Non-heather shrub (%)	**9.256***, dev. expl. = 0.207**	**9.199***, dev. expl. = 0.185**	**4.076***, dev. expl. = 0.110**	**4.368***, dev. expl. = 0.091**
Physical	Mean distance to streams (m)	**-0.008***, dev. expl. = 0.089**	**-0.009***, dev. expl. = 0.102**	**-0.004***, dev. expl. = 0.057**	**-0.005***, dev. expl. = 0.058**
	Peat cover (%)	**2.224***, dev. expl. = 0.447**	**2.361***, dev. expl. = 0.415**	**1.137***, dev. expl. = 0.214**	**1.252***, dev. expl. = 0.178**
Fragmentation	Enclosed grassland (%)	**-6.724***, dev. expl. = 0.227**	**-8.206***, dev. expl. = 0.256**	**-2.789***, dev. expl. = 0.072**	**-4.081***, dev. expl. = 0.093**
	Woodland (%)	**-2.772***, dev. expl. = 0.120**	**-2.130***, dev. expl. = 0.070**	**-1.546***, dev. expl. = 0.085**	**-1.006**, dev. expl. = 0.029**
Land use	Controlled burn (%)	-0.139, dev. expl. = 0.000	-0.676, dev. expl. = 0.007	**-0.527*, dev. expl. = 0.016**	**-1.053***, dev. expl. = 0.041**
	Disturbance index	**-4.196***, dev. expl. = 0.068**	**-4.940***, dev. expl. = 0.076**	**-1.381*, dev. expl. = 0.014**	**-2.137**, dev. expl. = 0.022**

5.4.2 Predicting changes in Golden Plover abundance

GLMs were created with colonisation, extinction and log-transformed proportional change in abundance as response variables (Table 5.3). Mean projected abundances in year *t* (i.e., 1990 and 2004), and *t-1* (i.e., 1989 and 2003) were used to represent cranefly abundance. Due to correlations between predictors, an individual model was fitted for each variable.

Nine habitat variables were significant predictors of colonisation. Most deviance was explained by peat cover (12.4%), which showed a positive relationship with colonisation. Cotton grass (positive, 6.1% deviance explained), vegetation height (negative, 6.1% deviance explained) and enclosed grassland (negative, 6.0% deviance explained) were the next best predictors. Both cranefly abundance variables showed positive, significant relationships: year *t* abundance explained 5.3% of deviance, which was better than all other variables; year *t-1* abundance explained 3.9% of deviance, which was similar to other predictors.

Ten variables were significant predictors of extinction. Most deviance was explained by peat cover (16.5%), which had a negative relationship with extinction. Cotton grass (negative, 15.5% deviance explained) was the next best predictor. Cranefly abundance showed significant, negative relationships with extinction, with mean abundance in year *t* explaining 14.9% of deviance, and mean abundance in year *t-1* explaining 14.5%. All other predictors explained less deviance than did projected cranefly abundance.

Only three variables were significant predictors of abundance change in ‘occupied’ squares, and less model deviance was explained than in colonisation and extinction models. Cotton grass showed a positive relationship with abundance change, explaining 4.4% of deviance. Grass cover showed a positive relationship, explaining 2.8% of deviance, whilst heather showed a negative relationship, explaining 3.7% of deviance. However, these two relationships were not consistent with those found for colonisation and extinction; more grass was associated with greater probability of extinction, but also with abundance increases; more heather was associated with greater probability of colonisation but also with abundance decreases. Therefore, only cotton grass cover significantly predicted all three responses in a consistent manner.

Table 5.3. Results from GLMs of colonisation, extinction and abundance change for Golden Plover. Colonisation and extinction GLMs were fitted with binomial error and logit link function. Proportional abundance change GLMs were fitted with Gaussian error and identity link function. Individual models were fitted for each predictor variable due to high correlations between predictors. Colonisation was calculated using squares empty in 1990. Extinction was calculated using squares occupied in 1990. Proportional change was calculated only for squares occupied in both survey years. Significance of coefficients is indicated as follows: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. Results significant at $P < 0.05$ are highlighted in bold.

		Colonisation (binomial)	Extinction (binomial)	Proportional change (log+1, Gaussian)
Food	Mean cranefly abundance, year *t*	**0.600***, dev. expl. = 0.053**	**-0.810***, dev. expl. = 0.149**	0.036, dev. expl. = 0.004
	Mean cranefly abundance, year *t-1*	**0.244**, dev. expl. = 0.039**	**-0.403***, dev. expl. = 0.145**	0.021, dev. expl. = 0.003
Vegetation	Mean veg. height (cm)	**-0.182***, dev. expl. = 0.061**	**0.224***, dev. expl. = 0.078**	0.015, dev. expl. = 0.004
	Cotton grass (%)	**11.375***, dev. expl. = 0.061**	**-13.856***, dev. expl. = 0.155**	**1.892**, dev. expl. = 0.044**
	Grass (%)	1.518, dev. expl. = 0.012	**1.830*, dev. expl. = 0.014**	**0.931*, dev. expl. = 0.028**
	Heather (%)	**3.288**, dev. expl. = 0.038**	0.898, dev. expl. = 0.004	**-0.871**, dev. expl. = 0.037**
	Non-heather shrub (%)	**7.582**, dev. expl. = 0.039**	**-11.411***, dev. expl. = 0.098**	-0.176, dev. expl. = 0.000
Physical	Mean distance to streams (m)	-0.004, dev. expl. = 0.009	**0.011***, dev. expl. = 0.059**	0.001, dev. expl. = 0.008
	Peat cover (%)	**2.246***, dev. expl. = 0.124**	**-2.675***, dev. expl. = 0.165**	0.250, dev. expl. = 0.009
Fragment.	Enclosed grassland (%)	**-4.832***, dev. expl. = 0.060**	**7.265***, dev. expl. = 0.077**	-1.603, dev. expl. = 0.017
	Woodland (%)	-0.623, dev. expl. = 0.003	**1.786**, dev. expl. = 0.021**	0.249, dev. expl. = 0.003
Land use	Controlled burn (%)	**2.219***, dev. expl. = 0.038**	1.036, dev. expl. = 0.010	-0.476, dev. expl. = 0.017
	Disturbance index	**-3.761*, dev. expl. = 0.031**	1.928, dev. expl. = 0.005	-0.565, dev. expl. = 0.003

Differences in mean projected cranefly abundance between the four categories of squares (‘empty’, ‘colonised’, ‘occupied’ and ‘extinct’) were examined; distributions are shown for year *t* (Figure 5.3) and year *t-1* (Figure 5.4). Kruskal-Wallis tests indicated that abundance differed significantly between categories of square (year *t*, $\chi^2 = 210.629$, df = 3, $P < 0.001$; year *t-1*, $\chi^2 = 206.055$, df = 3, $P < 0.001$). *Post hoc* Wilcoxon rank-sum tests indicated that all pair-wise comparisons were significantly different at $P < 0.05$, other than ‘colonised’ vs. ‘extinct’ (year *t*, W = 1868.5, $P = 0.125$; year *t-1*, W = 1856, $P = 0.119$). Abundance was lowest in ‘empty’ squares, highest in ‘occupied’ squares, and intermediate in ‘colonised’ and ‘extinct’ squares (Figure 5.3 and Figure 5.4).

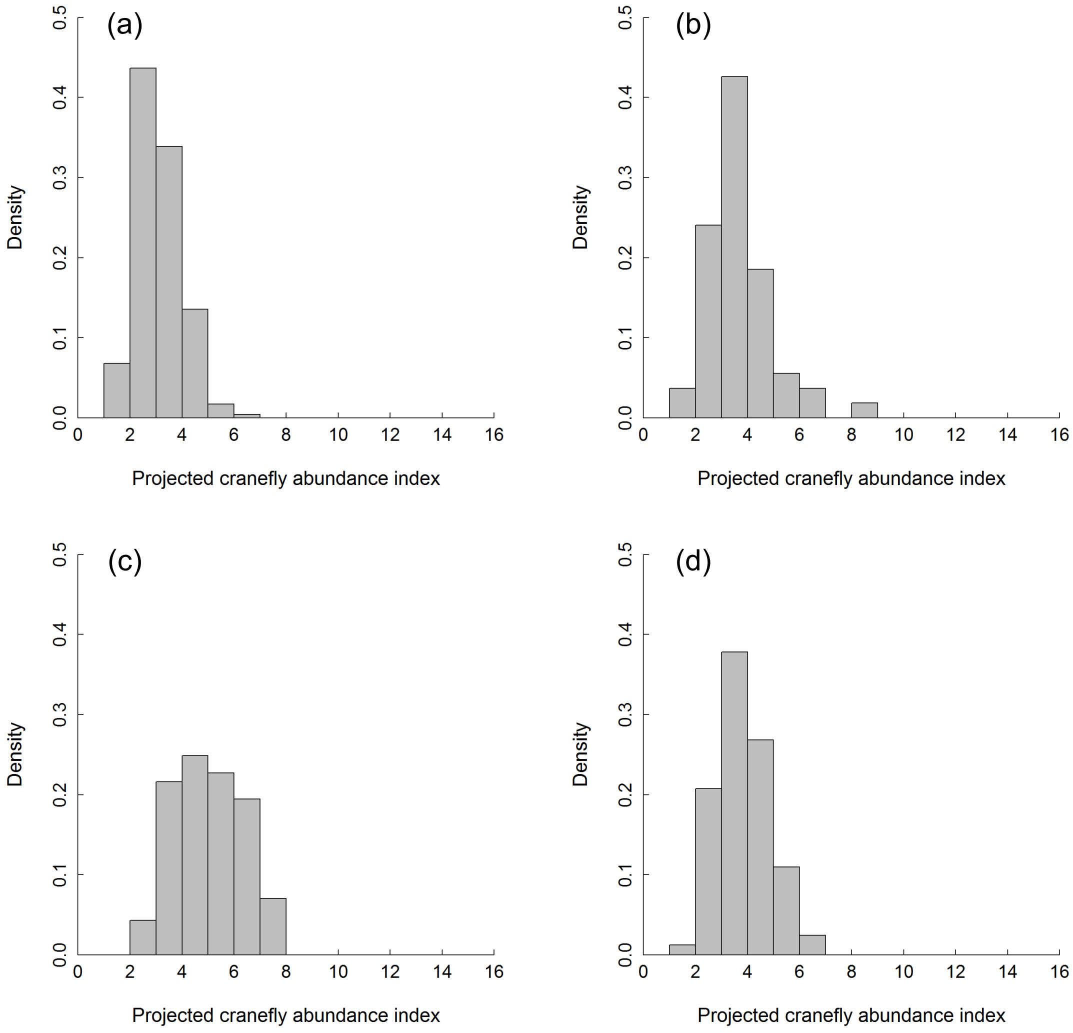


Figure 5.3. Histograms showing the distribution of mean year *t* cranefly abundance (i.e. 1990 and 2004) for different categories of 1 km square: a) ‘empty’ (no Golden Plovers in either year); b) ‘colonised’ (no Golden Plovers in 1990, at least one in 2004); c) ‘occupied’ (Golden Plovers in both years); and d) ‘extinct’ (at least one Golden Plover in 1990, none in 2004). Bars are scaled so that the total area of the histogram = 1.

