The effect of climate change on the distribution, phenology and abundance of British plants and animals.

Miss Rachael Hickling BSc.

A dissertation submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy
of the
University of York
Department of Biology

2006

Abstract

In this thesis the data from several recording schemes are analysed to examine the effects of climate warming (temperature) on distribution, abundance and phenology changes in Britain in a wide variety of animal and plant groups.

The majority of species studied have shifted polewards and uphill over a period of approximately 24 years, consistent with climate warming. The rates of range shift were not significantly different for well-recorded groups (birds and butterflies) compared with less well-studied taxa. Rates of shift for northerly-distributed invertebrate species were comparable with southerly invertebrate species.

The relationship between phenological and distributional change was also studied for birds, butterflies and plants. There was no relationship between phenological change and distribution change in birds and plants, but in butterflies, those species showing the greatest distribution change also showed the greatest advancement in spring emergence of adults. It is possible that similar relationships may emerge over time for plants and birds.

The effect of climate warming on abundance of populations was studied for birds, moths and butterflies. For moths and butterflies there was no conclusive evidence for an effect of climate warming on abundance, but these groups showed large year-to-year variation in abundance which may have masked any long term trends. For birds there was some evidence that northern species have declined more that ubiquitous species in the hottest parts of Britain.

In general, the majority of species studied appear to be responding to climate change, both by changing the timing of their reproductive events, and by shifting their distributions polewards. Large-scale recording and long-term datasets are essential to the further study of this subject. An understanding of how species are responding to climate change will become increasingly important as temperatures continue to rise.

Contents

List of Tables

List of Figures

Acknowledgements

I would like to thank the following for their assistance during the course of this project:

My supervisors, David Roy, Jane Hill and Chris Thomas, for their advice, imagination and reassurance.

Richard Fox, Alastair Fitter and Humphrey Crick for their collaboration and advice with manuscripts.

All the recording schemes and societies, the organisers of such schemes, and the recorders who contributed their datasets to the Biological Records Centre and the British Trust for Ornithology, without whom this project would not have been possible.

All the staff of Monks Wood and particularly the Biological Records Centre, who have been great friends and a constant source of support throughout this project. In particular, thanks to Henry Arnold for always being there when I had a question, and to Pete Rothery, who rescued me from statistical conundrums on many occasions.

NERC for their sponsorship of this project.

Finally I must thank my parents, Russell and Margaret, whose constant support and encouragement kept me going through the hardest times, when I otherwise would have lost my way.

Declaration

Some of the material included in this thesis was produced in collaboration with other workers:

Chapters 2 and 3 have been published:
Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology,* **11**, 502-506.
Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology,* **12**, 450-455.

Chapter 5 has been submitted for publication (Hickling *et al.* in press).

The UKCIP98 Climate Scenario CD-ROM has been supplied by the Climate Impacts LINK Project (DETR Contract EPG 1/1/68) on behalf of the UKCIP and The Met. Office (Hadley Centre).

R. Hickling

November 2006

Chapter 1

Introduction

1.1: The importance of climate for biological systems

It has long been known that even small variations in climate can have profound effects upon the Earth's ecology. Large or rapid changes in climate have led to extinctions in the past, and the biggest (95%) extinction event in Earth's history may have been due to a runaway greenhouse effect (Benton & Twitchett 2003). This runaway effect involved gas hydrates being released from the ground at ever increasing rates as warming continued, and therefore increasing the rate of warming such that normal systems that equilibrate atmospheric gases and temperatures took hundreds of thousands of years to come into play. It is unclear whether future climate changes and associated ecological responses will be similar to those observed in the geological past.

During the 21st century, global temperatures are predicted to increase by between 1.4°C and 5.8°C (IPCC 2001). Studies have shown that, so far, 80% of species are showing a response to the warming climate, and that the timing of biological events (phenology) has shifted an average of 5.1 days earlier (Root *et al.* 2003). As climate warming continues it can be expected that these figures will rise. Up to 35% of species may be committed to eventual extinction by the climate change expected by 2050 (Thomas *et al.* 2004). This may even be an underestimation, as this estimate does not take future land use and habitat loss into account.

Increased carbon dioxide is also an important factor in climate change (although all analyses presented in this thesis are related primarily to temperature effects). Increased levels of carbon dioxide can affect whole ecosystems. For example, Jones *et al.* (1998) showed that in high levels of carbon dioxide, plants may fix carbon below ground, eventually increasing the amount of organic carbon in the soil and so affecting the entire decomposer food chain. In another study, it was proven that elevated carbon dioxide levels change food plant quality, causing a decrease in foliar nitrogen concentration (Bezemer &

Jones 1998). This in turn can cause herbivorous insects to grow more slowly, consume more plant material and suffer heavier mortality, hence decreasing the abundance of a population.

It has been suggested that climate change could pose a greater threat to biodiversity than habitat loss (Thomas *et al.* 2004). Sala *et al.* (2000) suggest this is more likely in temperate regions, with habitat loss still more important than climate at low latitudes. It is therefore extremely important that we understand the drivers, mechanisms, and consequences of climate change for biological systems as fully as possible, in the hope that we can moderate the number of extinctions due to man-made climate change. On a more selfish note as scientists, the rapid warming of recent decades gives us a unique opportunity to examine the effects of climate change on ecological communities, on a spatial scale that laboratory experiments could never match.

1.2: Shifts in distributions

One way in which species may respond to climate change is by shifting their distributions to different latitudes or altitudes (Huntley 1991). Such shifts have already been modelled and documented for whole biomes in the Quaternary period (Kutzbach *et al.* 1998) by using remains of animals, and ancient seeds and pollen to estimate species' distributions (Peyron *et al.* 2005). Current climate warming has already been documented as having a significant impact on natural systems for whole groups of species (Table 1.1), including birds, butterflies and plants (Warren *et al.* 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003).

For example, 63% of 35 non-migratory European butterflies have shifted their ranges northwardsover the last 100 years, with the most parsimonious explanation being climate change (Parmesan *et al.* 1999). In the highland cloud forest of Costa Rica, increased temperatures have caused the cloud bank to rise, and lowland species are colonising higher altitudes (Pounds *et al.* 1999). Alpine plants are also shifting to higher altitudes (Grabherr *et al.* 1994).

1.2.1: Latitudinal shifts across the world

There are many examples of species' distributions shifting polewards in recent decades, as would be generally expected if they were responding to climate change (Parmesan & Yohe 2003). Several of these examples in Europe are of northward shifts in well-studied insects such as butterflies (Parmesan *et al.* 1999; Hill *et al.* 2002) and moths (Battisti *et al.* 2005), and climate change has been proposed as the most likely explanation of such range shifts.

Past northward shifts have been documented for small mammals during the Holocene period (Davis & Callahan 1992), and future shifts have been predicted by models of hibernating mammals (Humphries *et al.* 2002). Northwards shifts have also been documented in birds (Thomas & Lennon 1999). These taxonomic groups are all likely to experience strong energetic constraints at their northern range margin, and therefore might be expected to show a strong latitudinal response to climate change.

Some models have predicted that species may contract at both range margins, even under conservative climate change scenarios, rather than shift polewards (Beaumont & Hughes 2002). The fact that this particular study was based in Australia supports the suggestion that environmental constraints on species may differ geographically, with water availability rather than temperature per se being the primary limiting factor in tropical and warm-temperate zones such as Australia, and temperature being the primary factor limiting distributions at higher latitudes (Hawkins *et al.* 2003). Thus, distributional responses to climate change in Australia may be due more to changes in water availability rather than temperature.

There is a long-running debate about whether climate factors are equally important in limiting both high and low latitude range margins. For example, it has been suggested that climate is more important in limiting high latitude (cold) boundaries but that biotic factors (competition, predation etc.) are more important at low latitude (warm) boundaries (Davis *et al.* 1998). Whilst expansions at the northern (cold) range margin of southern species (in the Northern Hemisphere) have been relatively common in recent years, only a few studies have detected a corresponding retraction at the southern (warm) range margin of northern species (Franco *et al.* 2006; Thomas *et al.* 2006). For example, both Hill *et al.*

(2002) and Thomas & Lennon (1999) reported shifts at the northern range margin, but could only detect slight retractions at the southern range margin of species within the same taxonomic group. The two main theories to explain this are that either polewards retractions at southern range margins are simply not occurring, or that such retractions are occurring or will soon occur, but that current analyses have failed to detect them (Thomas *et al.* 2006).

1.2.2: Altitudinal shifts across the world

Distributional shifts uphill have been detected for a variety of species (Table 1.1), as would be generally predicted if they were responding to climate change (Parmesan & Yohe 2003, Pounds *et al.* 1999). Amongst European studies, uphill shifts have been detected in Czechoslovakian (Konvicka *et al.* 2003) and Spanish (Wilson *et al.* 2005) butterflies, Italian moths (Battisti *et al.* 2005), and Spanish (Penuelas & Boada 2003), Scandinavian (Kullman 2002) and alpine (Grabherr *et al.* 1994) plant species. In all these cases, climate change has been proposed as an explanation for the altitudinal shift.

The wide variety of species showing uphill shifts in distribution may be because it is often easier to detect altitudinal shifts which can occur over smaller geographic areas than latitudinal shifts. Alternatively, it may be that species appear to be responding more strongly to climate change altitudinally, because a lower dispersal capacity is required to shift uphill. Also within mountainous regions there is usually less urbanisation, leading to less loss of habitat and therefore an increased ability to disperse rapidly into climatically suitable areas.

1.2.3: Factors complicating distribution change

Distribution changes in response to climate change are often complicated by variables such as species' taxonomy and life history, or other, less predictable factors such as unforeseen responses to environmental variables, and interactions between species (Thomas *et al.* 2001; Davies *et al.* 2006). Climate changes may have indirect impacts on species. For example, Anurans within the Costa Rican cloud forest are suffering population crashes, possibly because warmer temperatures have increased their susceptibility to disease and parasites which in turn have benefited from recent warming (Pounds *et al.*

1999; Pounds *et al.* 2006), and this further confounds the likely persistence of local populations as the cloud bank rises and lowland species encroach on their habitat.

In British butterflies, whilst many generalist species are expanding their range northwards in response to climate warming, more sedentary, specialist species are in decline, as the loss and degradation of their habitat, and distance between patches of remaining suitable habitat hinders them from tracking isotherm shifts (Warren *et al.* 2001; Menendez *et al.* 2006). In North Sea fish, those species that have responded most dramatically to climate tend to have faster life cycles and smaller body sizes (Perry *et al.* 2005).

In some cases, the effects of climate on distribution changes have direct economic consequences. For example, changes in land management, alongside climate warming, has caused Barnacle Geese off Norway to use more northerly sites as a migration route, causing conflict with farmers (Prop *et al.* 1998). The birds now use fields as a food source in much greater numbers than they have previously. Further expansion may be expected if there is suitable habitat available to the birds. This example emphasizes how climate change could lead to increased tension between agriculture and nature as species distributions change, a pattern which may be reflected across the world.

1.2.4: Biodiversity change

In some cases, distributional or abundance responses of species to climate change may lead to changes in the entire biodiversity of a region. A good example of this is in Mexico, where ecological niche modelling has predicted large scale changes in the biodiversity of the region as climate warms, based on birds, butterflies and mammals (Peterson *et al.* 2002). In Africa, climatically suitable areas for thousands of plant species may shift location or decrease in size over the 21st Century (McClean *et al.* 2005). In general, historically cool regions are predicted to show increases in species richness with climate warming, but the new assemblages of species are likely to comprise predominantly mobile and generalist species, which are able to respond quickly to climatic changes (Menendez *et al.* 2006).

1.2.5: Adapting *in situ*

As well as the distributional changes already mentioned, species may also respond physiologically or behaviourally to climate change by adapting *in situ* (Davis *et al.* 2005) Depending on how rapid the life cycle of a species is, such adaptation can occur very quickly, for example in the case of bacteria (Bennet *et al.* 1992), or over decades in the case of herbaceous plants, or over centuries or millennia in the case of long-lived tree species (Davis *et al.* 2005). Whilst natural plasticity in the population may produce a temporary change in a population, true adaptation can only occur as a result of permanent changes at the genetic level.

A likely example of natural plasticity allowing a response to climate warming is phenological change, and many studies have already documented changes in phenology occurring over decades (Root *et al.* 2003). However, in some cases, as with distribution changes, the rate of response can lag behind the rate of predicted climate change (Etterson & Shaw 2001). Other examples of a plastic response to environmental pressures can often be seen in insects. . For example, the emergence of dispersive phenotypes in some species at their northern range margins may have resulted in faster colonization of new sites (Thomas *et al.* 2001; Simmons & Thomas 2004). In this case the butterfly species have increased the habitat and host plant range they can utilise, whilst the bush cricket species have increased the proportion of long-winged individuals. More long-term adaptation may occur because of fundamental genetic changes at the population level. There has been extensive study of changes in genetic diversity following post-glacial range expansion, and currently genetic markers can be used to identify past shifts in distribution (Hewitt 1999) and effects of habitat fragmentation (Hill *et al.* 2006).

1.3: Changes in phenology

As a result of climate change, spring is occurring earlier in the year and autumn later (Sparks & Menzel 2002), allowing for a longer growing season (Menzel & Fabian 1999). As a response to this, birds, butterflies and plants are shifting their phenology earlier in the year (Penualas & Flella 2001; Parmesan & Yohe 2003; Root *et al.* 2003; Root *et al.* 2005). The factor used to measure phenology in such species is usually the timing of reproduction, such as egg-laying in birds, or flowering in plants, but other measures such as arrival in the country of migratory birds, or first appearance by adult butterflies, may also be used (Table 1.1). In a meta-analysis of previous studies, 87% of species showed trends towards spring advancement (Parmesan & Yohe 2003). On average across species, phenology has advanced 5.1 days over the last 50 years (Root *et al.* 2003), with events occurring in spring showing the greatest advancement.