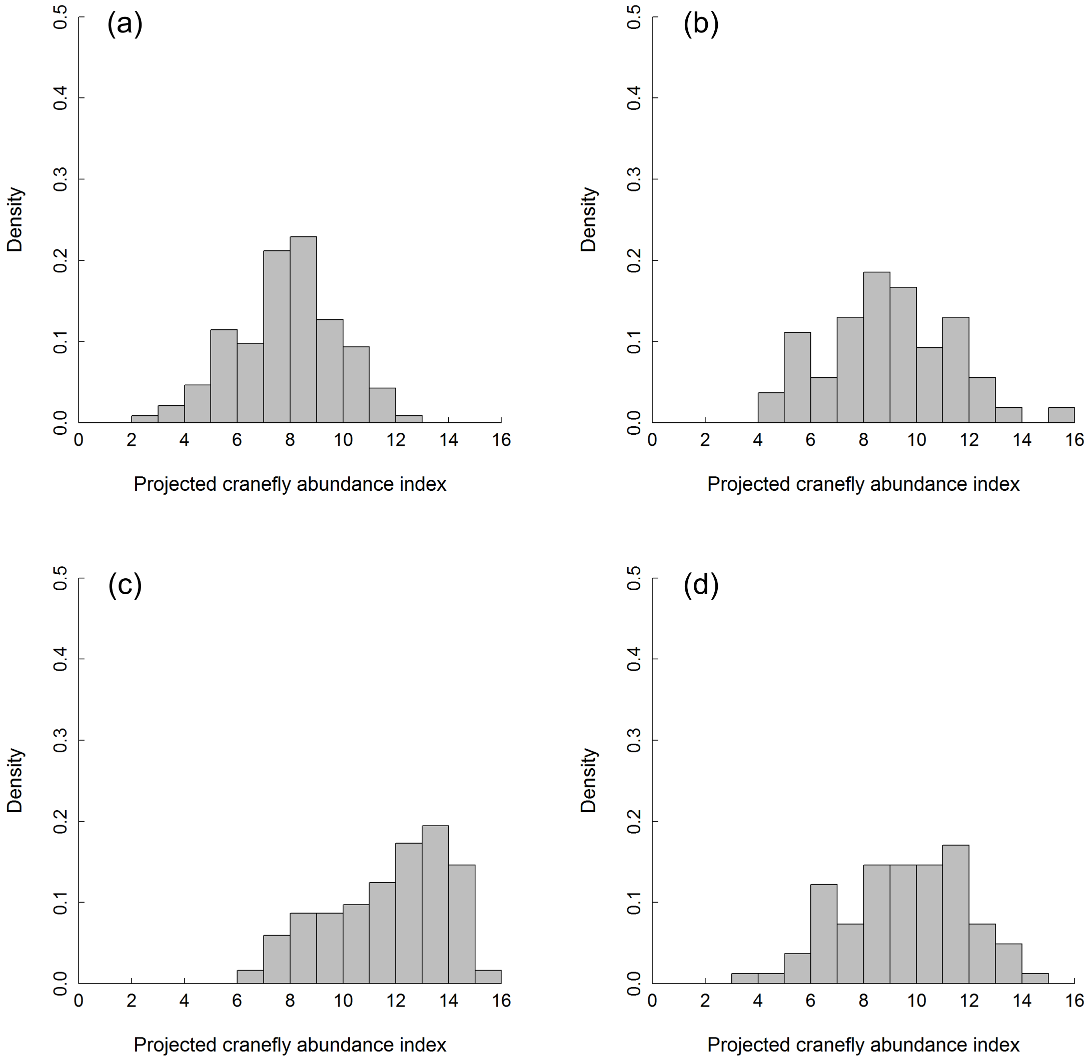


Figure 5.4. Histograms showing the distribution of mean year *t-1* cranefly abundance (i.e. 1989 and 2003) for different categories of 1 km square: a) ‘empty’ squares; b) ‘colonised’ squares; c) ‘occupied’ squares; and d) ‘extinct’ squares. Category descriptions are as for Figure 5.3. Bars are scaled so that the total area of the histogram = 1.

5.4.3 Cranefly abundance as a predictor of multiple species' diets

The predictive ability of cranefly abundance would be expected to degrade for bird species with a smaller proportion of craneflies in their diet. To test this, GLMs with cranefly abundance as the predictor variable were run for all species within the bird dataset. To simplify the analysis, only models using all survey squares were run. GLM results are presented in Table 5.4. Models were re-run using cranefly projections that were not limited to heath and rough grassland habitats to ensure that the relationship was independent of habitat selection; results are presented in Table 5.5.

The significance and amount of deviance explained by the models varied between species, observation year (i.e., 1990 or 2004) and projection year (i.e., year *t* or *t-1*). However, there was little difference between habitat-filtered and unfiltered projections; *P*-values and the proportion of deviance explained varied slightly, but not in a predictable, consistent manner, and overall patterns were highly similar between the two methods. Therefore, patterns observed appear to be independent of habitat selection.

Dunlin, Golden Plover, and Red Grouse showed significant, positive relationships with projected cranefly abundance in all models. Dunlin showed high proportions of deviance explained, with over 40% in 1990 and over 28% in 2004. Red Grouse showed lower proportions of deviance explained, with around 8% in 1990 and up to around 6% in 2004. Cranefly abundance was also a significant, positive predictor of 1990 Meadow Pipit and Skylark abundance, but little deviance was explained, and these relationships were not maintained in 2004. All other species either had no significant or a significant negative relationship with cranefly abundance.

Table 5.4. Results from GLMs of bird abundance for multiple species with projected cranefly abundance as the predictor variable. GLMs used negative binomial error distribution and log link. Abundance values are filtered to only include heath and rough grassland habitats. Significance of coefficients is indicated as follows: *** *P* < 0.001; ** *P* < 0.01; * *P* < 0.05. Significant results are highlighted in bold. Stonechat 1990 models were excluded due to very low numbers of squares with observations.

	1990 birds, 1989 craneflies	1990 birds, 1990 craneflies	2004 birds, 2003 craneflies	2004 birds, 2004 craneflies
Curlew	0.012, dev. expl. = 0.001	-0.054, dev. expl. = 0.002	-0.032, dev. expl. = 0.003	**-0.148***, dev. expl. = 0.021**
Dunlin	**0.520***, dev. expl. = 0.402**	**0.893***, dev. expl. = 0.294**	**0.607***, dev. expl. = 0.286**	**1.058***, dev. expl. = 0.259**
Golden Plover	**0.275***, dev. expl. = 0.323**	**0.542***, dev. expl = 0.259**	**0.371***, dev. expl. = 0.247**	**0.577***, dev. expl. = 0.217**
Lapwing	**-0.117*, dev. expl. = 0.025**	**-0.295*, dev. expl. = 0.031**	-0.015, dev. expl. = 0.000	**-0.418**, dev. expl. = 0.033**
Meadow Pipit	**0.034**, dev. expl. = 0.013**	**0.063*, dev. expl. = 0.009**	-0.017, dev. expl. = 0.002	**-0.049*, dev. expl. = 0.006**
Red Grouse	**0.124***, dev. expl. = 0.079**	**0.272***, dev. expl. = 0.082**	**0.147***, dev. expl. = 0.064**	**0.176***, dev. expl. = 0.030**
Reed Bunting	**-0.169*, dev. expl. = 0.049**	**-0.425*, dev. expl. = 0.051**	0.003, dev. expl. = 0.000	**-0.412***, dev. expl. = 0.055**
Ring Ouzel	**-0.113**, dev. expl. = 0.034**	-0.031, dev. expl. = 0.001	**-0.251***, dev. expl. = 0.066**	**-0.575***, dev. expl. = 0.101**
Skylark	**0.039*, dev. expl. = 0.007**	0.069, dev. expl. = 0.004	0.014, dev. expl. = 0.001	0.004, dev. expl. = 0.000
Snipe	**-0.143**, dev. expl. = 0.040**	**-0.246*, dev. expl. = 0.022**	-0.011, dev. expl. = 0.000	**-0.276**, dev. expl. = 0.027**
Stonechat	--	--	**-0.195**, dev. expl. = 0.038**	**-0.484***, dev. expl. = 0.062**
Wheatear	**-0.204***, dev. expl. = 0.088**	**-0.298***, dev. expl. = 0.043**	-0.053, dev. expl. = 0.003	-0.209, dev. expl. = 0.013
Whinchat	**-0.324***, dev. expl. = 0.144**	**-0.788***, dev. expl. = 0.148**	**-0.276***, dev. expl. = 0.071**	**-0.872***, dev. expl. = 0.186**
Wren	-0.132, dev. expl. = 0.034	-0.206, dev. expl. = 0.014	**-0.168***, dev. expl. = 0.078**	**-0.240***, dev. expl. = 0.049**

Table 5.5. Results from GLMs of bird abundance for multiple species with projected cranefly abundance as the predictor variable. GLMs used negative binomial error and log link. Abundance values are not filtered by habitat, so include mineral soils and low altitude habitats. Significance of coefficients is indicated as follows: *** *P* < 0.001; ** *P* < 0.01; * *P* < 0.05. Significant results are highlighted in bold. Stonechat 1990 models were excluded due to very low numbers of squares with observations.

	1990 birds, 1989 craneflies	1990 birds, 1990 craneflies	2004 birds, 2003 craneflies	2004 birds, 2004 craneflies
Curlew	0.012, dev. expl. = 0.001	-0.037, dev. expl. = 0.001	-0.029, dev. expl. = 0.003	**-0.133***, dev. expl. = 0.018**
Dunlin	**0.497***, dev. expl. = 0.396**	**0.903***, dev. expl. = 0.306**	**0.553***, dev. expl. = 0.271**	**1.006***, dev. expl. = 0.257**
Golden Plover	**0.340***, dev. expl. = 0.193**	**0.336***, dev. expl. = 0.290**	**0.316***, dev. expl. = 0.192**	**0.307***, dev. expl. = 0.178**
Lapwing	**-0.109*, dev. expl. = 0.023**	**-0.267*, dev. expl. = 0.026**	-0.022, dev. expl. = 0.000	**-0.409**, dev. expl. = 0.034**
Meadow Pipit	**0.035**, dev. expl. = 0.013**	**0.074**, dev. expl. = 0.012**	-0.014, dev. expl. = 0.001	-0.040, dev. expl. = 0.004
Red Grouse	**0.126***, dev. expl. = 0.082**	**0.282***, dev. expl. = 0.090**	**0.152***, dev. expl. = 0.070**	**0.191***, dev. expl. = 0.036**
Reed Bunting	**-0.171*, dev. expl. = 0.051**	**-0.391*, dev. expl. = 0.047**	-0.002, dev. expl. = 0.000	**-0.387***, dev. expl. = 0.051**
Ring Ouzel	**-0.104**, dev. expl. = 0.028**	-0.014, dev. expl. = 0.000	**-0.256***, dev. expl. = 0.065**	**-0.547***, dev. expl. = 0.096**
Skylark	0.035, dev. expl. = 0.006	0.074, dev. expl. = 0.005	0.006, dev. expl. = 0.000	0.002, dev. expl. = 0.000
Snipe	**-0.131**, dev. expl. = 0.035**	-0.205, dev. expl. = 0.016	-0.002, dev. expl. = 0.000	**-0.245**, dev. expl. = 0.022**
Stonechat	--	--	**-0.219***, dev. expl. = 0.049**	**-0.480***, dev. expl. = 0.065**
Wheatear	**-0.202***, dev. expl. = 0.086**	**-0.284***, dev. expl. = 0.040**	-0.057, dev. expl. = 0.004	-0.208, dev. expl. = 0.013
Whinchat	**-0.304***, dev. expl. = 0.134**	**-0.703***, dev. expl. = 0.130**	**-0.255***, dev. expl. = 0.060**	**-0.798***, dev. expl. = 0.164**
Wren	-0.131, dev. expl. = 0.036	-0.196, dev. expl. = 0.014	**-0.157***, dev. expl. = 0.068**	**-0.215***, dev. expl. = 0.041**

To test whether model predictive ability varied with dietary composition, proportions of deviance explained (from Table 5.4 and Table 5.5) were compared to the proportion of craneflies in bird diets (adult diet, Figure 5.5; pullus diet, Figure 5.6); in all cases, there was a positive relationship, and results were nearly identical for habitat-filtered and unfiltered cranefly projections (Table 5.6). All adult correlations were significantly different from 0, with Pearson correlation coefficients around 0.7 – 0.8 indicating a strong relationship. Correlations with pullus diet were still positive, but were weaker, ranging from 0.4 – 0.6, and none were significantly different from 0. However, the lack of significance should be interpreted cautiously, as there were relatively few data points, hence low statistical power. Overall, projected cranefly abundance appeared to predict bird abundance significantly better for species with more craneflies in their diet.

Table 5.6. Pearson correlation coefficients of proportion of deviance explained by cranefly abundance against proportion of craneflies in bird diets. Values were arcsine square root transformed before being used in correlation. Significant results are highlighted in bold; non-significant results with $P < 0.1$ are *italic*.

	1990 obs., 1989 projection	1990 obs., 1990 projection	2004 obs., 2003 projection	2004 obs., 2004 projection
a) Adult diet				
Filtered by habitat	**0.724, *P* = 0.027**	**0.750, *P* = 0.020**	**0.786, *P* = 0.012**	**0.742, *P* = 0.022**
Unfiltered	**0.697, *P* = 0.037**	**0.753, *P* = 0.019**	**0.779, *P* = 0.013**	**0.748, *P* = 0.020**
b) Pullus diet				
Filtered by habitat	0.473, *P* = 0.198	0.448, *P* = 0.227	*0.592, P = 0.071*	0.499, *P* = 0.142
Unfiltered	0.443, *P* = 0.233	0.473, *P* = 0.198	*0.599, P = 0.067*	0.524, *P* = 0.120

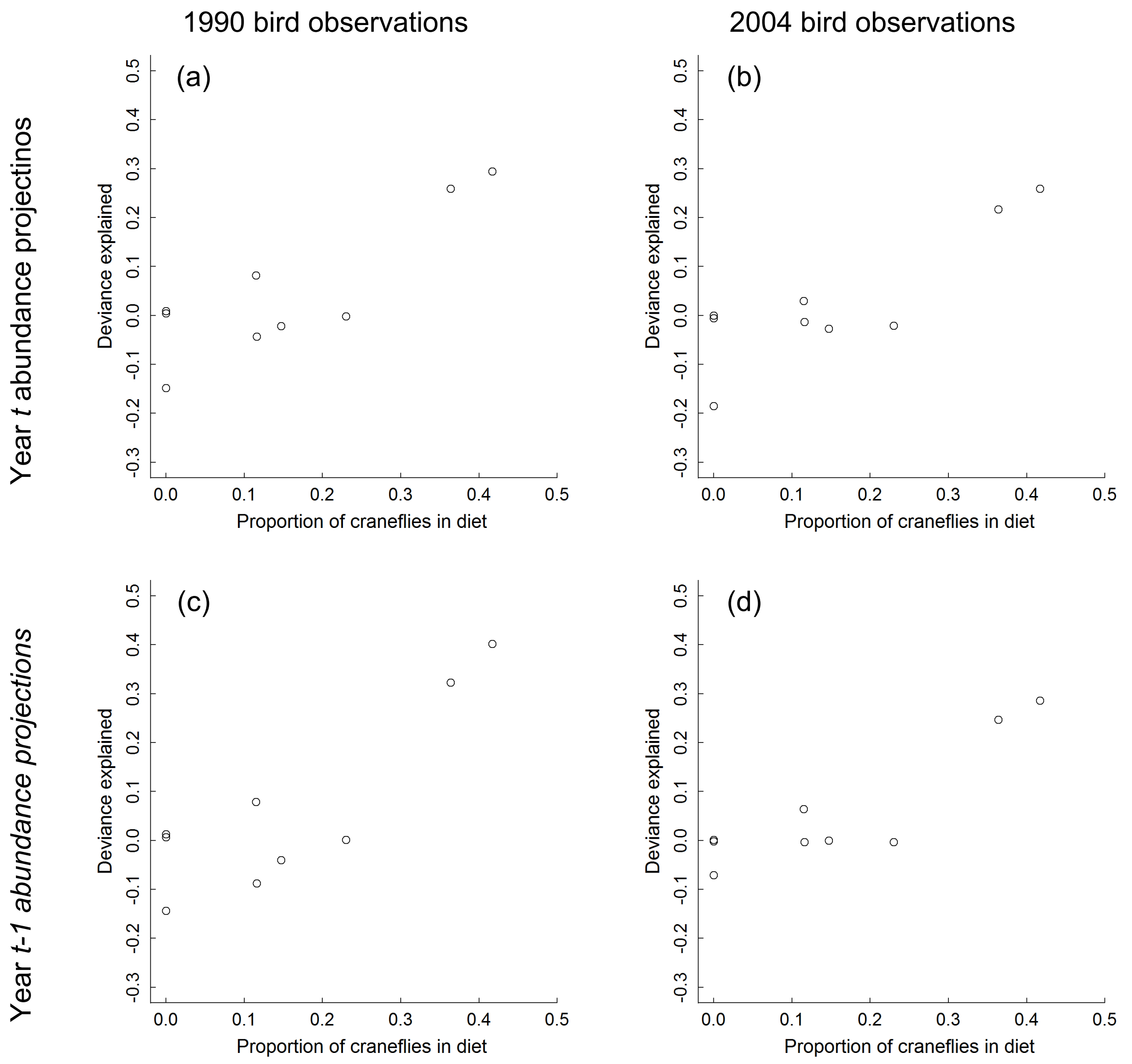


Figure 5.5. Plots of proportion of craneflies in adult diet against the proportion of deviance explained by cranefly abundance in GLMs of bird abundance (Table 5.4), for a) 1990 bird observations, 1990 cranefly projections, b) 2004 bird observations, 2004 cranefly projections, c) 1990 bird observations, 1989 cranefly projections, and d) 2004 bird observations, 2003 cranefly projections. Due to high similarity with unfiltered projections, figures show only values from habitat-filtered projections.

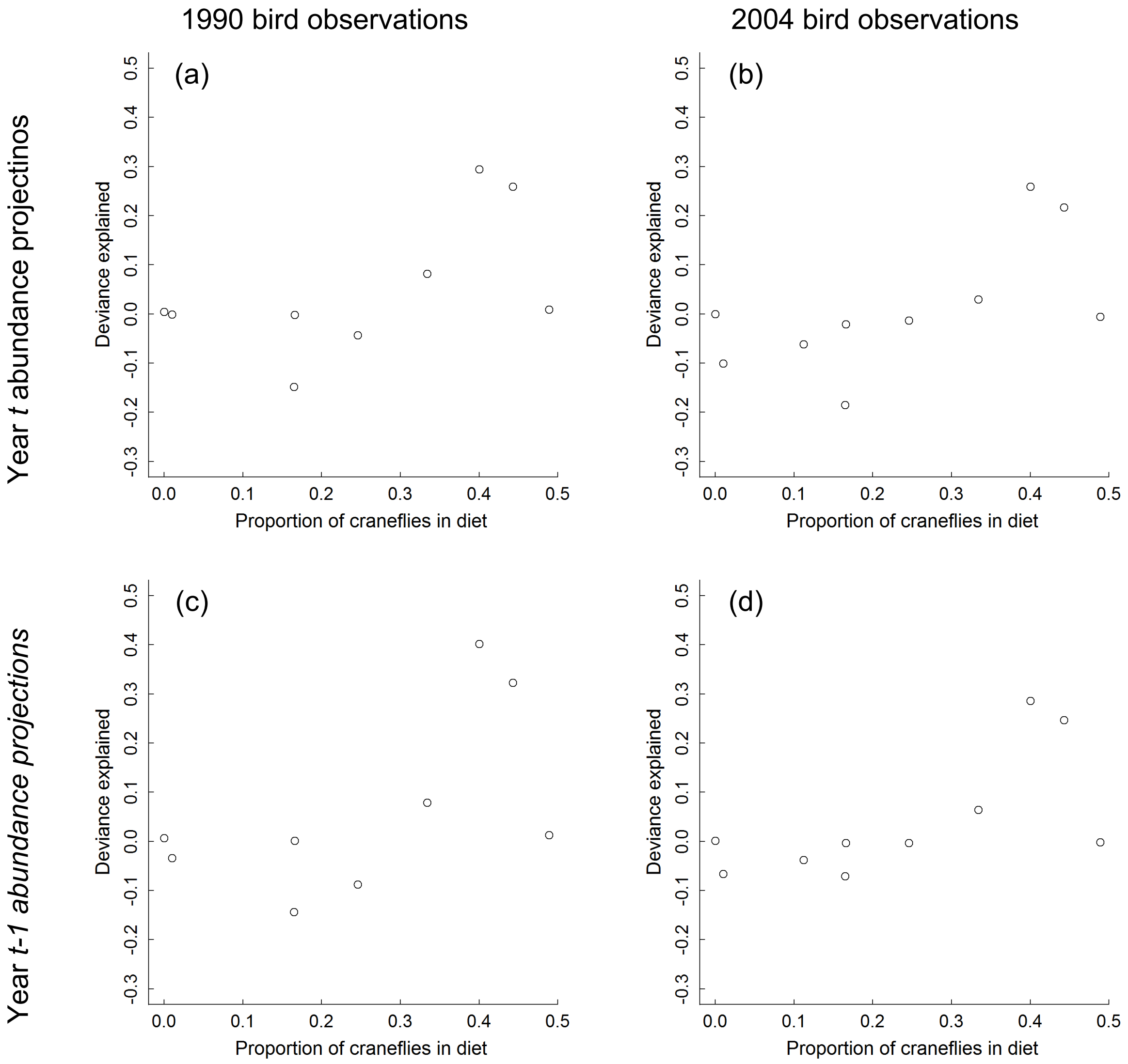


Figure 5.6. Plots of proportion of craneflies in pullus diet against the proportion of deviance explained by cranefly abundance in GLMs of bird abundance (Table 5.4), for a) 1990 bird observations, 1990 cranefly projections, b) 2004 bird observations, 2004 cranefly projections, c) 1990 bird observations, 1989 cranefly projections, and d) 2004 bird observations, 2003 cranefly projections. Due to high similarity with unfiltered projections, figures show only values from habitat-filtered projections.

5.5 Discussion

Projected cranefly abundance was found to be a highly significant predictor of Golden Plover abundance on a large spatial scale in both 1990 and 2004. When compared to other potential drivers of bird abundance, only peat cover consistently described more variation in Golden Plover abundance; the fact that peat cover was positively correlated with projected cranefly abundance suggests that one variable may be a surrogate of the other. Cranefly abundance was also a significant predictor of colonisations and extinctions between the two years, but was not a significant predictor of abundance change in squares that were occupied in both years. When modelling distribution changes, only peat cover and cotton grass always performed better than cranefly abundance, which performed better than or similarly to the other predictors. When several bird species were modelled, cranefly abundance described most variation in species that eat a greater proportion of craneflies. Together, these results suggest that food availability influences bird abundance at large scales. Understanding such drivers of bird abundance could aid conservation planning both in the present and under climate change.

5.5.1 Craneflies as a predictor of Golden Plover abundance

Analyses focussed on Golden Plover, as its links with craneflies are well studied. Most model deviance was explained when summer WTD two years before the bird survey drove spring cranefly abundance the year before the bird survey. This fits well with previous modelling work, which found that Golden Plover abundance was best explained by August temperature two years before, acting via adult cranefly abundance in spring (Pearce-Higgins *et al.*, 2010). That this pattern was found even when ‘empty’ squares were excluded suggests that cranefly abundance may help to determine suitable breeding sites, but may also influence abundance within suitable sites, probably acting via breeding success (Pearce-Higgins & Yalden, 2004).

Cranefly abundance was a significant predictor of Golden Plover abundance in both survey years. Even though these were 14 years apart and distributions changed between the two years, the proportion of deviance explained was similar in both years (although slightly lower in 2004); this suggests that the ability of cranefly abundance to drive Golden Plover distributions is a general result. This was further supported by the finding that cranefly abundance was a significant predictor of colonisations and extinctions between the survey years. Hence, areas that were colonised had greater cranefly abundances, and areas that lost Golden Plover populations had lower cranefly abundances. Therefore, cranefly abundance may also drive temporal distribution trends. Such a finding could aid conservation planning, as areas with lower cranefly abundance appear to be associated with greater risk of Golden Plover extinction.

Cranefly abundance was not a significant predictor of abundance change in squares that were occupied in both survey years. This may imply that the model lacks sufficient resolution to predict these smaller changes; given the broad nature of the model, such a lack of resolution could be expected. Alternatively, other processes may have driven abundance change. For example, a threshold of food availability might exist that makes a site suitable or not, with cranefly abundance having less influence on bird abundance changes once over this threshold. Indeed, use of fields by Golden Plover for foraging may have a threshold of 10 g m^{-2} of invertebrate prey (Pearce-Higgins & Yalden, 2003a). Similarly, other factors such as predation (Pearce-Higgins & Yalden, 2003b) or poor weather (Pearce-Higgins & Yalden, 2002) could influence abundance change but would not be captured by the model. However, longer time series of bird data would be required to fully examine temporal relationships, as the effect of food availability on bird populations over time is likely to involve interactions with other factors such as population density (e.g., Arcese & Smith, 1988).

Squares displaying different Golden Plover population trends differed in cranefly abundance. Squares not occupied in either year had the lowest abundances, whilst squares occupied in both years had the highest abundances. Squares showing colonisations and extinctions had intermediate abundances, implying that they may be marginally suitable, with conditions in a given year determining where birds choose to breed, or where chicks can be successfully raised. These marginal areas are likely to be those most at threat from climate change, as cranefly abundances are likely to fall (see Chapter 4), thus making the areas unsuitable and making local extinctions more likely.

It would have been plausible that due to the broad, simplistic nature of cranefly abundance projections that they would compare unfavourably to observed variables, which integrate multiple drivers of bird abundance. However, only peat cover and cotton grass cover consistently performed as well as or better than cranefly abundance across all models. Enclosed grassland performed similarly to cranefly abundance when modelling the distribution across all squares, but its predictive power dropped substantially when 'empty' squares were removed, implying that it may be more effective at determining suitable breeding areas than at influencing abundance within suitable areas. Although they were strong predictors of Golden Plover abundance, peat and cotton grass may provide no direct resources; instead they are likely to be surrogates for key resources. Both are known to be associated with high cranefly abundances (e.g., Coulson, 1962), and both displayed positive correlations with cranefly abundance (Appendix 2); this suggests that they could be surrogates for food availability. Indeed, Golden Plover chick preference for foraging in cotton grass-rich areas may be linked to cranefly availability (Pearce-Higgins & Yalden, 2004). Other studies have linked Golden Plover distributions to high plateaus and *Calluna-Eriophorum* or *Empetrum* heath (Haworth & Thompson, 1990), or high altitudes, shallow slopes and blanket bog (Stillman & Brown, 1994). These broad habitat features are likely to be surrogates for food and nest site availability, with heather mosaics and *Juncus* providing protection for chicks (Whittingham *et al*., 2001), and deep peat and cotton grass supporting high cranefly abundances. It is therefore encouraging that cranefly abundance projections, which were effectively derived from first principles, performed at a similar level to observed surrogates that are more finely resolved and integrate more influences. The use of cranefly abundance to model Golden Plover distributions reduces the reliance on these surrogates, adds biological realism, allows climate-driven fluctuations in food availability to be assessed, and allows effects of conservation interventions to be examined.