Within British plants, average first flowering has advanced by 4.5 days (Fitter & Fitter 2002). Flowering time has been shown to be highly dependent on temperature, but the wide variation between species implies that responses to climate warming may be difficult to predict (Fitter *et al.* 1995). The consequences for communities may therefore be both dramatic and unforeseen, as some species within the food chain respond at different rates to others. Certain studies have already demonstrated how climate change may alter trophic interactions (Harrington *et al.* 1999). For example, an increase in temperature in Britain has led to bud burst in oaks and the development of winter moth caterpillars occurring earlier, but a similar number of days earlier. In spite of this, survival of tit (*Parus major* and *Parus caeruleus*) hatchlings has been reduced because the caterpillars are at a later stage of their life cycle when the young tits are born (Buse *et al.* 1999; Visser & Holleman 2001).

1.4: Changes in abundance of species

Changes in abundance have been documented for a wide variety of species globally, although not as widely as distributional changes (Table 1.1). In most cases species are declining, and very often these declines can be directly related to habitat change or other anthropogenic effects. It is more difficult to relate declines directly to climate change, partly because responses tend to be less rapid or less obvious, partly because the mechanisms leading to such declines are still an area of active study, and partly because the effect of habitat loss tends to obscure any effect of climate change. However, over the long-term, climate change may lead to more drastic declines than habitat loss (Thomas *et al.* 2004).

1.4.1: Changes in abundance as a response to climate change

The most commonly predicted response of species to climate change is that as temperatures increase, warm-loving species such as tropical or warm-temperate species will increase in abundance, whereas species from colder areas such as boreo-montane or arctic species will decrease in abundance, and in the majority (81%) of documented cases this has occurred (Parmesan & Yohe 2003). For example, in the eastern North Atlantic and European shelf seas, numbers of warm water copepod species are increasing in comparison with cold water species (Beaugrand *et al.* 2002). In recent years in the Netherlands, warm-temperate and sub-tropical species of lichen have increased whereas boreo-montane and arctic-alpine species have decreased (van Hark *et al.* 2002).

However, not all species have responded in this way. In the UK, the opposite is occurring, with northern moth species increasing and southern moth species decreasing in abundance (Conrad *et al.* 2004). However, even in this example, the authors suggest that climate change may play a role in the observed changes. Species that overwinter as adults are increasing in abundance, suggesting milder winters are favouring these moths, whereas species overwintering as eggs are decreasing, suggesting that hardiness and resistance to pathogens is reduced by milder winters (Conrad *et al.* 2004). This suggests that in some cases, species' ecological traits rather than distributional extent may be a better predictor of response to climate change.

1.5: Sensitivity of species to climate change

Across species, distribution limits often match climatic features, such as maximum or minimum temperatures (Root 1988). However, it is likely that some species will be more sensitive to change in these climatic features than other species. It has long been recognised that insects are particularly sensitive to temperature (Uvarov 1931), and it is therefore unsurprising that many studies have detected a distributional response to changing climate in this group. For example, larval chironomid remains preserved in lake sediments have been used to determine past climate change because they are known to be very sensitive to temperature (Brooks & Birks 2001).

Within insects, a strong response to climate change has been detected in the Lepidoptera. The northern limits of most European butterflies are closely correlated with summer isotherms (Turner *et al.* 1987), whilst abundance is strongly associated with summer temperature, monthly rainfall (Roy *et al.* 2001) and yearly climate (Morecroft *et al.* 2002), so predictably, the period of recent climate change has caused many species, particularly mobile generalists, to shift their distributions, tracking the movement of the isotherm (Hill *et al.* 2002). Moth species (Conrad *et al.* 2004) and bush crickets (Thomas *et al.* 2001; Simmons & Thomas 2004) have also been shown to be sensitive to temperature change in recent years. It can be predicted that, within insects, those which are most constrained in their distribution by climatic variables will be the most sensitive to global warming.

This hypothesis can be extended to other species, such as small mammals, where energetic constraints limit their distribution (Humphries *et al.* 2002). Such climatic limitations may also apply to small birds, reptiles and amphibians, and many marine species. Therefore changing distributions might be expected to occur in a wide variety of taxonomic groups where species are highly mobile or strongly limited by climate (Hughes 2000).

Table 1.1: Key examples of the effect of climate change on different species groups.

	Species	**Response**	**Reference**
Latitudinal shift	Butterflies	Polewards	Warren *et al.* 2001
	Butterflies	Polewards	Parmesan *et al.* 1999
	Butterflies	Polewards	Hill *et al.* 2002
	Moths	Polewards	Battisti *et al.* 2005
	Birds	Polewards	Thomas & Lennon 1999
Altitudinal shift	Cloud Forest biome	Uphill	Pounds *et al.* 1999
	Alpine plants	Uphill	Grabherr *et al.* 1994
	Butterflies	Uphill	Konvicka *et al.* 2003
	Butterflies	Uphill	Wilson *et al.* 2005
	Moths	Uphill	Battisti *et al.* 2005
	Plants	Uphill	Penuelas & Boada 2003
	Plants	Uphill	Kullman 2002
Phenology	Plants	Advanced	Fitter & Fitter 2002
	Butterflies	Advanced	Roy & Sparks 2000
	Birds	Advanced	Crick & Sparks 1999
Abundance Change	Warm-water copepods	Increasing	Beaugrand *et al.* 2002
	Boreo-montane & arctic-alpine lichens	Decreasing	van Hark *et al.* 2002
	Northern moths	Increasing	Conrad *et al.* 2004

1.6: Response to climate change: limiting factors

The two most important limiting factors for a species in terms of shifting its distribution are habitat availability and dispersal ability. For species which are strongly limited by these factors, the consequences for their survival could be severe.

1.6.1: Dispersal ability

Dispersal ability is important for all species in determining colonisation of new areas. However, the rapid rate of recent climate change favours those species with particularly high dispersal ability. In plants, it has been noted that seed regenerating species in the Swedish Scandes have tracked climate more rapidly than vegetative species (Kullman 2002). This pattern may be reflected in plant species globally. In some butterflies and bush crickets, the evolution of increased dispersal ability in populations at range margins may have allowed more rapid colonisation at northern range margins (Hill *et al.* 1999b; Thomas *et al.* 2001). Similarly, changes in larval host plant usage may have facilitated range expansion of some species, for example comma and brown argus (Asher *et al.* 2001).

1.6.2: Habitat availability

Where habitat is unavailable, or patches of habitat have become too fragmented (for example, by urbanisation or agricultural improvement), species may be unable to track shifts in isotherms. This problem will be most severe for species which have poor dispersal ability. For example, many European forest plant species are unable to colonize new sites at their northern range margin in fragmented habitats, and many more have very low dispersal and migration rates (Honnay *et al.* 2002). These species may be unable to track climate change even if habitat corridors are maintained. In other cases, habitat corridors have been proven to be very important in dispersal (Levey *et al.* 2005).

Within butterflies, this problem has received much attention. It has been noted that for many species, and particularly sedentary specialist species, habitat patches are too isolated for range shifts to occur (Warren *et al.* 2001; Hill *et al.* 2002). Even for more generalist species that are shifting northwards, habitat availability affects the rate of expansion: the speckled wood butterfly is absent in areas where models predict it should occur, and this is probably due to reduced expansion rates in areas with fragmented habitat (Hill *et al.* 1999b). This suggests that even some generalist species may lag behind climate changes in highly fragmented landscapes.

In cases where species are unable to track climate change at their northern margins due to loss of habitat or low dispersal ability, encroachment at their southern range margin from other expanding species together with continued climate warming and habitat loss due to urbanisation may mean that regional or global extinction becomes inevitable in the long term. Faster rates of climate change are more likely to cause extinctions, as greater climate change raises the threshold of habitat availability above which a population can persist (Travis 2003).

1.7: Mechanisms behind responses to climate change

1.7.1: Temperature requirements and thermoregulation

Many invertebrates, especially in temperate regions, have their activity levels limited by air temperature or solar radiation (Bergman *et al.* 1996). However, over the course of evolution some species' life histories have become modified in order to persist in areas which would otherwise be climatically unsuitable. These complicated mechanisms need to be understood as fully as possible if distribution changes with a warming climate are to be analysed or predicted successfully.

In a study of the temperature requirements of four British butterfly species, the most northerly distributed species was able to survive in the lowest temperatures, but it still performed better (for mortality, pupal weight and relative growth rate) at high temperatures (Bryant *et al.* 1997). This may help to explain some of the conflicting results of previous studies, where some northern species appear to be doing well under increasing temperatures whilst others appear to be in decline. Species' taxonomy and evolutionary history may mean the responses of species to climate change are very variable.

Other studies have found that invertebrates have a variety of ways in which they can thermoregulate to some degree. For example, lepidopteran larvae can alter their temperature by adjusting orientation, convective heat loss, and exploiting thermal heterogeneity within their environment (Weiss *et al.* 1988). In some species, adults increase fecundity by selecting host plants with more favourable micro-climates for oviposition (Davies *et al.* 2006). This may allow them to persist further north than would otherwise be possible (Bryant *et al.* 2002).

1.7.2: Acclimation to long-term changes in temperature

Some species or populations may become acclimated to higher or lower temperatures over time, and therefore may differ in their response to climate change compared with other species or populations. This can be a complicating factor when examining the response of different species or populations to climate change. For example, a short-term change in temperature can have more effect on a cold-acclimated plant species than a warm acclimated plant species (Tjoelker *et al.* 2001). Species can also become acclimated to other environmental factors such as drought (Bryla *et al.* 2001) or light availability (Atkin *et al.* 2000), and as climate warming will often change these factors as well as temperature, the response of populations or species may be even more variable. Weather is predicted to become more variable in many parts of the world as climate change accelerates, but whilst some species may suffer from such variability, other species have been shown to acclimate to new weather conditions within a few days (Covey-Crump 2002), and such taxa may show a different response to climate warming.

The majority of studies investigating acclimation focus on plants. There are examples of acclimation in a variety of animals including butterflies (Fischer *et al.* 2003), Diptera (Miyazaki et al. 2006), and mammals (Shimada *et al.* 2006), and it is likely that many of the species investigated in this study will be capable of some degree of acclimation to environmental pressures. Where a strong response to climate change (either distribution change, abundance change or phenological change) is not detected in a species or group, it is possible that the species in question has so far been able to acclimate to climate changes. In such situations, a detectable response to climate change may occur as the rate of warming accelerates.

1.7.3: Natural fluctuations of populations

The abundance of individuals within a population varies naturally, and it is desirable to understand the drivers of such variability in order to draw robust conclusions from data. Differing rates of mortality and fecundity, stochastic random natural events, and flux between metapopulations, all lead to natural fluctuations in populations of species. Fluctuations in abundance of nearby populations are often very similar but correlations gradually break down over a few hundred kilometres (Pollard 1991; Hanski & Woiwod 1993; Sutcliffe *et al.* 1996). Furthermore, resource-limited populations with low potential growth rates are likely to fluctuate widely (Pollard & Rothery 1994), and this may be why butterfly populations fluctuate with increased amplitude towards the northern edges of their ranges (Thomas *et al.* 1994).

It is necessary to understand these stochastic fluctuations of populations, as well as the ecological factors driving overall changes in populations, in order to understand the way species respond to climate change at their range margins. However, with data currently available it is often very difficult to extract overall signals of change from the 'noise' of natural fluctuations. Many more species may be shifting their distributions than is currently known, simply because not enough data have been gathered to detect statistically significant trends within 'normal' levels of variation.

1.8: The complicated nature of nature

Many problems can arise when attempting to link climate fluctuations with ecology (Stenseth *et al.* 2002) and in general, species' responses to climate warming may be difficult to predict (Fitter *et al.* 1995). When examining the effect of climate on biodiversity, it was found that the biomes which are most affected depends upon how the various factors interact (Sala *et al.* 2000). An example of such a problematic factor is the feedback loops of plants and carbon dioxide concentrations (Woodward *et al.* 1998). This is an area which is still receiving a great deal of study and is not fully understood. For example, previous research has established that as carbon dioxide concentrations increase, the stomatal conductance of vegetation decreases, causing a warming effect. However, at a global scale, this positive feedback loop can become a negative feedback loop as vegetation structure changes (Woodward *et al.* 1998). Furthermore, the effect of vegetation structure on climate warming may be dependent on latitude or geographic region.

Computer models may provide a way for us to predict possible changes, but ecological interactions and global climate are so complicated and variable that it is often very difficult to know which factors to include. It has been argued that whilst climate-envelope models which fit species distributions to climate variable can be useful for making predictions, species' dispersal ability and interactions with other species need to be incorporated for reliable models (Davis *et al.* 1998). It is therefore an essential part of our understanding to study empirical responses to climate change as they have occurred in the field, as a complementary technique to modelling.

1.9: Data and methods

1.9.1: Available data and recording methods

Britain has extensive fine-scale and long-term distribution data for a wide range of taxa and thus is probably the only region in the world where it is possible to assess whether comparable range margin shifts are taking place in many different groups. The Biological Records Centre at CEH Monks Wood, Cambridgeshire, holds a large number of records for a wide variety of taxonomic groups, many of which have never been analysed previously in terms of shifts in range.

As well as holding distributional data for UK birds, the British Trust for Ornithology holds detailed abundance data on birds from its Common Bird Census, whilst the Rothamsted Insect Survey has collected abundance data for moths for many decades. The Butterfly Monitoring Scheme has collected detailed abundance data for butterflies from weekly transects walked over a period of many years. Whilst these abundance datasets have been analysed in the past, the recording methods and particularly the form of analysis has varied, and so until now there have been no attempts to compare across taxa.

1.9.2: Choice of basic methods

Throughtout this study, techniques used to analyse data are basic and simple to apply across different taxonomic groups. The primary methodology examines the latitudinal and altitudinal shift (in kilometres and metres respectively) of different species groups over similar time periods.