5.5.2 Craneflies as a predictor of multiple species' abundance

Projected cranefly abundance was used to model distributions of thirteen other bird species. Including Golden Plover, five species were waders, eight were passerines, and one was a grouse. All were fully or partly insectivorous, and all were associated with upland moorland. The range of diets, breeding behaviours and feeding behaviours meant that projected cranefly abundance should not predict all species equally well. Were it to do so, it would imply that the model was simply picking out areas suitable for moorland breeding birds, rather than describing variation in cranefly-reliant species. Therefore, it is encouraging that varying relationships with cranefly abundance were found.

Other than Golden Plover, Dunlin and Red Grouse showed strong positive associations with cranefly abundance in both years. In 1990, Meadow Pipit showed a significant, positive relationship, but this became non-significant or significantly negative in 2004. All of these species are known to have relatively high proportions of craneflies in their diets as either adults or chicks (Pearce-Higgins, 2010), which suggests that projected abundance only predicts distributions of cranefly-reliant species.

The varying relationship with Meadow Pipit abundance suggests that the extent to which some species rely on craneflies varies between years. As only the first Meadow Pipit brood each year is reliant on peatland craneflies (Coulson & Whittaker, 1978), a successful second brood could buffer populations from fluctuating cranefly abundance. However, counts of Meadow Pipit abundance are susceptible to considerable variation at region, plot, date and observer levels (Buchanan *et al*., 2006b), so it is equally plausible that such variation contributed to the changing relationship.

The relationships with Red Grouse and Dunlin distributions are highly encouraging. For Dunlin, 25.9 – 40.2% of deviance was explained by cranefly abundance, implying a strong link. Field observations have previously implicated cranefly abundance in driving Dunlin distributions, notably the absence from some South Pennine moors with drier peat (Yalden, 1974). The higher proportion of deviance explained compared to Golden Plover may be linked to the higher proportion of craneflies in the Dunlin diet (Pearce-Higgins, 2010). This relationship may also go to explain the suggestion that warmer summers cause poorer Dunlin recruitment (Beale *et al*., 2006b).

For Red Grouse, only 3.0 – 8.2% of deviance was explained by cranefly abundance, but as Red Grouse numbers are strongly influenced by the intensity of grouse moor management (Tharme *et al*., 2001), it is unsurprising that cranefly availability explains less variation. Moreover, craneflies only form part of the Red Grouse diet, with heather shoots forming the majority (Park *et al*., 2001). Craneflies are an important part of Red Grouse diet though, providing a high concentration of nutrients (Butterfield & Coulson, 1975), and increasing chick growth and survival (Park *et al*., 2001).

Golden Plover, Dunlin and Red Grouse share a combination of traits that could explain why their distributions are influenced by cranefly abundance. Their chicks are precocial, so forage for invertebrates themselves; food availability in the area surrounding the nest therefore becomes very important (Whittingham *et al*., 2001). Conversely, birds with altricial chicks would be less restricted by locally-available food. Additionally, these are all species associated with high, wet moorland, whereas other species with precocial chicks, Curlew, Snipe and Lapwing, are associated with lower moorland, and not with blanket bog

(Stillman & Brown, 1994). Snipe prefer acid grassland and wet flushes (Hoodless *et al.*, 2007), and Curlew forage on marginal pasture (Robson *et al.*, 2002). Therefore, even though these species have large proportions of craneflies in their diets (Pearce-Higgins, 2010), it is likely to be mineral soil species such as *Tipula paludosa* (Coulson & Whittaker, 1978). As patterns of deviance explained were similar when abundance projections were not restricted to high altitude heath and rough grassland, it suggests that the model is only predicting peatland cranefly abundance, with mineral soil cranefly abundance driven by different relationships. Therefore, the model would not be expected to predict birds reliant on mineral soil craneflies as successfully as those taking blanket bog craneflies.

When the proportion of deviance explained by cranefly abundance was correlated against the proportion of craneflies in adult diets, a significant, positive relationship was found. This confirms that across multiple species, the more craneflies a species takes, the more its distribution is influenced by cranefly abundance. Correlations with pullus diet were positive but were not significant; bird abundance data were based on adults, so it would not be expected that model deviance would relate as strongly to pullus diet. This result is similar to that presented by Pearce-Higgins (2010), who found that the climatic sensitivity of adult diets was significantly correlated with a population change index, but that pullus diets showed a weaker, non-significant relationship. Overall however, the result shows that by integrating topography, climate and a relationship with moisture, the model can create a single index of food availability that captures aspects of real bird ecology.

5.5.3 Implications and conclusions

This analysis confirms that cranefly availability, which influences bird habitat selection on smaller scales, also drives patterns on a regional scale. A significant relationship was found between projected cranefly abundance and observed Golden Plover abundance for two separate years, suggesting that the relationship is generally-applicable. Significant relationships with colonisations and extinctions suggest that food availability determines whether sites are suitable for breeding. Observed habitat variables also predicted Golden Plover abundance, but the dynamic model provides the opportunity to make projections for future climate scenarios and for conservation management interventions.

Bird species with larger proportions of craneflies in their diets were better predicted by the model. It would provide a good test of the model if regional-scale distribution data were available for areas supporting Dotterel (*Charadrius morinellus*), Whimbrel (*Numenius* *phaeopus*) and Snow Bunting (*Plectrophenax nivalis*), as these species also take high proportions of craneflies (Pearce-Higgins, 2010). Species that rely more heavily on craneflies are likely to be more sensitive to climate change (Pearce-Higgins, 2010), so the ability to predict spatial distributions over time would be highly beneficial.

The relationships identified provide some indication of threats and opportunities for conservation. For Golden Plover, Red Grouse and Dunlin, abundance was higher in areas of high cranefly abundance, so any processes that reduce cranefly abundance should also reduce bird abundance. In Chapter 2, field measurements showed that moorland drainage could decrease cranefly abundance by up to 75% in the vicinity of open drains. In Chapter 4, model projections suggested that climate change could cause cranefly abundance to decline by 20 – 40%. Both of these processes could lead to bird populations declining or being concentrated into relatively wet areas, driven primarily by food availability. Blocking drains and attempting to maintain moisture in peat throughout the summer would provide the best opportunities to counteract these threats.

Using a dynamic model of peatland water tables and a statistical relationship between moisture and craneflies, cranefly abundance projections can be made that predict bird distributions on a large spatial scale. This is the first time that the predictive power of a key food source has been shown to be significantly associated with the proportion of that food source in the diet across multiple species. This provides useful information for conservation, by highlighting the species most at risk from declining cranefly availability, by inferring processes likely to drive declines, and by indicating that increasing or maintaining moisture is a plausible conservation method. Overall, managing land to maximise availability of key invertebrates could be a crucial step in conserving the important upland bird assemblage.

5.6 Acknowledgments

James Pearce-Higgins provided habitat data and summarised bird data. I am grateful to Natural England and Moors for the Future for allowing use of the bird survey data.

Chapter 6

General Discussion

6.1 Summary of findings

This thesis has combined large-scale field experiments and predictive modelling to examine impacts of drainage, restoration and climate change on the abundance of keystone invertebrates in upland peatlands, and has further explored the relationship between cranefly abundance and the distribution of upland breeding birds. In **Chapter 2**, field experiments were used to describe and quantify the relationship between adult cranefly abundance and soil moisture, showing that high soil moisture was required for large abundances to occur. This was linked to drainage and restoration, showing that drain blocking significantly increases soil moisture and cranefly abundance, and making it one of the first studies to explicitly examine effects of drain blocking on peatland invertebrates. In **Chapter 3**, an extension of a peatland development model was presented, which used numerically-derived equations, was parameterised using freely-available water table data, and was driven using simple monthly climate data. The model predicted water table depth position well, and predicted up to two thirds of the variance in water table depth over time when tested against datasets from four British peatlands. **Chapter 4** used the water table model and relationships derived from field data to make projections of cranefly abundance at the landscape scale. Projections indicated that warmer, drier summers would cause water tables to fall, causing cranefly abundance to decrease. Blocking drains would not stop declines, but could slow declines and potentially prevent landscape-wide losses of cranefly populations. Finally, **Chapter 5** examined the relationship between modelled cranefly abundance and observed upland bird distributions on a regional scale. Projected cranefly abundance was found to predict Golden Plover abundance, as well as extinctions and colonisations, better than many observed habitat variables. Across multiple bird species, the amount of variation explained by cranefly abundance was significantly correlated with the proportion of craneflies in the diet.

Many of the findings presented in this thesis represent broad impressions of current patterns and possible future trends. These could inform peatland restoration projects and plans for conservation under climate change. However, for a complete understanding of the system, further study of some aspects would be required. The following sections discuss the findings in the context of wider issues, make suggestions for further work, and discuss implications for conservation in the British uplands.

6.2 Modelling ecosystem properties and biodiversity

A central component of the thesis has been the use of modelling to make projections of climate change and land use impacts on peatlands. The intention was to produce widely-applicable, ‘first impression’ projections; the key difference from previous models was that abundance was driven by soil moisture variation, which is a major driver of cranefly mortality (e.g., Coulson, 1962; Milne *et al*., 1965; Meats, 1967b), thus improving biological realism. Although further work would be required to make predictions for specific locations and times (see Chapters 3 and 4), results presented here complement existing models, increasing confidence in projected trends and providing useful conservation information. Britain is at the southern extent of northern peatland occurrence (Moore, 2002), and climatic changes are already being observed in the uplands (Burt & Holden, 2010), so rapid assessments of likely climate change impacts are required. Modelling can provide important information on directions and magnitudes of change (e.g., Hannah *et al*., 2002; Pearson & Dawson, 2003), which can then be integrated into conservation management and policy (e.g., Pressey *et al*., 2007; Bellard *et al*., 2012). This approach should ensure that appropriate conservation actions are taken before irreversible changes occur.

Many models of species abundance and distribution under climate change are based solely on statistical associations with surrogate variables. Here, a mechanistic moisture model was combined with an empirically-derived relationship, thus allowing abundance to be driven by a proximate environmental driver. Encouragingly, results supported trends predicted by a previous model of cranefly abundance that was driven by summer temperature (Pearce-Higgins *et al*., 2010; Pearce-Higgins, 2011b); this increases confidence in the projections of both models, suggesting that climate-driven declines are a distinct likelihood. The approach used here also brings extra benefits over models driven only by correlations with climate. Models are often based on simple relationships with climate variables, which may not adequately describe the real relationship (Dormann, 2007), or may have little direct ecological impact (Heikkinen *et al*., 2006). Here, an environmental variable was first identified that has a direct effect on survival; the relationship was then experimentally determined in the field across multiple sites and years (Chapter 2). We may therefore have more confidence in the relevance of the environmental driver and the nature of the relationship, and in turn more confidence in model projections.

The use of a mechanistic model to drive projections based on empirical relationships is relatively uncommon. The approach is different from the 'semi-mechanistic' models described by Mokany and Ferrier (2011), which "use correlative habitat modelling to predict the potential distribution of a species… within which realized abundance is further constrained and shaped by mechanistic processes." The approach pursued here reverses this, mechanistically defining habitat characteristics and then using correlations to make abundance projections. However, it could still be viewed as a 'semi-mechanistic model', or, as Lambin *et al*. (2000) describe similar models, as an 'integrated model'. Perhaps the most important benefit derived from using the mechanistic model is that it integrates temperature and precipitation changes, meaning that novel climatic conditions, which can cause problems for purely correlative models (Heikkinen *et al*., 2006), should not harm projections. Further, complex behaviours under novel climates, such as spring moisture remaining high due to replenishment of water tables in winter (Chapter 4), can be modelled. It is unclear whether this approach could be used for many other situations; other systems may have more species, more complex interactions, multiple environmental drivers, or environmental drivers that cannot be mechanistically modelled. However, if suitable systems could be identified, this approach would provide an alternative to models based solely on simple correlations with climate.

The modelling approach could still be improved (see Chapters 3 and 4 for full discussions). Notably, the hydrological model cannot replicate fine-scale spatial and temporal patterns. Hydrological models with 2-D processes are relatively common, such as those based on the TOPMODEL concepts (Beven & Kirkby, 1979; Beven, 1997). However, peatland hydrological processes may differ substantially from those in mineral soils (Evans & Warburton, 2007), and more field data would be required to parameterise more complex models (Ballard *et al*., 2011). Furthermore, 2-D processes make results dependent on the grid scale used (Lane *et al*., 2004), but high resolution calibration and driving data are not widely available. Similarly, models of peatland hydrology at fine temporal scales (e.g., Weiss *et al*., 2006; Ballard *et al*., 2011) may have intensive data requirements, and driving climate data are rarely available at appropriate time scales, particularly for future climate scenarios. Therefore, for the purpose of the studies presented here, the relatively coarse approach taken is perhaps more suitable, as limitations are clearly understood, extensive parameterisation was not required, and driving data were easily-accessible.

In order to identify dominant trends whilst keeping the modelling process relatively simple, uncertainty was sometimes disregarded. A sensitivity analysis (Appendix 1) indicated that uncertainty in hydrological model parameters did not strongly affect model performance, although some aspects of water table position were sensitive to parameter values. However, only one suitable dataset was available to calibrate the model against, so it is unclear if alternative calibrations would have improved the model. Further uncertainty came from the abundance-moisture relationship, which was wedge-shaped due to spatial aggregation (Chapter 2). For simplicity, expected abundance was modelled in projections, meaning that it would not always match realised abundance. Adding random noise would not have improved results, as dominant trends would have remained similar. Although suggestions for causes of spatial aggregation exist (e.g., Coulson, 1962; Freeman, 1967), the processes have not been quantified, so could not have been modelled without adding considerable complexity and uncertainty. Further uncertainty came from future climate data, as there is often considerable uncertainty inherent in future climate projections (e.g., Murphy *et al.*, 2009; Solomon *et al.*, 2009). This was partly dealt with by using the median of 100 randomised climate sequences, so projections were based on relatively conservative estimates of change. Further, three SRES scenarios were modelled, all of which showed the same trends, adding confidence to projections. However, blanket peat occurrence may be relatively insensitive to changes beyond a certain rainfall threshold (Gallego-Sala *et al.*, 2010), so uncertainty in precipitation projections will affect any models of peatlands under climate change. More complex models, dealing with more uncertainty, could of course be developed; such models would be required for specific, localised conservation plans. Here, however, broad, ‘first impression’ patterns were identified; these can be used to guide further research and model development, and inform initial conservation plans.

On the philosophy of modelling systems, Prof. George Box stated, “since all models are wrong the scientist cannot obtain a "correct" one by excessive elaboration” (Box, 1976); this seems pertinent here, where modelling excluded more complex processes to allow broad trends to be identified. In the absence of improved data for parameterisation, using a more elaborate model would have introduced more uncertainty and would still not have produced a ‘correct’ model. Here, the aim of the model was not to reproduce reality, but to reproduce realistic patterns; evaluations presented in Chapters 3 and 4 suggested that this was achieved. Therefore, although results must be interpreted within the context of methodological limitations, the model has added biological realism to cranefly abundance projections, has avoided problems associated with novel climatic conditions and sub-annual behaviours, and has produced informative, realistic patterns and trends.

6.3 Impacts of climate change and land management on peatland biodiversity and ecosystem services

Results of both fieldwork and modelling suggested that drainage and climate change could harm cranefly populations. Field results showed that drained peat is drier than peat around blocked drains (Chapter 2), and model results indicated that climate change would cause summer water tables to fall (Chapter 4). By reducing soil moisture, cranefly mortality would increase, thus reducing abundance. The effects of drainage on peatland water tables are becoming increasingly well-known, with lower mean water tables, modified fluctuations, and spatially wide-ranging impacts (e.g., Price *et al*., 2003; Wilson *et al*., 2010; Holden *et al*., 2011). Similarly, climate change is anticipated to cause warmer, drier conditions (Holden *et al*., 2007c; Clark *et al*., 2010b). Here, it was shown that sub-annual climatic changes are important, with differing effects at different times of year (Chapter 4). Results in this thesis describe impacts of these changes on keystone invertebrates, and inferences are made about the birds that rely on them. However, further inferences can be made about wider peatland biodiversity and ecosystem services.

The primary results of the thesis relate to upland peatland craneflies. Earlier in the thesis, it is argued that craneflies are keystone invertebrates, with the larvae constituting a major component of the blanket bog soil fauna (Coulson, 1988), both adults and larvae being important prey items for birds (Pearce-Higgins, 2010), and larvae playing roles in herbivory and litter decomposition (Coulson & Whittaker, 1978). In mineral soils, larval craneflies may also influence local hydrology (Holden & Gell, 2009). Enchytraeids, another major component of the blanket bog soil fauna, influence peatland carbon mineralisation, DOC concentrations and microbial communities (Cole *et al*., 2000; Cole *et al*., 2002a; Cole *et al*., 2002b); given that cranefly larvae can have larger relative impacts on litter decomposition than enchytraeids (Standen, 1978), it may be assumed that craneflies also have substantial impacts on some of these other processes in blanket bogs. Further research into the role of cranefly larvae and carbon fluxes, nutrient cycling and hydrology in blanket bogs is required to improve understanding of their wider role in the ecosystem. It is likely, however, that reduced cranefly abundance would have considerable impacts on biodiversity and ecosystem functions.

Soil invertebrates are somewhat buffered from temperature variation (Bale *et al*., 2002), but species concentrated in upper soil layers will be affected by environmental change (Briones *et al*., 2007), and cranefly eggs and larvae are typically found within the top few centimetres of peat (Coulson, 1962; Freeman, 1967). For many soil invertebrates, particularly those within arctic or northern ecosystems, summer moisture availability may be more important than temperature in driving population trends (e.g., Hodkinson *et al*., 1998). Results presented here appeared to support this suggestion, with declining abundances driven by falling summer moisture. Complex community responses could also be expected; Briones *et al*. (1997) showed that drier conditions could affect the vertical distribution and species composition of soil invertebrate communities, and de Vries *et al*. (2012a) showed that droughts affect soil food webs and microbial and faunal community composition even after the drought has ended. Such changes can have impacts on ecosystem functions such as carbon and nitrogen cycling (de Vries *et al*., 2012b) and organic matter decomposition (Briones *et al*., 2007). It is possible that winter rainfall could reverse some community-level impacts of summer drought (Staley *et al*., 2007), but a continued trend of warmer, drier summers would deplete cranefly populations, preventing subsequent re-establishment under wetter conditions. Further, as craneflies show higher density-dependent mortality under drier conditions (Blackshaw & Petrovskii, 2007), there may even be an interactive effect, whereby climate change causes more intra-specific competition and mortality. Therefore, although results presented here show trends of declining moisture and abundance, many complex changes could occur with more complex impacts. It is clear though, that due to the dominance of craneflies, climate change could have a disproportionately large impact on the peatland soil fauna.

To fully understand risks to cranefly populations, other aspects of the system should be explored. As moisture availability influences egg and larval survival, understanding impacts of moisture variation on survival and growth would be beneficial; a series of experiments on *Tipula paludosa* and *T. oleracea* (Meats, 1967a; Meats, 1967b; Meats, 1967c; Meats, 1968) could act as the template for experiments on *T. subnodicornis* and *Molophilus ater*, the key upland peatland species. Such experiments could identify which life cycle stages are particularly sensitive to desiccation, the duration of droughts required to cause mortality, and effects of fluctuating water tables caused by drainage. Higher temperatures increase growth rates in *T. subnodicornis* (Butterfield, 1976a), raising the prospect that if high moisture could be maintained, sensitive early larval instars could be more quickly passed through; only manipulative experiments could examine this possibility. It is also important to conduct more studies on responses to drain blocking. Other than work presented here (published in Carroll *et al.*, 2011), published work on biodiversity responses to drain blocking is limited to vegetation communities (Bellamy *et al.*, 2011) and aquatic invertebrates (Ramchunder *et al.*, 2012); there is therefore a great need for more studies on biodiversity responses. To complement work on craneflies, whole community responses should also be studied; Briones *et al.* (1997) performed experiments using gley soils, but the soil fauna differs between blanket peats and other upland soils (Coulson & Butterfield, 1985), so community responses may also differ. Long-term manipulative experiments, such as that described for plant communities by Peñuelas *et al.* (2007), would provide the best opportunity to study mechanisms and community-level effects of climate change.

A major reason for studying peatland craneflies was their importance to upland bird populations. Results in Chapter 5 support work showing strong links between cranefly abundance and Golden Plover, Red Grouse and Dunlin (Yalden, 1974; Park *et al.*, 2001; Whittingham *et al.*, 2001; Pearce-Higgins & Yalden, 2004). Other models have shown that cranefly declines could drive Golden Plover declines (Pearce-Higgins *et al.*, 2010), and that by increasing cranefly abundance, we could help to avoid bird declines (Pearce-Higgins, 2011b). Although not modelled explicitly here, the risk of climate-driven bird declines can be inferred from results in Chapters 4 and 5. It is possible, however, that other invertebrate species could replace craneflies in bird diets. Prey-switching driven by climatic shifts is already observed in some birds (e.g., Litzow *et al.*, 2002), but it is unclear which species could replace craneflies on blanket bogs. Golden Plover already take a large proportion of Coleoptera (Pearce-Higgins, 2010), but Coleoptera abundance appears to decrease with drought (Morecroft *et al.*, 2002; Staley *et al.*, 2007), and increased temperatures could disrupt carabid beetle life cycles (Butterfield, 1996). For Dunlin and Red Grouse, Diptera are the only major invertebrate dietary component (Pearce-Higgins, 2010), so no large-bodied alternative is immediately evident. Enchytraeids reach high densities in peat (Coulson, 1988), but could move deeper under drier conditions (Briones *et al.*, 1997), and are not large enough to be profitable prey (Buchanan *et al.*, 2006a). Therefore, the possibility of prey-switching making up for cranefly declines appears somewhat unlikely. It would, however, be highly beneficial to compare bird dietary composition between areas with blocked and open drains, to see whether local dietary shifts can already be detected.

Although the focus of this thesis has been invertebrates and birds, the projections of falling water tables and evidence of drainage impacts could be used to infer wider-ranging impacts on peatland ecosystem services. Arguably the most important impact would be on carbon storage. If water tables fall, active bog growth could slow or stop (Gallego-Sala *et al.*, 2010) and CO_2 production would increase (Freeman *et al.*, 1992), leading to bogs becoming carbon sources. Previous modelling indicates that the peatland carbon store could be relatively stable throughout the 21st Century (Clark *et al.*, 2010a). However, as shown in Chapter 4, water table trends in different seasons may differ substantially under climate change, meaning that patterns of gas emissions could differ from those predicted annually. As summer weather can have dominant effects on overall bog wetness and peat structure (Charman, 2007), further examination of source-sink behaviour at a sub-annual scale could improve projections of carbon storage. Further, droughts cause enzymatic changes within peat, with subsequent re-wetting leading to increased loss of dissolved organic carbon (DOC) (Fenner & Freeman, 2011). Given this mechanism and the temperature-sensitivity of DOC production (Clark *et al.*, 2009), increased temperatures combined with drier summers could lead to increased DOC concentrations, reducing both water quality and carbon storage. Similarly, as drought can lead to structural changes in peat (Holden & Burt, 2002), runoff regimes may change, thus affecting water supply, erosion and flood risk. It is not possible to predict all impacts of drier summers on peatlands, but it is clear that many important ecosystem services provided by peatlands are linked to high water tables; ensuring that peatlands stay wet will be a vital step in maintaining the provision of ecosystem services under climate change.

It is well known that climate change and land management can interact in complex ways (Dale, 1997). Model results (Chapter 4) indicated that peatland drainage could interact with drier summers to make population declines more severe. Reduced grouse moor management and grazing for economic reasons (Sotherton *et al.*, 2008; Reed *et al.*, 2009) would increase vegetation cover, which could interact with increased wildfire risk

(Albertson *et al*., 2010) to increase the frequency of large, uncontrollable fires. Conversely, overgrazing could interact with increased temperatures and atmospheric pollution to shift vegetation communities towards grass domination (Holden *et al*., 2007c; McGovern *et al*., 2011). Land management that alters vegetation communities or leads to areas of bare peat can affect carbon fluxes (Ward *et al*., 2009). Similarly, grazing and burning can increase CO_2 fluxes and reduce carbon storage in blanket bogs, with increased impacts under higher temperatures in summer (Ward *et al*., 2007). We may therefore expect both direct and indirect interactions between land management and peatland carbon storage; if carbon fluxes from peatlands increase, this could interact with climatic warming, creating a positive feedback loop (Davidson & Janssens, 2006). Therefore, land management and climate change effects cannot be considered independently.

Given the southerly location of British blanket bogs and extensive drainage present, it is important that climate change and land use impacts are understood so that appropriate conservation actions can rapidly be taken. Of course, caution should be exercised in applying results to other northern peatlands, which may experience different hydrological regimes or climatic conditions (e.g., Moore, 2002; Rydin & Jeglum, 2006). There is also variation in future precipitation projections over the northern peatland region (Solomon *et al*., 2009), so not all peatlands will experience drier summers. However, Britain contains a large proportion of the world’s blanket bog (Ratcliffe & Thompson, 1988), and many other areas of peatland will experience drier conditions, so results still have wider relevance. Results regarding drainage are applicable to a range of peatlands; drainage occurs for various reasons, such as peat extraction (e.g., Price *et al*., 2003) and afforestation (e.g., Holden *et al*., 2007c), so soil invertebrates in these systems could also experience similar impacts. Due to the ecosystem services provided by northern peatlands, most importantly carbon storage (Turunen *et al*., 2002; Limpens *et al*., 2008), there is an urgent need to develop models that explore multiple aspects of peatland ecosystems, that can help us to understand the effects of important local drivers of change.