The use of climate envelopes is a common method currently used to look at past species distributions and to predict future distributions. This approach was considered for this study, but was found unsuitable for several reasons, and hence the more simple approach was decided upon. Climate envelopes only work effectively where a good coverage of data is available for a wide area; whilst the species chosen in this study were the most well recorded in the UK, for many groups recording did not cover a sufficient area for climate envelope modelling to be effective. Secondly, climate envelopes can be easily confounded by montane areas (or other isolated areas), which are climatically suitable, but may be too geographically isolated for a species to occupy. Finally, this study was intended to produce results that would be easy to interpret, by using as little complex modelling or analysis as possible. Interpretation of climate envelope results can sometimes be quite difficult, and comparison of results across hugely variable taxonomic groups could prove extremely complicated.

1.10: Thesis: aims, layout and conclusions

Many studies from across the world strongly suggest widespread responses of species to climate change, but the methods and locations are heterogeneous, and most of these data come from a relatively small number of terrestrial taxa. Furthermore, studies vary in terms of whether they consider distribution, abundance or phenology changes. The first main goal of this thesis is to evaluate, for one region, whether distributional responses to climate change are widespread among taxa, when data are analysed in a consistent way. The second major goal is to assess, for selected taxa, whether different measures of responses to climate changes are related to one another.

The first half of this thesis deals specifically with changes in distribution as a result of climate change. In Chapter 2, the Odonata are analysed to assess whether insects with aquatic larval stages have shifted polewards during a period of climate warming. This study also provides a forum to test and develop a basic analysis, which is then applied to a wider range of less well-studied taxonomic groups in Chapter 3. It has been suggested that well-studied groups such as British butterflies may be a good indicator group for the distributional changes occurring in other taxonomic groups (Thomas *et al.* 2004), but since different analytical methods are usually applied to different groups, direct comparison can be difficult. The primary aim of Chapters 3 and 4 is thus to apply a standard methodology to a variety of taxonomic groups, to determine how their distributions are changing and how comparable these species are with previously well-studied groups such as butterflies. Chapter 3 considers changes at species' northern range boundaries. Chapter 4 completes this large analysis by comparing distributional changes of southern species with those occurring in northern species.

In the second half of the thesis, other ecological responses to climate which may be occurring at the population level are examined. Phenological change is analysed for three well-studied groups in Chapter 5, and the results are compared with results from distributional changes from previous chapters. In Chapter 6, I focus on northerly-distributed species, and analyse changes in abundance. Again, the results are discussed in relation to results from previous chapters. The final Chapter 7 discusses distributional changes, phenological changes and abundance changes together, and attempts to clarify the possible mechanisms behind the observed changes.

Specific aims:

- To design an analysis of distribution change that can be applied across taxonomic groups (groups are defined on page 53).
- To determine whether less well-studied taxonomic groups are showing the same degree of northward shift as better-studied groups.
- To determine whether northern species are retracting at their southern range margin to the same degree that southern species are expanding at their northern range margin.
- To determine whether phenological change is correlated with distributional change and how these responses to climate change might interact.
- To design an analysis of abundance change that can be applied across taxonomic groups.
- To determine if abundances of northern species are decreasing in abundance compared with ubiquitous species, and whether these changes can be related to climate change and to distributional changes.

Chapter 2

Design of analysis for quantifying distribution shifts, using Odonata as a test group.

2.1: Abstract

Many species are predicted to shift their ranges to higher latitudes and altitudes in response to climate warming. In order to study such changes across a range of taxa with different ecologies and recorded at different intensities, a simple method must first be developed. Odonata is a suitable group with which to design this general analytical approach because they contain both scarce and common species and have been comparatively well-recorded over time. This chapter describes the process by which a methodology was developed, and presents evidence for 37 species of non-migratory British dragonflies and damselflies shifting northwards at their range margins over the past 40 years, seemingly as a result of climate change. This response by an exemplar group of insects associated with fresh water parallels polewards range changes observed in terrestrial invertebrates and other taxa.

2.2: Introduction

2.2.1: Previous studies of distribution change in aquatic insects

Amongst insects, some European butterfly species have shifted their ranges northwards (Parmesan *et al.* 1999; Warren *et al.* 2001), and it is expected that other winged insect species will show a similar response to climate change. However, few studies have focused on other groups of insects, and there is little information available on insects that lay their eggs in water, such as mosquitoes, chironomids and dragonflies, although it is believed that several southern Odonata species are expanding northwards in Britain (Brooks 2001).

2.2.2: Possible responses of aquatic insects to climate change

It is important to expand our knowledge about how aquatic insects are responding to climate change, as this group may respond differently to terrestrial invertebrates. In other insect groups, it has been hypothesized that the larval stages may be the most sensitive to climatic variation (Bryant *et al.* 2002). If this is the case, it is possible that species with aquatic larvae may be less buffered than terrestrial species against any positive or detrimental effects of climate warming, because selection of particular microclimates is difficult in water. Therefore aquatic species may be particularly sensitive to climate warming compared with terrestrial insect groups.

Sub-fossil remains of chironomids have been used to re-construct glacial climate changes (Brooks & Birks 2001) because they can be collected from lake sediments in large enough numbers for analysis, and because they respond quite rapidly to climate change over geological time. However, due to a lack of modern distribution data, it is not known whether chironomids have responded rapidly to recent changes in temperature. In contrast, a relatively large amount of data does exist on modern distributions of Odonata, particularly in Europe, and this makes the Odonata an ideal group for analysing range shifts in an aquatic group of insects.

2.2.3: Current documented distribution changes in Odonata

There is some evidence that dragonflies are being recorded at higher latitudes and altitudes (Ott 2001), but data are lacking and conflicting. In Belgium, most species have increased in range size over recent years (De Knijf *et al.* 2001), whereas, studies in Switzerland suggest that most species are declining or remaining stable (Gonseth & Monnerat 2001). These differences may arise due to contrasting methodologies and selection of study species. This is an area which would benefit from further investigation, and this is one of the primary reasons I chose to focus on the Odonata.

2.2.4: Design of a broad distribution analysis

When designing an analysis which can calculate range margin shifts across many taxonomic groups, there are several key points which must be addressed. Firstly, species must be selected according to basic rules which can be applied across groups. Secondly, the 'range margin' must be defined clearly. Thirdly, the shift of the range margin must be calculated using an appropriate scale (grid cell size). In order to design an effective analysis, I focused on one taxonomic group, and investigated in detail how variation in these three aspects could affect my results.

i) Definition of the range margin

Even within a single taxonomic group, where recording has been consistent for all species through time, there can be great variation in the spread of data at range margins. For example, Figure 2.1 shows four typical Odonate species from the Biological Records Centre (BRC) database. Notice that *Aeshna cyanea* and *Brachytron pratense* appear to be much more sparsely distributed throughout their range, and particularly in the north, compared with *Aeshna grandis* and *Aeshna mixta*, even after recorder effort 'filters' have been applied (see Methods). It is much more difficult to decide by eye where the range margin is located for *Aeshna cyanea* and *Brachytron pratense* than for *Aeshna grandis* and *Aeshna mixta*.

Most previous studies define the 'range margin' of a species by selecting a certain number of the most northerly/southerly 10km grid squares (Parmesan *et al.* 1999). However, there is variation between studies, which can make comparison of results difficult. For example, within many distribution datasets, other data are associated with each species record which is often used as criteria for including or excluding that data point. Thomas & Lennon (1999) chose to only include records where birds were confirmed to be (or probably) breeding. As another example, for some records held in the BRC database, the exact date of recording is not known, but the date that record was published is known, and often it is considered wise to exclude these data from analysis. In most cases, the exact way in which records are selected for analysis and range margins are defined is only a matter of opinion, and one method is not necessarily any more 'correct' than another. However, this variation between studies can make direct comparisons of results very difficult.

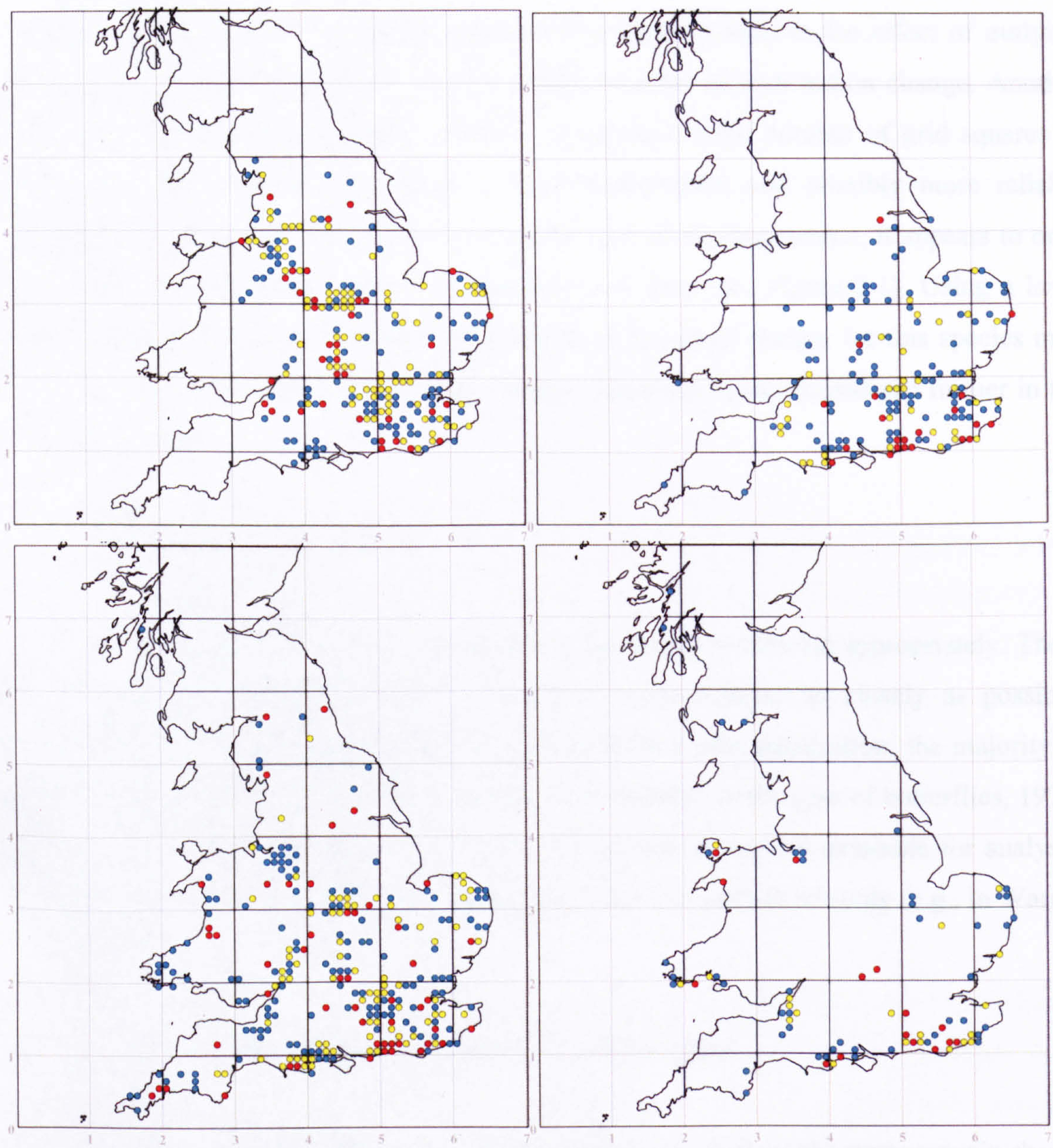

Figure 2.1: Distribution maps for A) *Aeshna grandis*, B) *Aeshna mixta*, C) *Aeshna cyanea*, D) *Brachytron pratense*. Data has been filtered for recorder effort (see Methods). Records from 1960-1970 (red), 1985-1995 (blue), and both time periods (purple) are shown.

BRC holds long-term and fine-scale data for a wide variety of species. One of the best-recorded groups within this database is the Odonata, for which many species have been recorded consistently across time and geographically. Using these data for British dragonflies and damselflies, I assess the effect of range margin definition on results. For example, if only a small number of grid squares are considered to make up the range margin of *Brachytron pratense*, it may appear to have shifted quite far northwards over time (see Figure 2.1). In this case, using the median rather than the mean to calculate the average latitude of the range margin in both time periods reduces the effect of outlying populations, and probably gives a more reliable estimate of distribution change. Another solution in the case of *Brachytron pratense* is to use a large number of grid squares to define the range margin, leading to a more conservative and possibly more reliable estimate of range margin shift. However, in the case of *Aeshna cyanea*, it appears to only have shifted a very small distance northwards over time (see Figure 2.1). Using a large number of grid squares to estimate the position of the range margin for this species may fail to pick up such a small distribution change. These issues are considered further in the Methods section.

ii) Selection of time periods

Time periods over which change is assessed must be selected appropriately. These time periods should reflect periods of rapid climatic changes as closely as possible. However, as most distribution datasets are collected for atlas publication, the majority of data often falls into two distinct time periods, for example, in the case of butterflies, 1970-1982 and 1995-1999. In order to maximize the number of records available for analysis, these time periods will usually form the basis for the time periods of study (e.g., in Warren *et al.* 2001).

iii) Calculation of latitudinal shift and recorder effort

Finally, the calculation used to produce figures for shifts at the range margin should be simple to apply and appropriate. Whilst more complicated methods of calculating latitudinal shift may give more reliable estimates for individual species or groups, when designing an analysis that can be applied across groups, it is important to keep it simple. Another benefit of simple design is that the results are more intuitive and therefore easier to interpret.

Correlations with changes in recorder effort should be avoided where possible. Within all long-term distributional datasets, there will be some change in recorder effort over time. Whilst many studies have attempted to account for recorder effort in various ways, no perfect method has yet been designed. For example, Thomas *et al.* (2001) used a method of subsampling data, whilst Telfer *et al.* (2002) used quite complicated mathematical equations to produce a reliable estimate of change in range size for British plants. Again, when designing an analysis which can be applied across a wide range of taxonomic groups, simpler methods of accounting for recorder effort will produce more intuitive results, and will be less likely to produce unexpected results for any species with unusual patterns of recording.