6.4 Conservation in the uplands

Results presented in this thesis have implications for conservation in the British uplands. Importantly, Chapter 2 showed that a widely-used peatland restoration method benefits keystone soil invertebrates. However, results in Chapter 4 suggested that even though drain blocking could slow declines and stop localised extinctions, it might not stop climate-driven declines altogether. Therefore, it may be necessary to consider alternative conservation methods for climate change adaptation. Further, it may be necessary to examine wider upland conservation and land use policy to understand possible drivers of change in upland ecosystems and how conservation benefits may be achieved.

Chapter 2 showed that drain blocking is beneficial in areas subject to drainage. Peatland drain blocking is already widespread (Armstrong *et al*., 2009), but many areas are still drained, and authors have proposed focussing blocking on older drains and steeper slopes to maximise effectiveness of restoration (e.g., Holden *et al*., 2007c). However, as the greatest cranefly abundances occur in relatively wet areas (Chapter 2), climate change adaptation management may be better served by blocking drains on shallower slopes and in wetter areas to ensure that high water tables are maintained under climate change. Beyond drain blocking, conservation strategies should consider ways of preventing summer drought; methods from restoration of mined peatlands may be informative for this purpose. Bunds could be built to reduce runoff (Price *et al*., 2003), but as summer water tables are strongly influenced by evapotranspiration (Evans & Warburton, 2007), reducing runoff may have little benefit and could disrupt catchment hydrology. Alternatively, if bunds created standing water, this would increase the risk of soil invertebrates drowning, particularly if winter rainfall increases. Another option may be to manage vegetation or apply mulches to reduce evapotranspiration (Price *et al*., 2003); if such methods were combined with bunds, it may be possible to maintain areas with appropriate soil moisture levels. These management strategies could also benefit upland bird populations; without such management, other conservation techniques may have limited effectiveness, as food would ultimately become limiting due to reduced prey densities (Pearce-Higgins, 2011b). Understanding biodiversity impacts of alternative conservation and restoration methods will be a key part of managing upland peatlands to aid climate change adaptation.

Several methods of peatland restoration are currently available. The methods used reflect the aims of restoration and the extent of restoration required (Anderson *et al*., 2009b). Reasons for restoration include overgrazing damage, the spread of invasive species, peat desiccation, and the exposure of bare peat (Anderson *et al*., 2009b). Possible interventions include stock reduction, changing burning regimes, removing unwanted species, blocking drains or gullies and stabilising bare peat (Anderson *et al*., 2009b). These methods are often conducted on a large scale, with over 15,000 ha of blanket bog involved in restoration schemes (Holden *et al*., 2008). Such large-scale projects attract substantial costs; the median cost has been estimated as £1,600 ha^{-1} (Holden *et al*., 2008). Many restoration projects also include monitoring of hydrology, vegetation and invertebrates (Holden *et al*., 2008). However, drain blocking projects rarely produce detailed, long-term monitoring datasets (Holden *et al*., 2007a; Holden *et al*., 2011), and there are relatively few publications on biodiversity responses to peatland restoration (but see Littlewood *et al*., 2006; Bellamy *et al*., 2011; Ramchunder *et al*., 2012). Therefore, if peatlands are to be successfully restored and managed, appropriate monitoring of different methods is required so that effective and cost-efficient management can be undertaken.

A complicating factor in peatland restoration is that there are multiple stakeholders, each with different aims. Stakeholders range from governmental organisations such as Natural England, Scottish Natural Heritage and Countryside Council for Wales, to non-governmental organisations such as conservation charities and utility companies, to individuals such as gamekeepers and farmers (Armstrong *et al*., 2009). Interestingly, given this range of stakeholders, many peatland restoration projects list biodiversity as a major justification (Holden *et al*., 2008). However, restoration methods for other purposes could still benefit biodiversity, regardless of the original intention. For example, drain blocking is often carried out to raise peatland water tables and thus reduce DOC concentrations, sediment loads and erosion (Armstrong *et al*., 2009), leading to reduced water treatment costs for utility companies (Worrall *et al*., 2007), but also to improved conditions for moisture-dependent species. Similarly, in the future, peatland restoration could be funded via carbon offsetting schemes, driven by the assumption that active peatlands are carbon sinks (Worrall *et al*., 2009). Given the limited understanding of biodiversity responses to peatland restoration, the benefits can typically only be inferred, but if biodiversity does benefit, conservation aims could be achieved without spending limited conservation funds.

Managing land for multiple uses could be an important part of future upland land management. Peatland restoration to restore hydrological function would also aid water quality, carbon sequestration and biodiversity, meaning that, as suggested by Maltby (2010), multiple ecosystem service benefits could be achieved through restoration. In Great Britain, areas of high carbon storage value do not necessarily overlap with areas of high species richness (Anderson *et al*., 2009a), but given that peatlands support species of conservation, economic and cultural interest, biodiversity benefits could still be driven by management for carbon storage. Indeed, in boreal forests, another important northern ecosystem, below-ground carbon storage is positively associated with above-ground plant and animal diversity (Wardle *et al*., 2012), suggesting that appropriate land management strategies for northern peatlands could achieve the desired multiple benefits. There are also other ‘win-win’ aspects of peatland restoration, such as restored vegetation reducing erosion and carbon loss (House *et al*., 2010). Given the fact that many peatland ecosystem services are underpinned by high water tables, peatland restoration provides an excellent opportunity to achieve multiple benefits.

The restoration approaches, land uses, climate change risks and ecosystem services discussed above are bound together by upland policy. The degradation of peatlands through drainage and overgrazing has primarily been driven by agricultural policies and subsidies (Holden *et al*., 2007c; Condliffe, 2009). Conversely, these policies have also become a major driver of environmental improvements (Condliffe, 2009). Therefore, land management changes over the coming decades are likely to be heavily influenced by policy and economic drivers. Further reforms to agricultural policies are likely to increase requirements for environmental protection, and could be used to fund peatland restoration (Whitfield *et al*., 2011). Outside of directly encouraging restoration, agricultural policy will also influence wider habitat management, as upland farms, and sometimes grouse moors, may only be economically viable due to subsidies (Dougill *et al*., 2006; Hubacek *et al*., 2008). As the economic viability of upland farming declines, the role of farmers may shift towards maintaining and improving upland habitats, but there is also the risk that some land may simply be abandoned (Condliffe, 2009; Reed *et al*., 2009); this could lead to improvements in some habitats, but further degradation in others (Dougill *et al*., 2006; Reed *et al*., 2009). It is therefore encouraging that peatland management and restoration are explicitly considered in a recent UK government review of upland policy (Defra, 2011).

Novel solutions may be required to drive peatland restoration and conservation. Carbon sequestration could be used to pay for peatland restoration (Worrall *et al*., 2009), but the lack of consensus regarding impacts on carbon fluxes means that policies and mechanisms to enable this cannot easily be developed (Bussell *et al*., 2010; Whitfield *et al*., 2011). Other potential opportunities for funding are water companies, the tourism industry and the renewable energy industry (Bonn *et al*., 2009). To translate the importance of the uplands to the public and industrial stakeholders, monetary values of ecosystem services could be estimated (Bonn *et al*., 2009). However, problems exist with reducing complex functions to simple monetary values, particularly as data from upland peatlands are limited (Cornell, 2010). New approaches to property rights in the uplands may also be required to reduce stakeholder conflicts and allow effective, beneficial land management (Quinn *et al.*, 2010). Given the range of possibilities and uncertainties in the future of upland policy and conservation, more data on impacts of restoration methods, such as results in Chapter 2, and more modelling to identify future risks, such as results in Chapter 4, are required to ensure that efficient, effective land management strategies can be established.

6.5 Concluding remarks

Managing peatlands will be a major challenge over the coming decades. Two broad aims will need to be achieved. First, the damage done by inappropriate land management will need to be remedied. In some cases, such as in tropical peatlands, ongoing detrimental land management must first be minimised or stopped. Within the UK, there is substantial interest in restoring degraded peatlands, but more monitoring is required to fully understand restoration impacts. Second, risks from climate change will have to be appropriately managed. This aim is harder to achieve due to the uncertainty in climate change projections, as well as regional variation in land use, peatland type and non-climatic drivers of change. Management strategies must therefore be based on the most likely scenarios for change, but must also take account of risks and contingencies. Such strategies can only be built around a solid empirical evidence base, supplemented by modelling work. Improved data would not only benefit management strategies, but may also open up new opportunities for funding peatland management and restoration.

The justification for peatland restoration is often linked to conservation of biodiversity, but physical and economic benefits are also highly important. Given the importance of the global peatland carbon store, the conservation of peatland biodiversity may ultimately be made possible by managing peatlands for carbon storage; it is particularly important to ensure that peatlands do not become net carbon sources in the long term. Global climate change mitigation actions may not be able to prevent the loss of the cool, wet climates associated with northern peatlands, but appropriate land management, focussed on maintaining hydrological function, could help to preserve important ecosystem services. As Joosten *et al.* (2012) state, the overall strategy for mitigating climate change impacts on peatlands should be, "1. Keep wet peatlands wet; 2. Rewet drained peatlands; 3. Adapt management where peatland cannot be rewetted.” Given recent interest in peatland restoration and conservation, there may be real possibilities to enable such a strategy over the coming years.

This thesis has shown that the abundance of craneflies, keystone invertebrates of upland peatlands, significantly increases with soil moisture. Driven by this relationship, peatland restoration through blocking drains has been shown to increase cranefly abundance. Modelling work has shown that drier summers under climate change could drive cranefly population declines, and that active drainage could make declines worse. On a regional scale, distributions of some upland breeding bird species are associated with cranefly abundance, implying that cranefly population declines would harm the unique bird species assemblage of the British uplands. Although the focus of the thesis has been peatland biodiversity, there are also implications for other ecosystem services such as carbon storage and water quality, which would be damaged by peatlands becoming drier. Previously, peatlands have been identified as a forgotten ‘Cinderella habitat’ (Lindsay, 1993), but this appears to be changing. By appreciating the benefits of peatlands, by improving our understanding of land use and restoration impacts, and by assessing risks posed by environmental change, it should be possible to ensure that, in the future, peatlands are managed appropriately, allowing them to continue to provide important ecosystem services and support unique biodiversity.

Appendix 1

Sensitivity analysis of hydrological model parameters

In Chapter 3, the following equations were parameterised by comparing model outputs to observed water table depths for Moor House NNR:

$$\left(1-\left(\alpha-\beta*\left(\exp(-0.01*WTD)^{\gamma}\right)\right)-\kappa\cos(\lambda*\mathrm{S})\right)*R_L \tag{A1.1}$$

$$(\delta-(0.01*WTD^{2})-\kappa\cos(\lambda*\mathrm{S}))*R_L \tag{A1.2}$$

$$\left(\varepsilon-\left(\eta*\left(\exp(0.01*WTD)^{\theta}\right)\right)-\kappa\cos(\lambda*\mathrm{S})\right)*R_L \tag{A1.3}$$

See Chapter 3 for details of equation function and model fitting; equations have been re-numbered in this appendix. Observed water table data for model calibration were supplied by the Environmental Change Network. Fitted values are given in Table A1.1.

Table A1.1. Parameters used in runoff equations and fitted values.

Parameter	Equation	Description	Fitted value
α	A1.1	Defines minimum runoff at slope = 0 (i.e. 1 - α - κ)	0.425
β	A1.1	Strength of WTD effect below surface (adjusts slope of relationship)	0.7
γ	A1.1	Exponent of WTD effect below surface (adjusts curve of relationship)	5
δ	A1.2	Maximum runoff at slope = 0 (i.e. δ - κ)	1.4
ε	A1.3	Maximum runoff at slope = 0 (i.e. ε - κ)	1.46
η	A1.3	Strength of WTD effect above surface (adjusts slope of relationship)	0.01
θ	A1.3	Exponent of WTD effect above surface (adjusts curve of relationship)	50
κ	A1.1, A1.2, A1.3	Minimum slope effect (i.e. when slope = 0)	0.5

After initial calibration, a simple sensitivity analysis was conducted, whereby parameter values were adjusted up and down by 10% of the fitted value. As with initial model fitting, this was performed using the first five years of Moor House water table data (i.e., 1999 – 2003 inclusive). Effects of parameter variation on water table fluctuations were assessed using R^2 values from linear regressions of observed vs. predicted water table depth. Effects of parameter variation on water table position were assessed by comparing modelled means, standard deviations, minima and maxima to those observed. Raw values are presented in Table A1.2; summary statistics for the values are presented in Table A1.3. Errors relative to observed values (i.e., modelled - observed) are presented in Table A1.4; summary statistics for absolute errors are presented in Table A1.5. To see qualitative effects of parameter value variation, modelled water tables were plotted against observed water tables for the model fitting period. Results are presented in Figure A1.1.