2.2.5: General aims of this chapter

i) Design of a general analysis

The fundamental aim of this chapter is to design an analysis of distribution change that can be easily applied to a wide range of taxonomic groups in Chapter 3. The analysis should produce results which are relatively easy to interpret, and can be compared directly across both well-recorded and less well-recorded species. The analysis should be designed with reference to previous studies of distribution change, and with the BRC dataset in mind (which forms the main source of data in Chapter 3).

ii) Distribution changes in Odonata

For such a relatively well-recorded group, studies of the effect of climate change on the distributions of Odonata are scarce. The secondary aim of this chapter is to determine whether or not Odonata have shifted their distributions northwards over the period of recent climate warming. Any response seen within the Odonata can help to further inform our predictions of the response of aquatic insects in general.

2.3: Methods

2.3.1: The BRC Odonata dataset, and selection of species

Out of 54 species listed in the Atlas of the dragonflies of Britain and Ireland (Merritt *et al.* 1996), 52 species had records in the BRC database. Information about extinctions, migrants, and other life history traits was obtained from the Atlas, and selected species were checked by an expert (Steve Brooks, Natural History Museum). Four species were excluded because they were only found in the Channel Islands, eight were excluded because they were migratory, and a further three species were excluded because they had only been recorded in five or fewer grid squares and were therefore considered too rare for analysis. All remaining 37 non-migratory British Odonata species were included in the study (Table 2.2). Classification of northern and southern range margins in Britain were established using the European distribution atlas (Askew 1988). Four species have northern ranges (*Aeshna caerulea, Coenagrion hastulatum, Somatochlora arctica, Leucorrhinia dubia*), and reach their southern range limits in Britain. 24 species have southern ranges and reach their northern range limits in Britain. Nine species are found throughout Britain and do not reach a range limit to their European range in Great Britain ('ubiquitous' species). However, the ubiquitous species are generally more abundant and widespread in the south than in the north, and so we present data on distributional changes at the northern-most parts of their British ranges. See Figure 2.2 for examples of typical southern, ubiquitous and northern distributions.

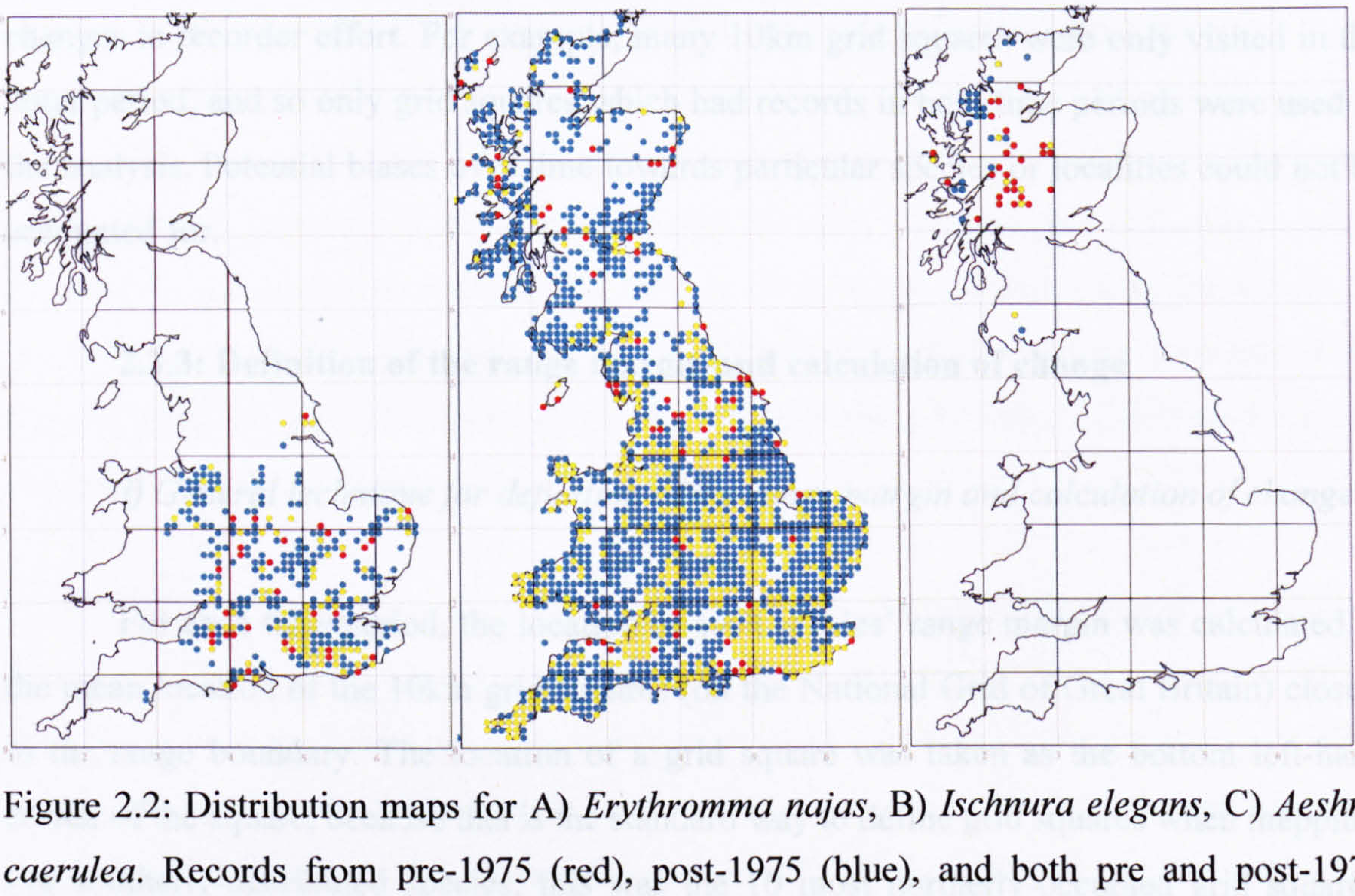

Figure 2.2: Distribution maps for A) *Erythromma najas*, B) *Ischnura elegans*, C) *Aeshna caerulea*. Records from pre-1975 (red), post-1975 (blue), and both pre and post-1975 (purple) are shown. Data has not been filtered for recorder effort.

2.3.2: Selection of time periods and accounting for recorder effort

Odonata distributions in Britain were obtained from data compiled by the Biological Records Centre (CEH Monks Wood and The Dragonfly Society of the British Isles). The records were split into two 10-year time periods (1960-1970 and 1985-1995), which coincide with a period of rapid climate warming both globally (IPCC 2001) and in Britain (CIP 2004). Between the time periods chosen for study (1960-1970 and 1985-1995), temperatures in Britain increased by 0.44°C (using Central England Temperature data), which corresponds with a shift in isotherms of approximately 66km (calculated using data derived from Parmesan *et al.* (1999)). These specific time periods were chosen to maximize the number of records available for analysis whilst maintaining a substantial (14 year) gap in between, over which shifts in distribution could occur. Analyses were based on records of species' presence/absence at a 10km Ordinance Survey grid resolution. Determining changes in range over time from these records may be confounded by changes in recorder effort. For example, many 10km grid squares were only visited in the latter period, and so only grid squares which had records in both time periods were used in the analysis. Potential biases over time towards particular species or localities could not be accounted for.

2.3.3: Definition of the range margin and calculation of change

i) General technique for definition of the range margin and calculation of change

For each time period, the location of each species' range margin was calculated as the mean location of the 10km grid squares (on the National Grid of Great Britain) closest to the range boundary. The location of a grid square was taken as the bottom left-hand corner of the square, because this is the standard way to define grid squares when mapping. For southerly-distributed species, this was the 10 most northerly-occupied grid squares. For northerly-distributed species this was the 10 most southerly-occupied grid squares. The shift of the range margin was calculated as the difference in these mean locations between 1985-1995 and 1960-1970. The range sizes of species in the two time periods were determined as the number of 10km grid squares with one or more individuals recorded. The change in range size was calculated as the difference in the number of occupied grid squares between the two time periods.

ii) Presentation of results and statistical tests

Data for ubiquitous species are presented in Table 2.2 and Figures 2.4 and 2.5 for comparison, but because these species do not reach their range limits in Britain, they were not included in statistical analysis comparing northern and southern species. Significant differences between change in range size and latitudinal shift of northern and southern species was assessed by Mann-Whitney U-test and adjusted for tied values.

iii) Suitability of general technique – how to define the range margin

The number of marginal grid squares used to estimate the latitude of the range margin can have an effect on the final result. For example, in most cases, using only 10 grid squares picks up small changes more effectively than using 40 grid squares, because if as many as 40 grid squares are used to calculate an average figure, only a relatively large northward shift across the whole range will be reflected as large shift in the overall average figure. However, using only 10 grid squares can give excessively large values of change where outlying populations influence the result. Equally, there are pros and cons to using the mean or the median to calculate the latitude of the range margin. Using the mean will usually give a more reliable estimate of the latitude, but where outlying populations are present, using the median reduces the effect of these in the calculation. These problems are presented graphically in Figure 2.3.

Figure 2.3 shows for example species how using different numbers of grid squares or mean / median to estimate the shift in the range margin can affect the result. In Figure 2.3A the species has been well-recorded throughout its range, and the margin is quite clear to the eye, with no outlying populations. In this case, using 10 or 40 marginal records makes little difference to the estimated range shift. In Figure 2.3B, an outlying population has been recorded, but records generally become less frequent towards the range margin anyway. Although the margin has clearly shifted northwards to quite a large degree, using 40 grid squares gives a much more conservative estimate of range shift because the impact of the outlier population is weakened. In Figure 2.3C, several recently recorded outlying populations skew the mean estimated range shift quite dramatically, and it could be argued that this gives an exaggerated result. Whilst there can be no justification for removing perfectly valid yet outlying populations from the analysis, it may be the case that these populations do not represent a shift of the entire range margin. In this case, using the median instead of the mean to calculate the latitude of the range margin in each time period reduces the effect of the outlying populations, giving an estimate of change that is less sensitive to the location of specific populations. On the other hand, rare long-distance colonisation events have a critical effect on range expansions (they may subsequently act as origins for expansion in the north), so it may be undesirable to down-play their importance by use of the median.

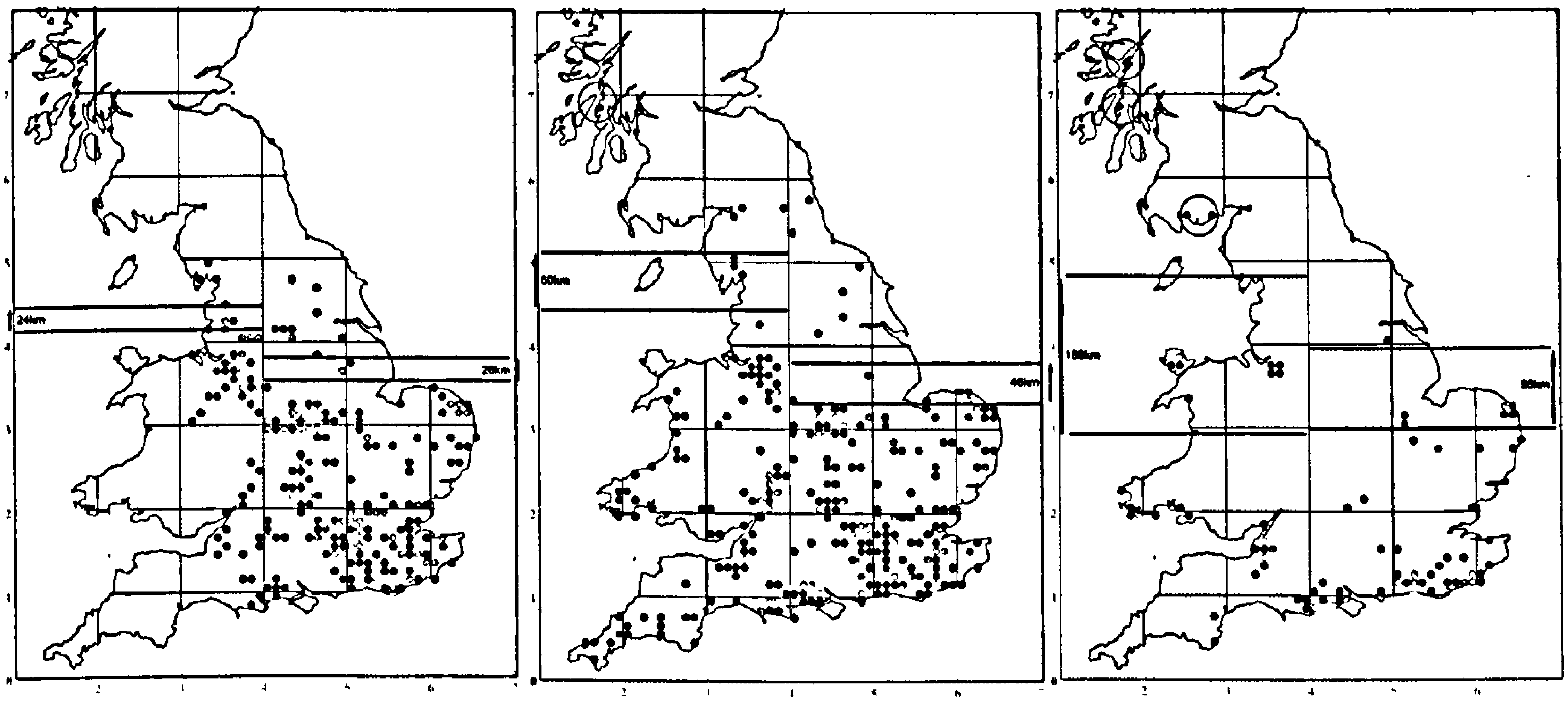

Figure 2.3: The effect on estimated range margin shift of using different methods to define the range margin. Mean estimated range shifts are shown allocating 10 (dark blue), and 40 grid squares (bright pink), and median of 10 grid squares (bright green), to define the range margin for A) *Aeshna grandis*, B) *Aeshna cyanea*, C) *Brachytron pratense*. Data have been filtered for recorder effort (see above). Records from 1960-1970 (red), 1985-1995 (blue), and both time periods (purple) are shown. Records of interest are circled in orange.

In order to determine quantitatively the sensitivity of the analysis to defining range margin as the mean of 10 marginal squares, the analysis was repeated using the mean allocation of 20, 30 and 40 grid squares to define the range margin. The results are shown in Table 2.1. This shows that it does not make much difference to the overall result how many grid squares are used to calculate the range margin, but using larger numbers of grid squares can make subtle changes at the range margin of southern species more difficult to detect. Given the robust nature of this technique (and given the fact that when using more than 10 squares to define the range margin some species must be excluded because they are too rare) it was decided that using the mean of 10 grid squares to calculate the latitude of the range margin was most effective for a range of different species. All results henceforth refer to this method of calculation.

Table 2.1: The effect on estimated range margin shift of using different numbers of grid squares to define the range margin. Mean estimated range shifts are shown allocating 10, 20, 30 and 40 grid squares to define the range margin. Results are presented for southern, northern and ubiquitous Odonata species, and for all species in total.

	Mean range shift (km)			
No. of grid squares	**Southern spp.**	**Ubiquitous spp.**	**Northern spp.**	**All spp.**
10	88	51	44	74
20	87	89	40	83
30	82	111	40	84
40	73	118	40	80

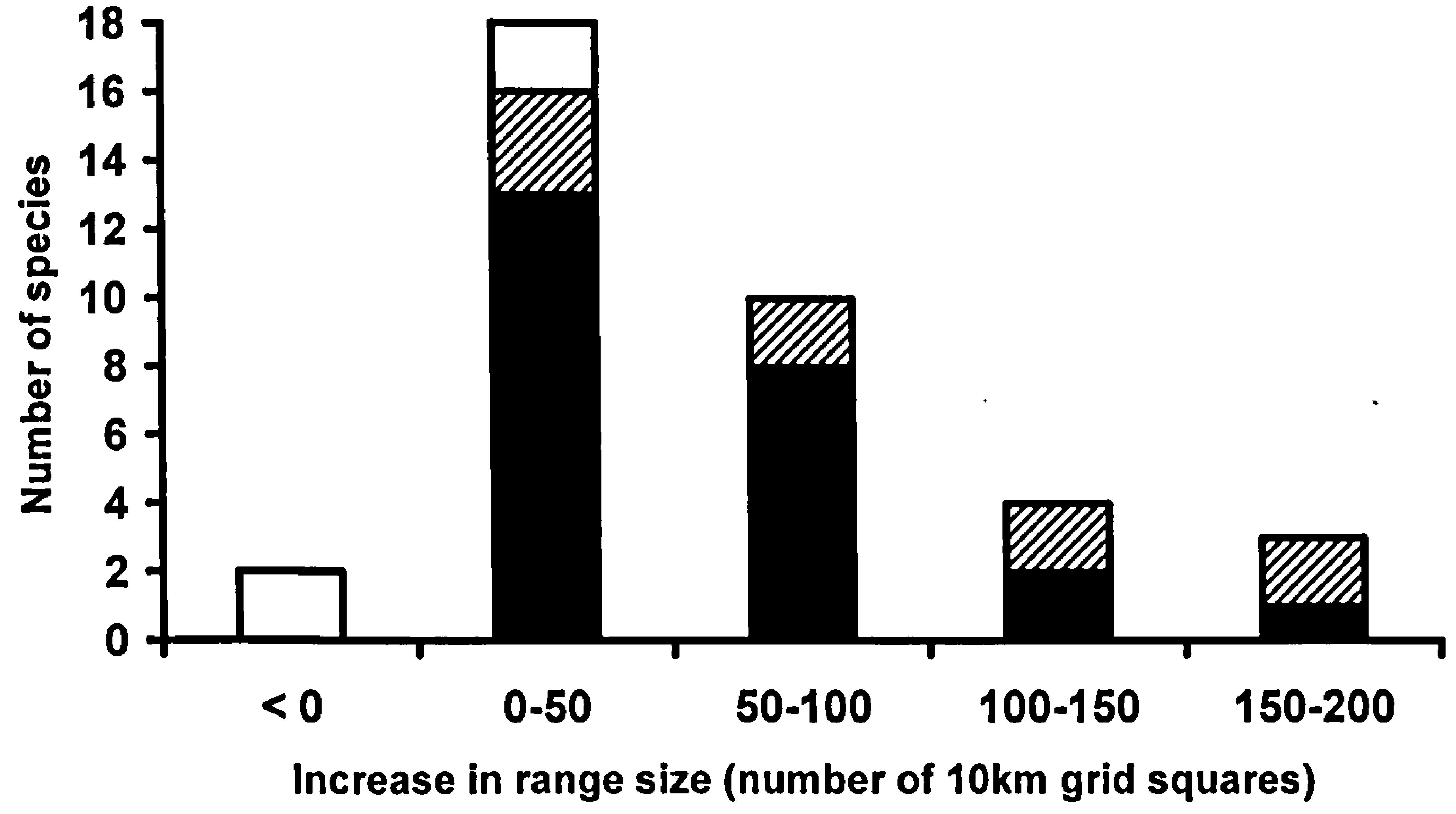

Figure 2.4: Change in range size in British Odonata between 1960-1970 and 1985-1995. Change in range size = number of occupied grid squares in first time period – number of occupied grid squares in second time period (after filtering for recorder effort). Northern species (white), ubiquitous species (hatched) and southern species (black) are shown. n = 37. < 0 indicates a reduction in range size.

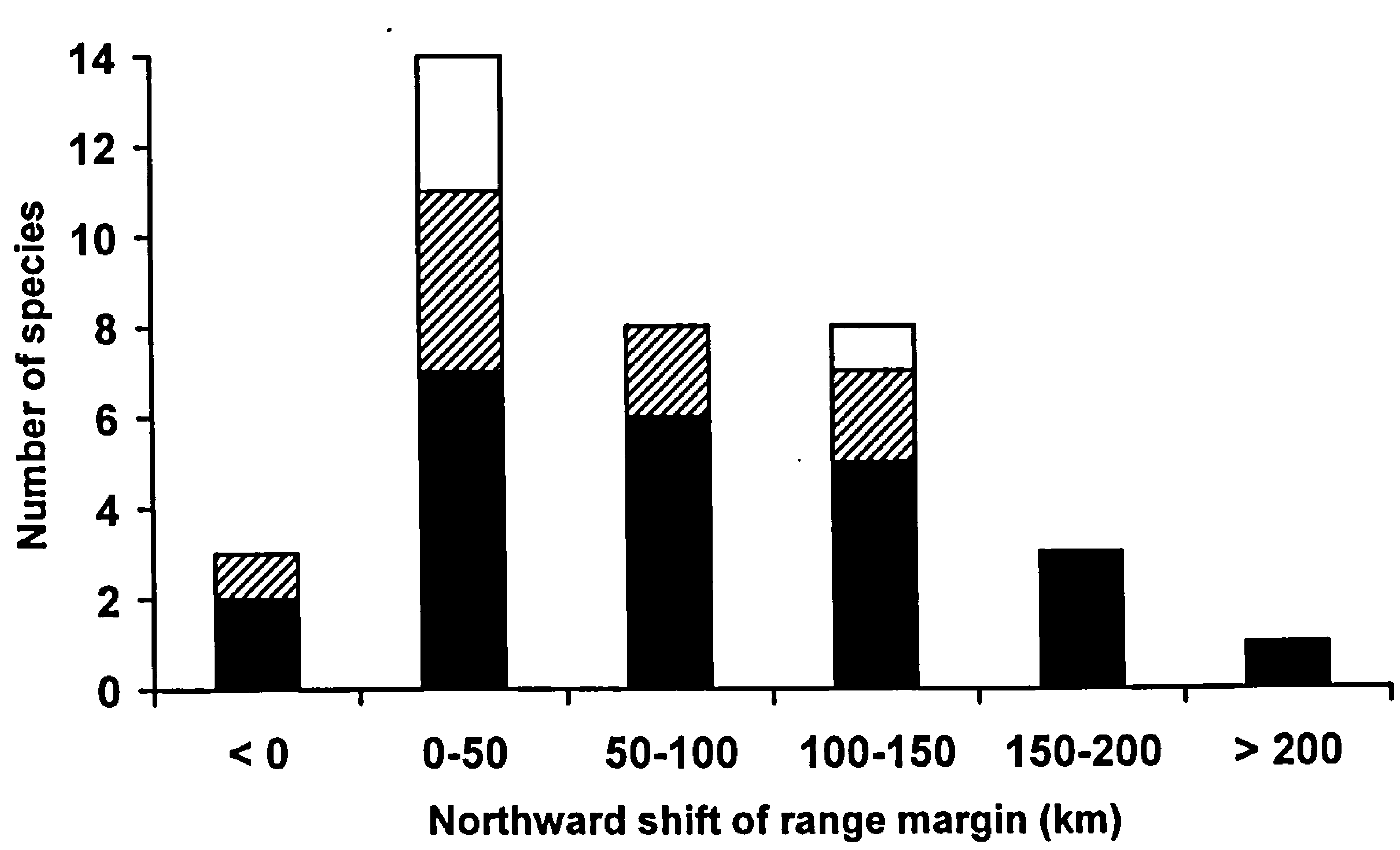

Figure 2.5: Northward shift of range margins of British Odonata between 1960-1970 and 1985-1995. Northern species (white), ubiquitous species (hatched) and southern species (black) are shown. n = 37. Mean northing of 10 most marginal squares (after filtering for recorder effort). < 0 indicates a shifts southwards.

Table 2.2: Change in range size and northward shift at the range margin of British Odonata between 1960-1970 and 1985-1995. S = Southern species, U = Ubiquitous species, N = Northern species. Range size: positive values indicate increases in range size (10 km squares). Range margin shift: positive values indicate northwards shift, negative indicates southwards shift.

Family	**Species**	**Range type**	**Change in range size**	**Range margin shift (km)**
Calopterygidae	*Calopteryx virgo* (Linnaeus 1758)	S	18	73
Calopterygidae	*Calopteryx splendens* (Harris 1782)	S	76	41
Lestidae	*Lestes dryas* Kirby 1890	S	1	-14
Platycnemididae	*Platycnemis pennipes* (Pallas 1771)	S	28	18
Coenagrionidae	*Ischnura pumilio* (Charpentier 1825)	S	34	171
Coenagrionidae	*Coenagrion mercuriale* (Charpentier 1840)	S	2	22
Coenagrionidae	*Coenagrion pulchellum* (Vander Linden 1825)	S	11	105
Coenagrionidae	*Coenagrion puella* (Linnaeus 1758)	S	177	103
Coenagrionidae	*Erythromma najas* (Hansemann 1823)	S	56	66
Coenagrionidae	*Ceriagrion tenellum* (Villers 1789)	S	1	49
Gomphidae	*Gomphus vulgatissimus* (Linnaeus 1758)	S	9	104
Aeshnidae	*Brachytron pratense* (Müller 1764)	S	30	189
Aeshnidae	*Aeshna grandis* (Linnaeus 1758)	S	67	24
Aeshnidae	*Aeshna cyanea* (Müller 1764)	S	95	60
Aeshnidae	*Aeshna mixta* Latreille 1805	S	73	65
Aeshnidae	*Aeshna isosceles* (Müller 1767)	S	4	-2
Aeshnidae	*Anax imperator* Leach 1815	S	101	85
Corduliidae	*Cordulia aenea* (Linnaeus 1758)	S	23	145
Libellulidae	*Libellula depressa* Linnaeus 1758	S	99	94
Libellulidae	*Libellula fulva* Müller 1764	S	9	17
Libellulidae	*Orthetrum coerulescens* (Fabricius 1798)	S	12	190
Libellulidae	*Orthetrum cancellatum* (Linnaeus 1758)	S	88	107

Table 2.2: continued.

Family	Species	Range type	Change in range size	Range margin shift (km)
Libellulidae	*Sympetrum striolatum* (Charpentier 1840)	S	149	346
Libellulidae	*Sympetrum sanguineum* (Müller 1764)	S	75	50
Lestidae	*Lestes sponsa* (Hansemann 1823)	U	117	138
Coenagrionidae	*Pyrrhosoma nymphula* (Sulzer 1776)	U	125	14
Coenagrionidae	*Ischnura elegans* (Vander Linden 1820)	U	168	143
Coenagrionidae	*Enallagma cyathigerum* (Charpentier 1840)	U	175	21
Aeshnidae	*Aeshna juncea* (Linnaeus 1758)	U	53	68
Cordulegastridae	*Cordulegaster boltonii* (Donovan 1807)	U	27	31
Corduliidae	*Somatochlora metallica* (Vander Linden 1825)	U	9	-63
Libellulidae	*Libellula quadrimaculata* (Linnaeus 1758)	U	93	39
Libellulidae	*Sympetrum danae* (Sulzer 1776)	U	22	67
Coenagrionidae	*Coenagrion hastulatum* (Charpentier 1825)	N	2	15
Aeshnidae	*Aeshna caerulea* (Ström 1783)	N	-1	36
Corduliidae	*Somatochlora arctica* (Zetterstedt 1840)	N	1	12
Libellulidae	*Leucorrhinia dubia* (Vander Linden 1825)	N	-1	114
Mean			55	74
SE			9	12

2.4: Results

2.4.1: Descriptive results

All but two non-migratory British Odonata species increased in range size (mean change = +55 10km grid squares, s.e. = 9). The two species that did decline in range size (*Aeshna caerulea* and *Leucorrhinia dubia*) were both northern species, but only declined by one grid square each.