Table A1.2. Water table position values and R^2 values from linear regressions of modelled vs. observed water table depth, using parameter values +10% and -10% of the fitted value.

	R^2	Mean WTD (cm)	Standard deviation (cm)	Minimum WTD (cm)	Maximum WTD (cm)
Observed	--	4.3	4.7	-0.5	22.9
Fitted	0.67	4.7	4.8	-0.5	21.1
α - 10%	0.64	5.1	5.1	-0.5	21.8
α + 10%	0.69	4.4	4.5	-0.6	20.3
β - 10%	0.68	4.4	4.5	-0.6	20.3
β + 10%	0.64	5.1	5.1	-0.5	21.8
γ – 10%	0.65	4.9	5.0	-0.5	21.5
γ + 10%	0.68	4.6	4.6	-0.5	20.7
δ - 10%	0.66	4.4	4.9	-1.2	20.9
δ + 10%	0.70	5.3	4.5	0.2	20.8
ε – 10%	0.55	3.3	5.3	-4.4	21.0
ε + 10%	0.67	4.7	4.8	-0.5	21.1
η – 10%	0.67	4.7	4.8	-0.5	21.1
η + 10%	0.67	4.7	4.8	-0.5	21.1
θ – 10%	0.67	4.7	4.8	-0.5	21.1
θ + 10%	0.67	4.7	4.8	-0.5	21.1
κ – 10%	0.67	5.9	4.8	0.8	21.8
κ + 10%	0.65	3.7	4.8	-1.5	20.2

Table A1.3. Summary statistics for values calculated as part of the sensitivity analysis. Statistics are calculated including values from the model with fitted parameters, but excluding observed values.

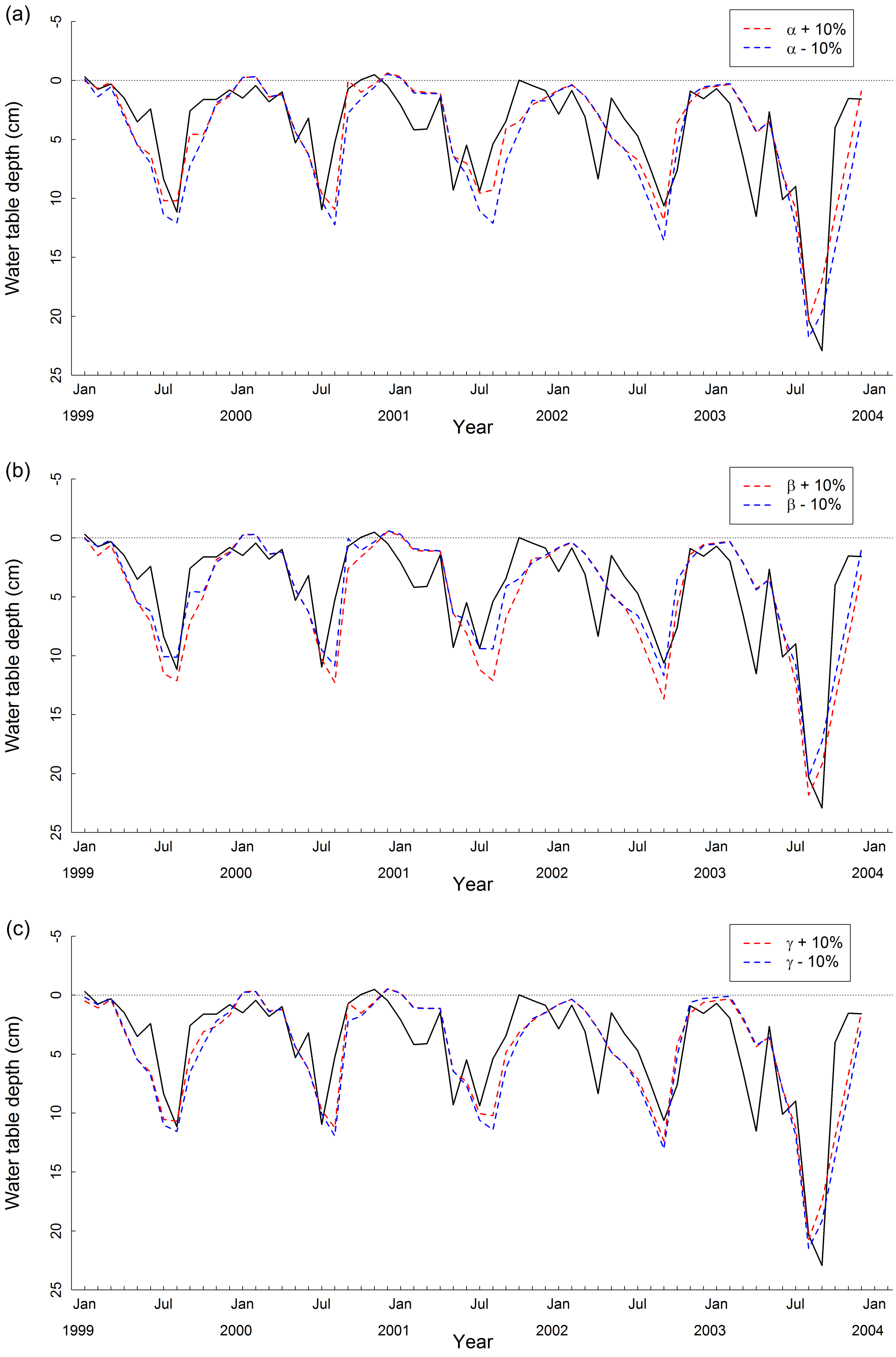
	R^2	Mean WTD (cm)	Standard deviation (cm)	Minimum WTD (cm)	Maximum WTD (cm)
Minimum	0.55	3.3	4.5	-4.4	20.2
Maximum	0.70	5.9	5.3	0.8	21.8
Range	0.15	2.6	0.9	5.2	1.6
Mean	0.66	4.7	4.8	-0.7	21.0
St. dev.	0.033	0.58	0.23	1.06	0.50

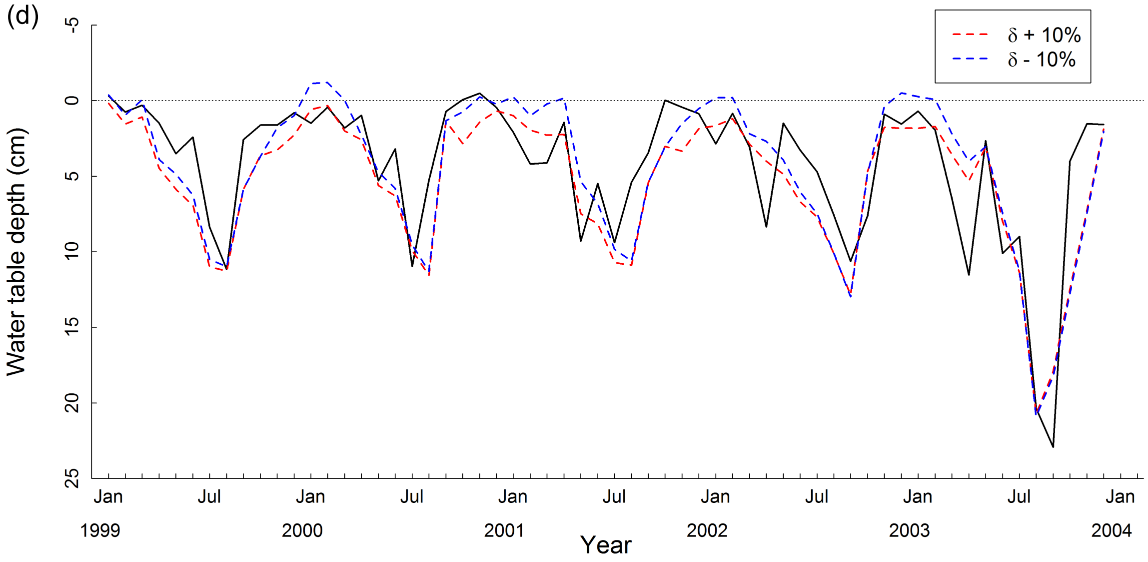
Table A1.4. Error in modelled values relative to observed values (i.e. modelled - observed) from sensitivity analysis using parameter values +10% and -10% of the fitted value.

	Error in mean WTD (cm)	Error in standard deviation (cm)	Error in min. WTD (cm)	Error in max. WTD (cm)
Fitted	0.4	0.1	0.0	-1.8
α - 10%	0.8	0.4	0.0	-1.1
α + 10%	0.1	-0.2	-0.1	-2.6
β - 10%	0.1	-0.2	-0.1	-2.6
β + 10%	0.8	0.4	0.0	-1.1
γ – 10%	0.6	0.3	0.0	-1.4
γ + 10%	0.3	-0.1	0.0	-2.2
δ - 10%	0.1	0.2	-0.7	-2.0
δ + 10%	1.0	-0.2	0.7	-2.1
ε – 10%	-1.0	0.6	-3.9	-1.9
ε + 10%	0.4	0.1	0.0	-1.8
η – 10%	0.4	0.1	0.0	-1.8
η + 10%	0.4	0.1	0.0	-1.8
θ – 10%	0.4	0.1	0.0	-1.8
θ + 10%	0.4	0.1	0.0	-1.8
κ – 10%	1.6	0.1	1.3	-1.1
κ + 10%	-0.6	0.1	-1.0	-2.7

Table A1.5. Summary statistics for absolute errors calculated as part of the sensitivity analysis. To calculate absolute errors, the sign of the errors in Table A1.4 was disregarded.

	Mean WTD (cm)	Standard deviation (cm)	Minimum WTD (cm)	Maximum WTD (cm)
Min. absolute error	0.1	0.1	0.0	1.1
Max. absolute error	1.6	0.6	3.9	2.7
Mean absolute error	0.6	0.2	0.5	1.9


(a)
α + 10%
α - 10%
(b)
β + 10%
β - 10%
(c)
γ + 10%
γ - 10%
Water table depth (cm)
-5
0
5
10
15
20
25
Jan
Jul
Jan
Jul
Jan
Jul
Jan
Jul
Jan
Jul
Jan
1999
2000
2001
2002
2003
2004
Year