All but three species shifted northwards at their range margin (mean = 74km, s.e. = 12) between 1960-1970 and 1985-1995 (Table 2.2, Figure 2.4, 2.5). Southern species increased in range size (mean change = +52 squares, s.e. = 10) and, on average, shifted northwards at the range margin by 88km (s.e. = 16). Ubiquitous Odonata species increased in range size (mean change = +88 squares, s.e. = 21) and, on average, shifted northwards in the northern parts of their ranges by 51km (s.e. = 21). Overall, northern species did not exhibit changed range sizes (mean change = +0.25 squares, s.e. = 1) and, on average, shifted northwards at their southern range margin by 44km (s.e. = 24).

2.4.2: Statistical tests

There was a significant difference between southern and northern species for change in range size (Mann-Whitney U-test $n_1 = 24$ $n_2 = 4$, $W = 392.5$, $p = 0.0038$), but not for change at the range margin (Mann-Whitney U-test $n_1 = 24$ $n_2 = 4$, $W = 367.0$, $p = 0.2245$).

2.4.3: Different numbers of grid squares

The analysis was repeated using 20, 30 and 40 grid squares to define the range margin, to determine whether or not using 10 grid squares gives a representative measurement. On average, range margin shifts for southern and northern species appeared smaller using more grid squares, but range margin shifts for ubiquitous species appeared larger (Table 2.1). Three paired T-tests were run, comparing results for the same species using different numbers of grid squares. There was no significant difference between results using any number of grid squares: comparing 10 and 20 (Paired T-test n = 37 $t_{36} = -1.67$, p = 0.104), comparing 10 and 30 (Paired T-test n = 37 $t_{36} = -1.30$, p = 0.200), comparing 10 and 40 (Paired T-test n = 37 $t_{36} = -0.66$, p = 0.511). Therefore results using 10 grid squares to define the range margin appear to be robust.

2.5: Discussion

2.5.1: Species of note and shifts in isotherms

The species which colonised the most new grid squares in the second time period was *Coenagrion puella*, a common southern species, which increased its range size from 147 grid squares to 324 grid squares during the study period (Figure 2.2). The species which expanded furthest northwards at its range margin was *Sympetrum striolatum*, another common southern species, which shifted 346km (14km year^{-1}) north between the two time periods. This range shift is comparable with that of the southern generalist butterfly species *Polygonia c-album* (comma butterfly), which shifted 220km (10km year^{-1}) north in Britain between 1970-1982 and 1995-1999 (using data from Warren *et al.* 2001). Isotherms over the period of study for dragonflies (1960-1970 and 1985-1995) have shifted in the UK by approximately 66km. However, temperatures are highly variable between years, so that the exact dates used to calculate this isotherm shift can have a dramatic effect on the results. For example, if data from the midpoints of the periods of study are used (1965 and 1990) instead of average temperatures across those periods, the shift in the isotherm is calculated as 252km. This is because 1965 was a particularly cool year, and 1990 a particularly warm year. Due to this inter-annual variation, a particularly mobile species such as *Sympetrum striolatum* may be able to spread rapidly north in very hot years.

2.5.2: Possible reasons for observed changes

Overall, southerly-distributed British Odonata species increased in range size and expanded northwards at their range margins. The increases in range size could be attributed to increased temperatures due to climate change, but the study period considered also coincided with improved water quality in many locations (Environment Agency 2004), as well as climate warming, and so increased range sizes of species could also be attributable to improved habitat quality. A northward shift of range margin would be expected as a consequence of a general increase in range size, but could be attributed directly to increased climatic suitability of northern sites during the study period. Examination of the changes observed in the four northern species is informative, even though as with many British groups, there are few northern species. Two of the northern species (*Somatochlora* *arctica* and *Coenagrion hastulatum*) expanded their overall recorded range size, and yet retracted northwards at their southern boundary, whereas, if they had generally increased throughout their range, their southern range boundary should have moved south. The other two northern species (*Aeshna caerulea* and *Leucorrhinia dubia*) were the only two species in the entire study of 37 species to show declines in range size (as well as northwards shifts). This suggests that the shifts at the range margins are not simply due to general increases in range size, but are directly linked to climatic suitability.

2.5.3: Differences between northern and southern range margins

Statistically, there was no significant difference between the range margin shifts of northern or southern species. This may be because of the small sample size of northern species. However, there is weak evidence that Odonata are shifting northwards faster at their northern range margin than at their southern range margin. This result is consistent with the results of Parmesan *et al.* (1999), and could suggest that species at their southern range margins are less constrained by climate than by other factors such as, habitat or competition (Darwin 1859). Alternatively, this difference between northern and southern boundaries (documented in other studies and weakly but not statistically proven here) could be due to the fact that colonisation events at northern boundaries are recorded immediately, whereas, a species must be extinct in a whole 10km grid square before it is recorded as extinct in that square.

2.5.4: Changes in recording effort over time

Whilst I took account of variation in sampling effort by only considering grid squares examined in both time periods, I was unable to account for possible changes in sampling effort within grid squares. The number of recorders increased in the north of Britain more than the south between the two time periods. Therefore, it is probable that range size declines and northwards shifts of the southern boundaries of northern species have been under-estimated, whereas, range size increases of the southern and ubiquitous species may be exaggerated, as may northwards shifts and range size increases of the 'ubiquitous' species.

2.5.5: Comparison with other studies

These results show similarities to the results of previous studies of butterfly range shifts (Warren *et al.* 2001), which found that mobile generalist species appear to be increasing in range size and tracking climatic changes. To make a direct comparison, I used data from Warren *et al.* (2001) to calculate the average range shift of southern generalist butterflies between 1970-82 and 1995-99. I found southern dragonflies had shifted northwards, on average, by 88km (4km year^{-1}), and this is comparable to, or perhaps exceeds, the range shift calculated using data from Warren *et al.* (2001) of 53km (3km year^{-1}).

However, my results also exhibit some important differences from Warren *et al.* (2001). Whereas, the maximum range shifts in the two groups are comparable, most of the more habitat-specialised butterfly species have failed to shift northwards. It seems likely that the maximum expansions reflect changes in the physical environment. The low dispersal rates and high degree of habitat specialisation of many of the butterfly species, compared to most Odonata, may be resulting in butterfly distributions lagging further behind changes in the climate itself, with many species failing to colonise northwards across fragmented landscapes (Hill *et al.* 2001; Thomas *et al.* 2001).

2.5.6: Wider implications

It is possible that many other winged insects that lay their eggs in aquatic environments will share a similar response to climate warming as observed for British Odonata, since the thermal environment for the immature stages is likely to be important. Mosquito-borne diseases are now being reported at higher elevations in Latin America, Africa and Asia (Epstein *et al.* 1998), which might reflect an elevational shift in the ranges of their vectors. West Nile virus is now occurring at higher latitudes and may become a problem in Britain as warmer temperatures allow its mosquito vectors to expand their ranges (Higgs *et al.* 2004). There is evidence that some thermophilic mayfly species (for example *Ephemerella notata*) may be extending their distributions northwards in Britain, possibly as a result of climate warming (Bratton 1990; C. Macadam personal communication). In the Netherlands, there is evidence that some Heteroptera species are also shifting northwards (Aukema 2001), and trends in Heteroptera occurrence in Britain suggest climate warming may be affecting the ranges of some species (Kirby *et al.* 2001). Results from this study showing a northward shift of British dragonflies and damselflies during a period of climate warming may potentially be observed in other aquatic insects, which are also expected to expand their ranges to higher latitudes in forthcoming years if climates continue to warm as predicted.

The simple methodology developed here has proven to be robust for both rare and common species, and can be applied to a wider variety of taxa in Chapter 3, to determine if other species are showing a similar response to climate change.

2.6: Conclusion

Dragonfly and damselfly species in Britain have increased in distribution size and shifted northwards at their range margins over recent decades, possibly as a result of climate change. Southern and northern species appear to be shifting northwards at a similar rate. This response suggests that insects with aquatic stages in their life cycle are as sensitive, if not more sensitive, to changes in climate as other species. The methods used in this chapter can be applied to a wider range of taxonomic groups in Chapter 3.

Chapter 3

The distributions of a wide range of taxonomic groups are expanding polewards.

3.1: Abstract

Evidence is accumulating of shifts in species' distributions during recent climate warming. However, most of this information comes predominantly from studies of a relatively small selection of taxa (i.e. plants, birds and butterflies) which may not be representative of biodiversity as a whole. Using data from less well-studied groups, I show that a wide variety of vertebrate and invertebrate species have moved northwards and uphill in Britain over approximately 25 years, mirroring, and in some cases exceeding, the responses of better-known groups.

3.2: Introduction

3.2.1: Previous studies of latitudinal and elevational shift

Global climates are warming (IPCC 2001) and many species are responding to these changes by shifting their distributions to higher latitudes and/or altitudes (Pounds *et al.* 1999; Walther *et al.* 2002; Konvicka *et al.* 2003; Root *et al.* 2003; Parmesan & Yohe 2003; Wilson *et al.* 2005). However, evidence for these range changes comes predominantly from studies of plants, birds and butterflies, for which historical data are available (Root *et al.* 2003, Parmesan & Yohe 2003). It is not clear whether responses of these well-studied taxa are representative of biodiversity as a whole (Prendergast *et al.* 1993, Thomas *et al.* 2004) given that the pre-warming distributions of different taxonomic groups may vary, and that species with different generation times, habitat associations, dispersal capacities or thermal physiologies might show very different responses to changing climate (Hill *et al.* 2002, Thomas *et al.* 2001, Warren *et al.* 2001, Kullman 2002). Species which are capable of utilising a wider range of habitats will have more opportunities for dispersal, allowing them to track changes in climate more easily than more specialised species (Hill *et al.* 2002, Warren *et al.* 2001). Likewise, species whose life cycle includes particularly dispersive phenotypes are more likely to track climate changes than less dispersive species (Thomas *et al.* 2001, Kullman 2002).

3.2.2: Recording effort

Recording effort is often a big problem when analysing ecological distribution data, because recording tends to improve over time: more 10km squares are recorded in later time periods, and in those squares which have been recorded for many years, recording tends to be more intensive. Whilst it is very difficult to account for recorder effort within an analysis, subsampling of data can often be helpful. In this study, data were subsampled based on the species richness recorded in a square, to give results based on only the most highly and consistently recorded grid squares. This is explained in more detail in the Methods section.

3.2.3: General aims of this chapter

Britain has extensive fine-scale and long-term distribution data for a wide range of taxa and, thus, is probably the only region in the world where it is possible to assess whether comparable range margin shifts are taking place in many different groups. Here, I analyse distributional changes across a wide range of animal groups to investigate whether responses of less well-studied groups to recent climate warming are qualitatively similar to those for better-studied groups.

i) Reliability of the method

Does the method outlined in Chapter 2 produce results comparable with previous studies of birds and butterflies when applied to these groups?

ii) Comparison with less well-studied groups

Do less well-studied groups also show the latitudinal and altitudinal shifts associated with climate change, that have already been documented in more well-studied groups such as birds and butterflies?

iii) Recorder effort

Can subsampling of data help account for variation in recorder effort?

3.3: Methods

3.3.1: Species selection

i) Taxonomic groups chosen

I analysed distribution datasets for 16 taxonomic groups that occur in terrestrial and/or freshwater environments in Great Britain, at a 10km grid square resolution. The groups analysed were dragonflies and damselflies (Odonata), grasshoppers and allies (Orthoptera), lacewings (Neuroptera), butterflies (Rhopalocera), spiders (Araneae), herptiles (Amphibia & Squamata), freshwater fish (Teleostei), mammals (Mammalia), woodlice (Isopoda), ground beetles (Carabidae), harvestmen (Opiliones), millipedes (Diplopoda), longhorn beetles (Cerambycidae), soldier beetles and allies (Cantharoidea & Buprestoidea), aquatic bugs (Heteroptera), and birds (Aves). These groups were selected from the Biological Records Centre (BRC) database due to relatively large numbers of species in each group, large numbers of records for each species, and good coverage or recording across the UK and over time.

ii) Distribution of species

For each group, species were only included in analyses if they were southern/low elevation species; these species would be expected to increase their range sizes, move northwards, and/or shift to higher elevations if they were responding solely to temperature. Northern species were excluded from our analyses due to a lack of data; with the exception of birds, the taxa included in our study contain very few species which reach the southern (warm) boundary of their distributions in Britain and generally these species are poorly recorded, precluding the possibility of making among-taxon comparisons. In Chapter 4, a similar analysis is applied for groups where enough northern species are available for analysis, and within-taxon comparisons are made.

iii) Criteria for inclusion / exclusion of species

Species were classified as southern if, according to UK and, where available, European distribution maps, they reached their northern range margin in Britain. For each group, species classifications were checked by an expert where possible. Dragonflies and lacewings were checked by Steve Brooks (Department of Entomology, Natural History Museum), grasshoppers were checked by Peter Sutton (National Orthoptera Recorder), spiders were checked by Peter Harvey (Spider Recording Scheme National Organiser), herptiles, fish and mammals were checked by Henry Arnold (BRC Database Manager), woodlice, longhorn beetles, soldier beetles and aquatic bugs were checked by Paul Harding (former head of BRC, CEH fellow), carabids were checked by Mark Telfer (Carabid National Recorder), millipedes were checked by Paul Lee (Millipede National Recorder) and birds were checked by Shelley Hinsley (CEH Ornithologist). Classification of butterfly range margins was not in doubt and was therefore not checked by an expert. I was unable to find an expert willing to check harvestmen and therefore this group was classified only using atlas information.

Species were excluded from analyses if they were found only on the Channel Islands (close to the coast of northern France), were migratory, were clearly synanthropic, were introduced, if their taxonomy was still under debate, or if, after squares had been excluded by recorder effort and date, the species occupied fewer than 20 10km grid squares (i.e. less than approximately 1% of all 10km grid squares) across the two time periods. Thus, we excluded species which may be expanding as a consequence of human activities (i.e. through recent introductions or due to their close associations with humans), as well as migrant species where records may not reflect the extent of their breeding distributions. We excluded poorly-recorded species because our method of identifying the northern margin (below) is probably unreliable for such species, and susceptible to sampling error.

Within each group, a large percentage of species were excluded because they were too rare, or, less commonly, for one or more of the other reasons stated above. A large percentage of species in each group also had a ubiquitous distribution (i.e. not showing a clear range boundary within Britain), leaving only a relatively small percentage of species in each group suitable for analysis, even with selection criteria being relatively inclusive of species. (Table 3.1).

Table 3.1: Selection of British, southerly distributed species from the Biological Records Centre database.

Taxonomic group	**No. of spp. in database**	**% excluded**	**% ubiquitous**	**% northern**	**No. of southerly spp. in analysis**
Dragonflies and damselflies	52	46	15	0	20
Grasshoppers and allies	55	51	9	0	22
Lacewings	76	71	21	0	6
Butterflies	66	23	24	8	30
Spiders	654	44	42	1	85
Herptiles	14	21	57	0	3
Fish	71	61	17	1	15
Mammals	67	46	39	1	9
Woodlice	38	53	26	0	8
Ground beetles	351	48	34	2	59
Harvestmen	25	28	56	0	4
Millipedes	54	46	43	0	6
Longhorn beetles	63	71	11	0	11
Soldier beetles and allies	61	33	39	2	16
Aquatic bugs	60	22	52	3	14
Birds	546	77	16	3	22

3.3.2: Selection of time periods

For each taxonomic group, two distinct time periods within the past 40 years (coincident with global (IPCC 2001) and regional (CIP 2005) warming) were selected. The time periods for each group were chosen so as to maximise the number of records available for analysis whilst still maintaining a substantial time interval between recording periods (Figure 3.1). In most cases, each recording period was 11 years long, with a 14 year gap in between, corresponding with a 25-year period between the mid-points of the two recording periods.

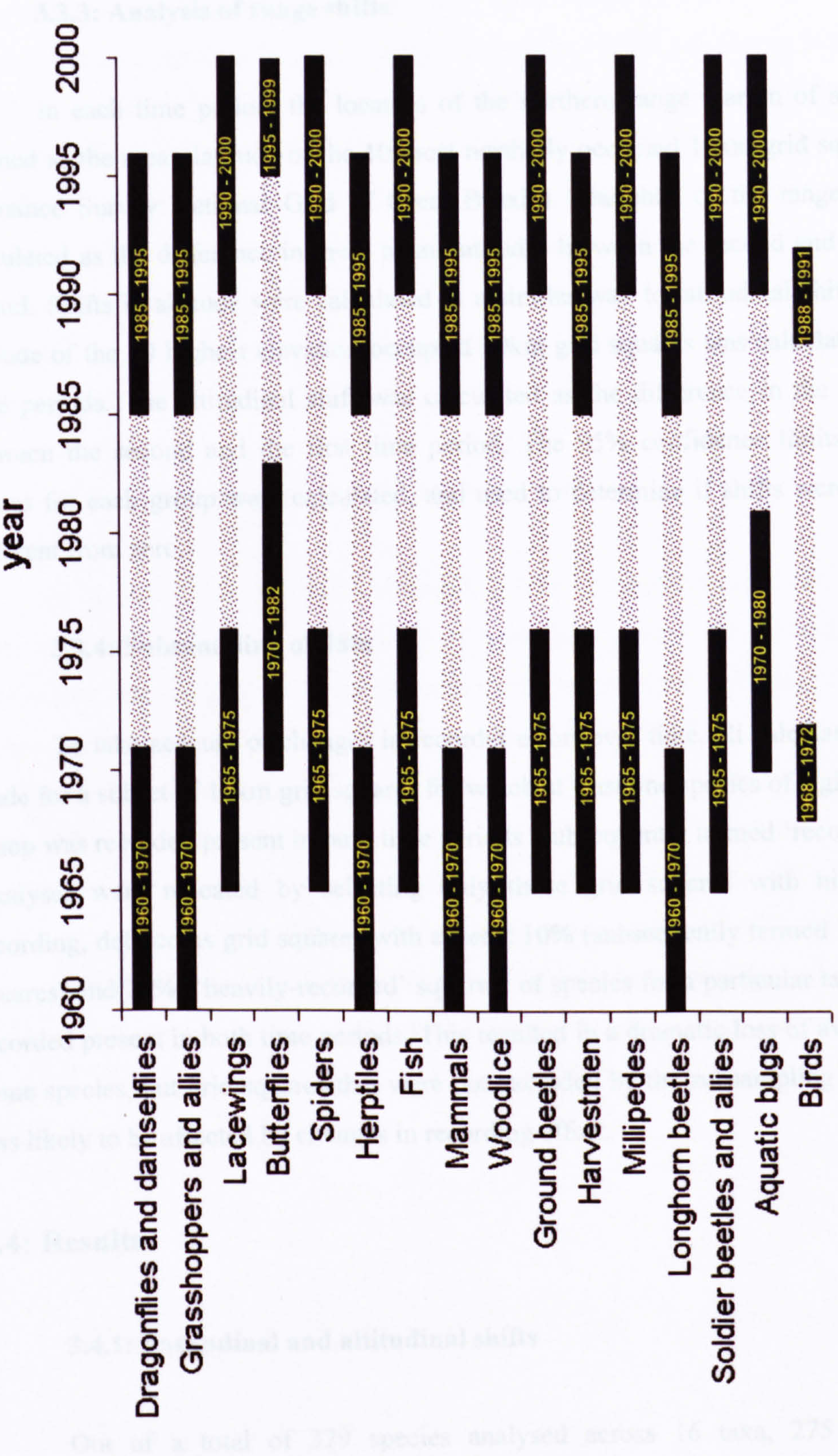

Figure 3.1: Time periods chosen for analysis (solid black) for each taxonomic group, and time gap in between (speckled black). The exact years (inclusive) within which records were analysed are shown in yellow.

3.3.3: Analysis of range shifts

In each time period, the location of the northern range margin of a species was defined as the mean latitude of the 10 most northerly occupied 10km grid squares (on the Ordnance Survey National Grid of Great Britain). The shift of the range margin was calculated as the difference in these mean latitudes between the second and the first time period. Shifts in altitude were calculated in a similar way to latitudinal shifts. The mean altitude of the 10 highest elevation occupied 10km grid squares was calculated in the two time periods. The altitudinal shift was calculated as the difference in the mean altitude between the second and the first time period. The 95% confidence limits of the mean values for each group were calculated, and used to determine if shifts were significantly different from zero.

3.3.4: Subsampling of data

To take account of changes in recorder effort over time, all calculations were first made for a subset of 10km grid squares for which at least one species of a given taxonomic group was recorded present in both time periods (subsequently termed 'recorded' squares). Analyses were repeated by selecting only those grid squares with higher levels of recording, defined as grid squares with at least 10% (subsequently termed 'well-recorded' squares) and 25% ('heavily-recorded' squares) of species for a particular taxonomic group recorded present in both time periods. This resulted in a dramatic loss of available data for some species, but grid squares that were not excluded by the subsampling technique were less likely to be affected by changes in recording effort.

3.4: Results

3.4.1: Latitudinal and altitudinal shifts

Out of a total of 329 species analysed across 16 taxa, 275 species shifted northwards at their range margin, 52 species shifted southwards, and 2 species' range margins did not move, with an average northwards shift across all species of 31 to 60 km (depending on level of sub-sampling of data). Comparable findings were obtained with respect to elevation shifts: 227 species shifted to higher altitude and 102 species shifted to lower altitude, resulting in a mean increase of 25 m overall. Twelve of the 16 taxonomic groups showed significant ($p < 0.05$) northwards shifts (Table 3.2; Figure 3.2A) and shifts to higher elevation (Table 3.2; Figure 3.2B). Only amphibians and reptiles (3 species) shifted significantly southwards and to lower elevation. For most groups, taking account of recording effort decreased the number of species available for analysis, but had little qualitative impact on our findings (Table 3.2; Figure 3.2). Species from well-studied groups (butterflies, mammals, and birds) on average moved north by 30-32 km, whereas previously less well-studied groups moved north by 32-66 km (depending on level of sub-sampling of data).

3.4.2: Distribution change and isotherm shifts

In general, species which showed a large latitudinal shift also increased in distribution size. However, in the case of mammals, ground beetles and birds, overall distribution size in grid squares decreased over the two time periods, whilst the range margins of these groups still shifted northwards (Table 3.3). Most species shifted northwards less than calculated isotherm shifts over equivalent time periods (using data from CET), but to the same order of magnitude (Table 3.3). Inter-annual fluctuations in temperature are sufficiently large that calculated isotherm shifts over different time periods also vary to a large degree. Rate of change per year was correlated with absolute calculated range shift: i.e. dragonflies showed the largest shift at the range margin and also the most rapid rate of change, followed closely by soldier beetles, whilst harvestmen showed a negligible shift at the range margin and correspondingly negligible rate of change (Table 3.3).

Table 3.2: Number of southern species available for analysis, mean northward shift at the range margin (km), altitudinal shift (m), and time period of analysis, for 16 taxonomic groups, analysing 'recorded', 'well-recorded' and 'heavily recorded' grid squares. Asterisks indicate $p < 0.05$. SE signifies Standard Error.

	Recorded squares			Well-recorded squares			Heavily-recorded squares			
Taxonomic group	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Time Period (years)**
Dragonflies and damselflies	20	104 (17.0) *	61.9 (13.08) *	19	80 (11.3) *	31.1 (8.47) *	19	36 (8.9) *	16.8 (6.17) *	25
Grasshoppers and allies	22	34 (8.0) *	30.5 (7.48) *	22	21 (6.3) *	18.8 (5.30) *	19	11 (4.3) *	6.1 (4.25)	25
Lacewings	6	44 (27.9)	7.4 (13.46)	1	-	-	0	-	-	25
Butterflies	29	37 (9.7) *	11.1 (6.75)	29	35 (9.6) *	7.4 (5.71)	29	30 (9.0) *	-1.2 (6.06)	21
Spiders	85	84 (8.0) *	24.3 (4.97) *	54	59 (7.2) *	15.5 (4.92) *	15	68 (10.5) *	-0.9 (7.54)	25
Herptiles	3	-83 (29.8) *	-33.0 (27.14)	3	-68 (28.5) *	-22.8 (10.76) *	3	-45 (44.0)	-22.9 (5.93) *	25
Fish	15	47 (15.4) *	32.7 (12.71) *	15	51 (15.7) *	22.0 (11.12) *	15	33 (9.3) *	9.0 (8.68)	25
Mammals	9	22 (38.4)	31.0 (27.70)	8	24 (33.0)	41.0 (29.11)	5	37 (13.7) *	103.9 (22.65) *	25
Woodlice	8	79 (18.4) *	55.3 (12.02) *	7	65 (12.1) *	37.9 (11.52) *	2	-	-	25
Ground beetles	59	55 (8.4) *	12.7 (6.31) *	28	47 (12.4) *	7.3 (8.04)	6	0 (28.6)	0.2 (28.55)	25
Harvestmen	4	8 (29.9)	35.8 (11.22) *	2	-	-	0	-	-	20

Table 3.2: continued.

	Recorded squares			Well-recorded squares			Heavily-recorded squares			
Taxonomic group	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Number of species**	**Mean northward shift at the range margin, km (SE)**	**Mean altitudinal shift, m (SE)**	**Time Period (years)**
Millipedes	6	74 (17.0) *	24.0 (10.21) *	3	48 (26.8)	-5.7 (12.76)	1	-	-	25
Longhorn beetles	11	40 (10.4) *	39.3 (9.24) *	8	43 (7.3) *	26.1 (6.37) *	0	-	-	25
Soldier beetles and allies	16	91 (13.3) *	62.1 (9.89) *	5	50 (22.1) *	41.3 (18.37) *	0	-	-	25
Aquatic bugs	14	64 (19.7) *	19.2(8.49) *	8	84 (24.4) *	25.6 (9.35) *	4	81 (13.2) *	8.4 (7.76)	20
Birds	22	29 (20.0)	-2.1 (13.14) *	22	29 (20.0)	-2.1 (13.14)	22	28 (20.0)	-2.1 (13.14)	19.5

Table 3.3: Change in distribution size, latitudinal shift, equivalent shift of the isotherm over each time period (calculated using CET data [note below]; isotherm shift of 150km for every 1°C increase in temperature derived from Parmesan *et al.* (1999)), number of years studied, and rate of latitudinal shift per year, for recorded squares for 16 taxonomic groups. Asterisks indicate $p < 0.05$. SE signifies Standard Error.