(d)
δ + 10%
δ - 10%
Water table depth (cm)
-5
0
5
10
15
20
25
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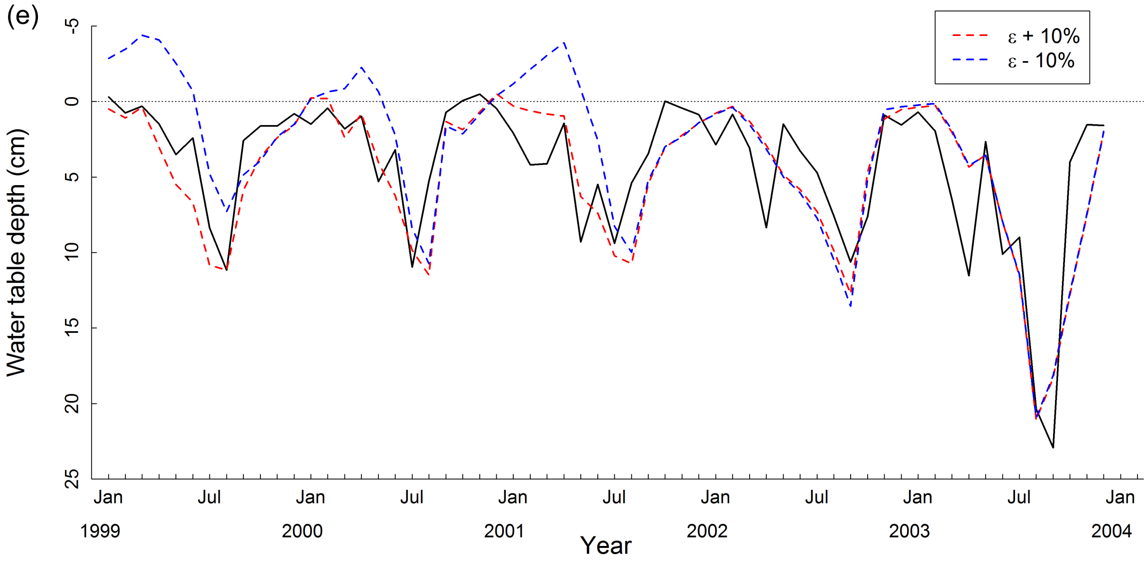
(e)
ε + 10%
ε - 10%
Water table depth (cm)
-5
0
5
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15
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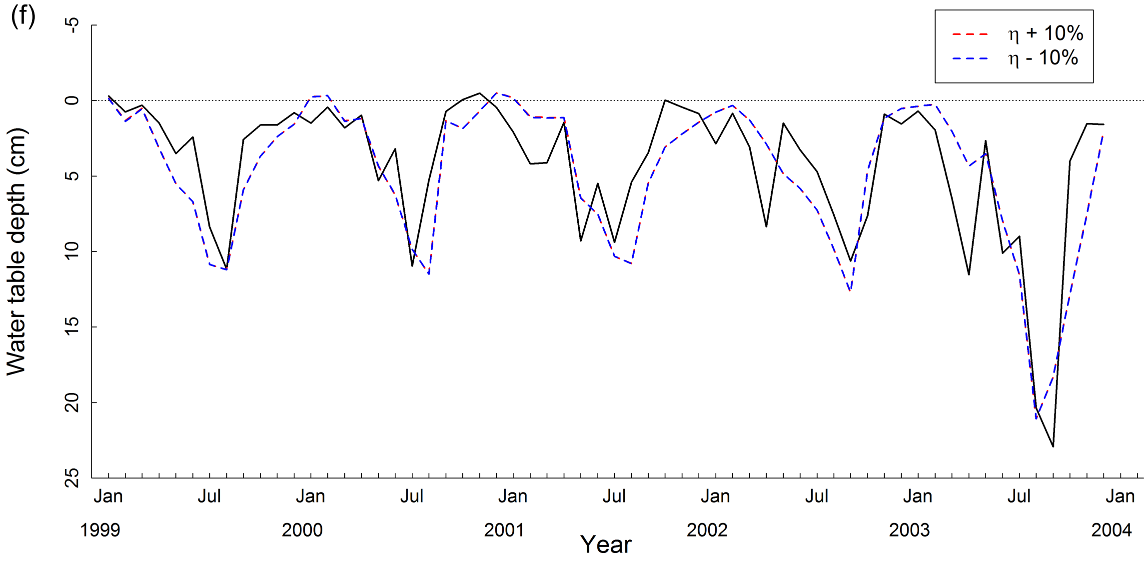
(f)
η + 10%
η - 10%
Water table depth (cm)
-5
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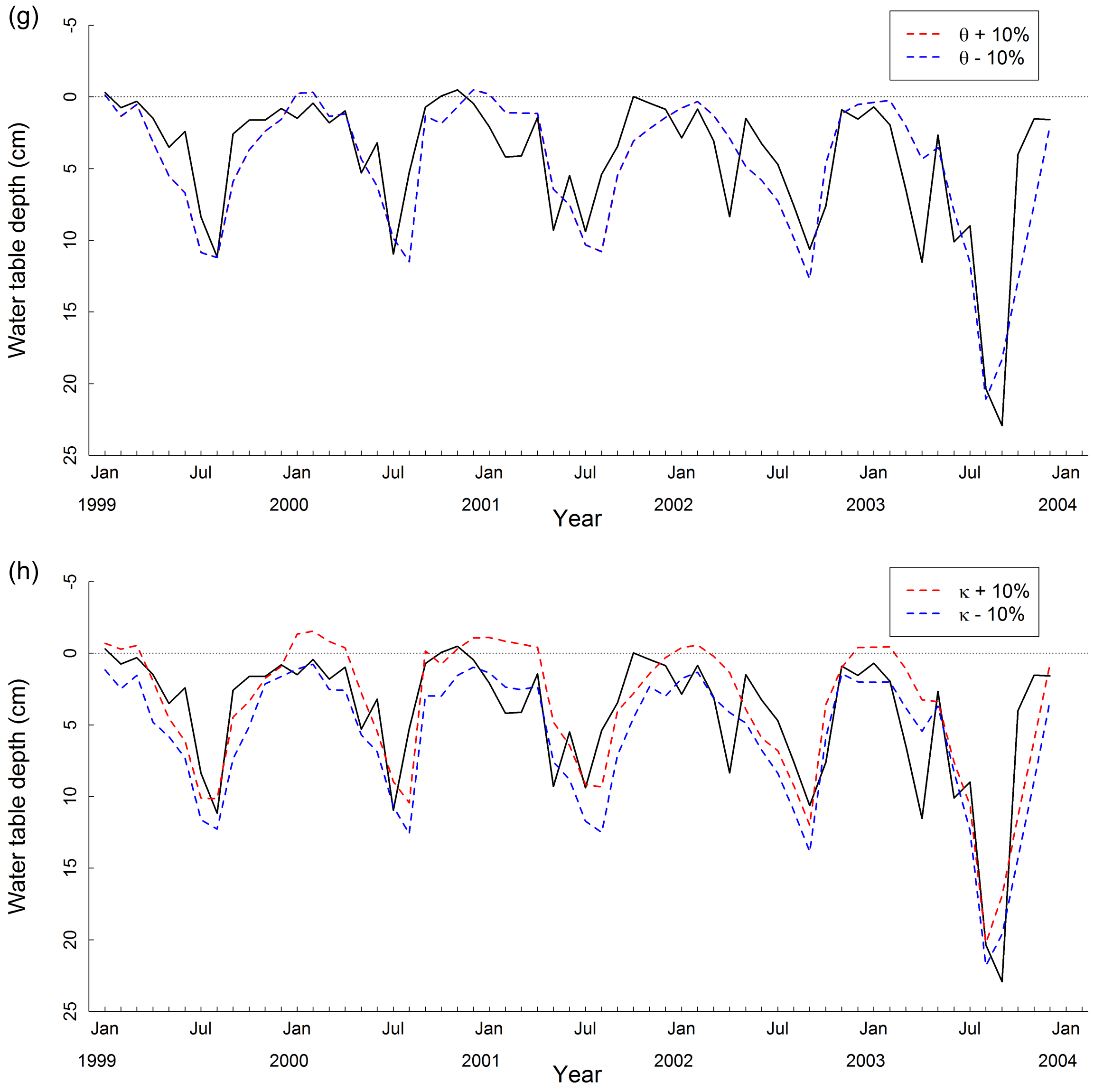

Figure A1.1. Effects of +10% and -10% variation in fitted parameter values on modelled water table depths, for parameters a) α, b) β, c) γ, d) δ, e) ε, f) η, g) θ and h) κ. See Table A1.1 for parameter descriptions. Modelled values are plotted as dashed red and blue lines. Observed water table depths are plotted as a solid black line.

Appendix 2

Correlations between habitat variables and between bird species

Data used in bird analyses (Chapter 5) were explored for correlations between and within bird species, and between habitat variables. Table A2.1 shows correlations between the abundances of different bird species for both 1990 and 2004 surveys, and the correlations between abundance in the two surveys for each species. Table A2.2 shows correlations between different habitat variables used in analyses. Bird survey and habitat data were kindly provided by Natural England, Moors for the Future and Dr. James Pearce-Higgins.

Table A2.1. Spearman's rank correlation coefficients for correlations between abundances of the different bird species used in analyses. Values in the lower-left section refer to correlations for 1990 survey data; values in the upper-right section refer to correlations for 2004 survey data. Values in shaded boxes on the diagonal refer to correlations between 1990 and 2004 abundance for the same species.

	Curlew	Dunlin	Golden Plover	Lapwing	Meadow Pipit	Red Grouse	Reed Bunting	Ring Ouzel	Skylark	Snipe	Stonechat	Wheatear	Whinchat	Wren
Curlew	0.324	0.013	-0.058	0.259	0.142	0.054	0.072	0.117	0.278	0.307	0.115	0.093	0.057	0.062
Dunlin	-0.046	0.405	0.365	-0.041	-0.024	0.092	-0.104	-0.069	0.115	-0.023	-0.070	-0.050	-0.070	-0.154
Golden Plover	0.090	0.312	0.579	-0.040	0.098	0.346	-0.232	-0.087	0.109	-0.030	-0.139	-0.045	-0.174	-0.242
Lapwing	0.206	-0.040	-0.046	0.202	0.035	-0.031	0.115	-0.017	0.178	0.324	-0.018	0.112	-0.001	-0.071
Meadow Pipit	0.149	0.059	0.199	0.113	0.275	0.524	0.070	0.182	0.189	0.125	-0.028	0.151	0.131	0.056
Red Grouse	0.078	0.096	0.410	0.030	0.354	0.512	-0.077	0.153	-0.219	0.037	-0.012	0.059	0.031	0.044
Reed Bunting	0.046	-0.066	-0.027	0.044	0.101	-0.271	0.194	-0.023	0.064	0.207	0.157	0.019	0.248	0.058
Ring Ouzel	-0.078	-0.015	-0.046	0.050	0.221	0.139	-0.014	0.257	-0.031	0.062	0.150	0.136	0.175	0.289
Skylark	0.345	0.064	0.133	0.032	0.249	0.069	0.199	0.015	0.393	0.128	0.045	0.111	-0.034	0.105
Snipe	0.174	-0.034	-0.058	0.136	0.099	-0.075	0.175	0.086	0.187	0.215	-0.014	0.080	0.136	0.008
Stonechat	-0.036	-0.014	0.010	-0.016	0.108	-0.037	-0.008	-0.020	0.002	-0.020	-0.016	0.090	0.307	0.255
Wheatear	0.004	-0.099	-0.125	0.095	0.026	-0.049	0.096	0.264	0.124	0.077	-0.021	0.114	-0.023	0.091
Whinchat	0.053	-0.088	-0.108	0.167	0.072	-0.109	0.107	0.163	-0.051	0.196	-0.014	0.226	0.189	0.202
Wren	0.065	-0.052	0.046	-0.013	0.177	0.173	0.132	0.005	-0.169	0.038	-0.010	0.006	0.068	0.033

Table A2.2. Spearman's rank correlation coefficients for correlations between habitat variables used in bird analyses. Values above and below the shaded line are mirrors of one another. Moderate and strong correlations (ρ > 0.5) are highlighted in bold.

	1989 abund.	1990 abund.	2003 abund.	2004 abund.	Veg. height	Cotton grass	Grass	Heather	Non-heather heath	Stream dist.	Peat	Encl. grass	Woods	Burns	Disturb.
1989 abund.		**0.878**	**0.851**	**0.867**	**-0.576**	**0.547**	-0.174	0.198	0.462	-0.485	**0.779**	**-0.521**	-0.442	0.066	-0.375
1990 abund.	**0.878**		**0.793**	**0.887**	**-0.528**	**0.548**	-0.086	0.145	0.494	-0.425	**0.726**	**-0.516**	-0.392	-0.031	-0.391
2003 abund.	**0.851**	**0.793**		**0.778**	**-0.662**	0.474	-0.229	0.251	0.427	-0.363	**0.678**	-0.494	-0.379	0.097	-0.410
2004 abund.	**0.867**	**0.887**	**0.778**		-0.494	**0.511**	-0.120	0.132	0.457	-0.391	**0.702**	-0.424	-0.434	-0.079	-0.350
Veg. height	**-0.576**	**-0.528**	**-0.662**	-0.494		-0.458	0.394	-0.452	**-0.566**	0.401	**-0.646**	**0.623**	0.372	-0.270	0.338
Cotton grass	**0.547**	**0.548**	0.474	**0.511**	-0.458		0.358	-0.003	**0.682**	-0.308	**0.652**	**-0.527**	-0.443	-0.160	-0.198
Grass	-0.174	-0.086	-0.229	-0.120	0.394	0.358		-0.481	0.053	0.110	-0.067	0.084	-0.085	-0.453	0.120
Heather	0.198	0.145	0.251	0.132	-0.452	-0.003	-0.481		0.378	-0.058	0.261	-0.302	-0.208	**0.786**	-0.196
Non-heather heath	0.462	0.494	0.427	0.457	**-0.566**	**0.682**	0.053	0.378		-0.359	**0.564**	**-0.588**	-0.457	0.128	-0.205
Stream dist.	-0.485	-0.425	-0.363	-0.391	0.401	-0.308	0.110	-0.058	-0.359		**-0.523**	0.408	0.271	0.077	0.224
Peat	**0.779**	**0.726**	**0.678**	**0.702**	**-0.646**	**0.652**	-0.067	0.261	**0.564**	**-0.523**		**-0.665**	**-0.524**	0.055	-0.322
Encl. grass	**-0.521**	**-0.516**	-0.494	-0.424	**0.623**	**-0.527**	0.084	-0.302	**-0.588**	0.408	**-0.665**		0.499	-0.138	0.274
Woods	-0.442	-0.392	-0.379	-0.434	0.372	-0.443	-0.085	-0.208	-0.457	0.271	**-0.524**	0.499		-0.077	0.215
Burns	0.066	-0.031	0.097	-0.079	-0.270	-0.160	-0.453	**0.786**	0.128	0.077	0.055	-0.138	-0.077		-0.141
Disturbance	-0.375	-0.391	-0.410	-0.350	0.338	-0.198	0.120	-0.196	-0.205	0.224	-0.322	0.274	0.215	-0.141	

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