Taxonomic group	Average change in distribution size (grid squares)	Mean northward shift at the range margin, km (SE)	Shift in isotherm (km)	Time Period (years)	Rate of shift per year (km)
Dragonflies and damselflies	61	104 (17.0) *	66	25	4
Grasshoppers and allies	31	34 (8.0) *	66	25	1
Lacewings	15	44 (27.9)	97	25	2
Butterflies	187	37 (9.7) *	107	21	2
Spiders	23	84 (8.0) *	97	25	3
Herptiles	-38	-83 (29.8) *	66	25	-3
Fish	179	47 (15.4) *	97	25	2
Mammals	-10	22 (38.4)	66	25	1
Woodlice	44	79 (18.4) *	66	25	3
Ground beetles	-2	55 (8.4) *	97	25	2
Harvestmen	12	8 (29.9)	41	20	0
Millipedes	11	74 (17.0) *	97	25	3
Longhorn beetles	22	40 (10.4) *	66	25	2
Soldier beetles and allies	35	91 (13.3) *	97	25	4
Aquatic bugs	17	64 (19.7) *	88	20	3
Birds	-38	29 (20.0)	106	19.5	1

[note] ((Average temperature in °C over all months in time period two) - (Average temperature in °C over all months in time period one) * 150

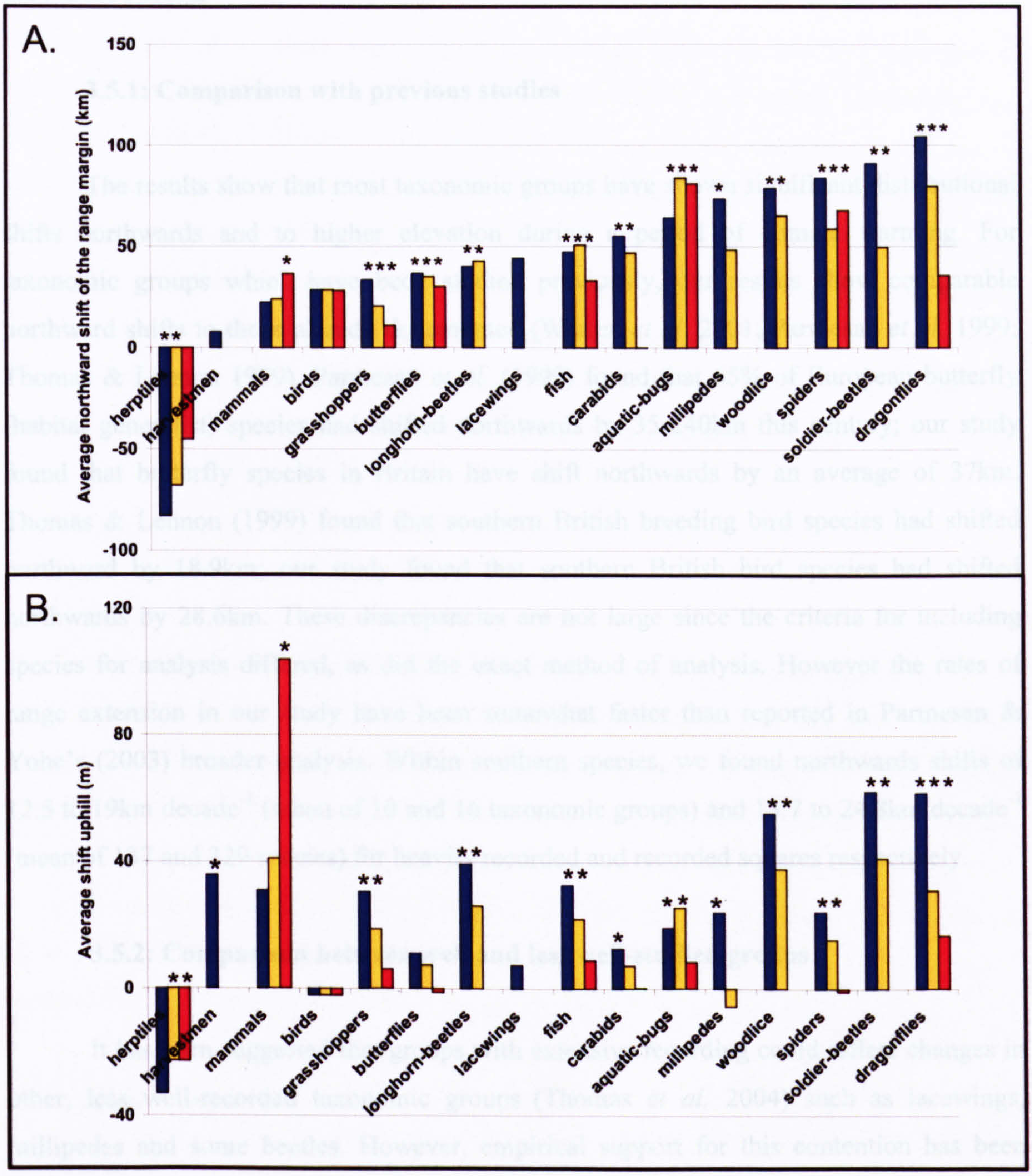

Figure 3.2: Shifts in range margins for southern species of 16 taxonomic groups during recent climate warming in relation to (A) latitude and (B) altitude. Results are given for three levels of sub-sampling of data ('recorded' = blue, 'well-recorded' = yellow, 'heavily-recorded' = red). Only species occupying more than twenty 10 km grid squares across the two time periods are included. Asterisks indicate where the shift is significantly different from zero ($p < 0.05$).

3.5: Discussion

3.5.1: Comparison with previous studies

The results show that most taxonomic groups have shown significant distributional shifts northwards and to higher elevation during a period of climate warming. For taxonomic groups which have been studied previously, our results show comparable northward shifts to those already documented (Warren *et al.* 2001; Parmesan *et al.* 1999; Thomas & Lennon 1999). Parmesan *et al.* (1999) found that 65% of European butterfly (habitat generalist) species had shifted northwards by 35-240km this century; our study found that butterfly species in Britain have shift northwards by an average of 37km. Thomas & Lennon (1999) found that southern British breeding bird species had shifted northward by 18.9km; our study found that southern British bird species had shifted northwards by 28.6km. These discrepancies are not large since the criteria for including species for analysis differed, as did the exact method of analysis. However the rates of range extension in our study have been somewhat faster than reported in Parmesan & Yohe's (2003) broader analysis. Within southern species, we found northwards shifts of 12.5 to 19km decade^{-1} (mean of 10 and 16 taxonomic groups) and 13.7 to 24.8km decade^{-1} (mean of 137 and 329 species) for heavily recorded and recorded squares respectively.

3.5.2: Comparison between well and less well-studied groups

It has been suggested that groups with extensive recording could reflect changes in other, less well-recorded taxonomic groups (Thomas *et al.* 2004) such as lacewings, millipedes and some beetles. However, empirical support for this contention has been scarce. Our analysis suggests that the rates of range shifting are not significantly different for birds and butterflies compared with other taxa (given the current data), even though some of the less well-studied taxa give the appearance of showing an even stronger response to climate change (Figure 3.2A).

Whilst the majority of groups appear to be shifting by about 2km per year (Table 3.3), amongst the species shifting more rapidly are some initially surprising taxonomic groups, including millipedes, aquatic bugs and woodlice. These groups are often considered to have a low dispersal capacity, and so it is interesting to see that they are shifting more rapidly than butterflies. It is possible that some of this apparent northward shift is a result of increased recording in the north of Britain in the later time period. However, it is also likely that certain stages of invertebrates' life cycles, particularly egg stages, allow them to disperse wide distances into any habitat or microclimate that is suitable, regardless of the dispersal capacity of the final adult stage. For example, eggs can often be transported attached to the feet or coats of other animals. It is also likely that movement of soil and water by man can lead to surprisingly high rates of long-distance dispersal in seemingly sedentary taxa (Hodkinson & Thompson 1997). Such man-made dispersal will have been occurring for decades or even centuries, but it is possible that only under recent climatic conditions can species successfully establish new populations further north.

3.5.3: Altitudinal shifts

My results for altitudinal shifts are also comparable with previous studies (Kullman 2002; Konvicka *et al.* 2003; Penuelas & Boada 2003) (Figure 3.2B) and show that most groups have shifted to higher elevation. Altitudinal shifts documented in previous studies ranged from 70m uphill (Penuelas & Boada 2003) to 375m uphill (Kullman 2002); the maximum uphill shift of an individual species in my study was 223m and the average shift across all southern species was 24.7m. Within southern species, we found uphill shifts of 4.7 to 10.7m decade^{-1} (mean of 10 and 16 taxonomic groups) and 2.8 to 10.1m decade^{-1} (mean of 137 and 329 species) for heavily recorded and recorded squares respectively.

3.5.4: Recorder effort

Increased recorder effort over time may have led to some over-estimation of range changes in analyses of the full data sets ('recorded' squares), but qualitatively similar results were obtained with more stringent criteria for inclusion of data, which suggests that our general conclusions are robust.

It is very difficult to account for changes in recorder effort, both geographically and over time, and no method can give a completely precise result. The majority of studies account for geographical variation, as I did, by only including grid squares surveyed in both time periods (Telfer *et al.* 2002), or by repeating an analysis a certain number of times using a subsampled dataset (Thomas *et al.* 2004). Within square variation can be accounted for by ranking change according to the average change in all species (Telfer *et al.* 2002). This method assumes that rare species will remain rare and common species will remain common, and that recorders will record each species with equal vigour in both times periods. Such a method works best for species groups with lots of species. In groups with fewer species such as butterflies or dragonflies, such a method would probably produce less informative results.

Whilst various different techniques may be suitable when looking at a single species or taxonomic group, when studying a range of groups with different rates of change, ecological constraints and life history elements, it is my opinion that the technique applied here should be relatively robust. It also allows for more intuitive interpretation of data across different groups. By repeating the analysis with subsampled data, it is possible to confirm that the qualitative conclusions on the rates of northward expansion in British species are maintained. Furthermore, shift estimates for 'recorded' squares are not necessarily less accurate than for the 'heavily recorded' squares. The latter exclude so many northern squares that genuine northward expansions may be missed or underestimated by only including 'heavily recorded' squares.

3.5.5: Differences between latitudinal and altitudinal results

The results for latitudinal shifts appear stronger than those for elevation shifts, where significant shifts uphill generally were restricted to analyses of the full data set (i.e. not taking account of recording effort). This may be due to several reasons. First, the elevation range of Britain is not great, and so there are relatively few high elevation areas for southerly species to colonise near their range boundaries. Second, higher elevation locations tend to be less well recorded than lowland sites, and thus these areas will disproportionately be excluded from analyses which take account of recorder effort. In addition, high and low elevation sites often occur in close geographic proximity to one another, with the possibility that individual animals of many of these taxa could move tens of metres in elevation as a direct (e.g., behavioural) response to changes in the physical environment, but which would not be detected in our relatively course-scale analyses which were at a 10km grid square resolution. This is likely to lead to underestimates of the true elevation shift. The estimates of latitudinal shifts are likely to be more reliable:

latitudinal shifts of 30 to 60km for southern species clearly represent the establishment of large numbers of new northern populations over a succession of generations. Few of the species considered are likely to colonise more than a few kilometres per generation. Thus, the latitudinal shifts reveal substantial changes to species' breeding ranges.

3.5.6: Possible mechanisms behind range shifts

Despite the wide range of taxonomic groups considered, our results show no clear taxonomic, ecological or physiological pattern in terms of the response of groups to climate warming. A wide range of responses were found among species within almost all taxonomic groupings, which suggests that within-taxon variation in ecological traits and dispersal capacity (Warren *et al.* 2001) may preclude broader taxonomic generalisations. All distribution changes are taking place not only in the context of climate warming but also in the context of land use and other environmental changes. This is best exemplified by the three amphibian/reptile species that were included in the analysis. Each of them is at the north-western edge of its distribution in Britain and should, in principle, have benefited from the warming that has been experienced in recent decades. Nonetheless, their distributions have collapsed southwards. Each of the three species chosen are specific to particular habitats, and as those habitats have been drastically reduced and fragmented, these species now survive in remnant populations restricted to only a small fraction of their former distribution. This trend has been documented in other species that lack the dispersal ability to persist in fragmented habitats (Hill *et al.* 1999b; Honnay *et al.* 2002).

3.5.7: Importance of results

Most previous studies of range shifts focused on species which are particularly limited by climate, or are highly mobile (Hughes 2000) and excluded species whose distributions were likely to have been greatly affected by habitat changes (Parmesan *et al.* 1999). In our analyses, species were excluded only if recording effort was poor. Thus the fact that species' distributions are also responding to other factors makes it all the more impressive that it is possible to identify a significant average northwards shift in the distributions of almost all taxonomic groups for which a sample size of more than 10 species could be analysed.

3.6: Conclusion

Species from a wide range of taxonomic groups are moving north and to higher elevations, during a period of regional (CIP 2005) climate warming. For some less well-known groups, these responses may even be greater than those already observed for more widely-studied groups.

Chapter 4:

Comparison of northward shifts at the range margins of northern and southern species.

4.1: Abstract

Whilst studies of distribution changes in southern species are relatively common, there are fewer studies of how climate change might affect species at their southern range margin. In Britain this type of study is confounded by the challenging terrain over which many northern species' southern range margins lie. Here, I examine latitudinal shifts at the southern range margin and altitudinal shifts for northern species in five different taxonomic groups, and compare the distributional changes in the northern species with their southern counterparts. I show that in insect groups, northern species are retracting northwards at a comparable speed to the expansion of southern species. However, neither southern nor northern plant species appear to be responding strongly to climate warming, whilst northern birds are shifting in the opposite direction to that predicted. Possible explanations for these differences are discussed.

4.2: Introduction

Whilst it has been demonstrated in previous chapters that southern British species from both well recorded and less well recorded taxonomic groups are shifting northwards at their range margin, very little is known about the shifts of northern British species at their southern range margin. This is partly because northern species in Britain tend to be fewer in number, and partly because the geography and the lower human population density of the north of the UK makes recording more difficult.

4.2.1: Previous evidence for latitudinal shifts at southern range margins

Few studies have focused on the shift at warm (southern) range margins, and where this has been the subject of study, the evidence has been less compelling than for range shifts at cool (northern) margins (Parmesan *et al.* 1999; Thomas & Lennon 1999; Parmesan & Yohe 2003). The groups that have received the most attention are birds (Thomas & Lennon 1999), butterflies (Beaumont & Hughes 2002; Hill *et al.* 2002) and plants (Penuelas & Boada 2003). However, in a meta-analysis, Parmesan & Yohe (2003) found that only 75% of species showing a southern range margin shift were retracting northwards, compared to 81% of species expanding at their northern range margin.

4.2.2: Previous evidence for altitudinal shifts at southern range margins

In many cases, altitudinal shifts are detected where latitudinal shifts are not, possibly because altitudinal shifts can be detected over a smaller geographic area than latitudinal shifts. For example, at a mountainous southern range margin, large shifts in the altitude of a population could occur within a single 10km grid square, whereas in order to detect latitudinal shifts of similar magnitude, they would have to occur over large distances and even over several grid squares.

Therefore, there is more evidence for altitudinal shifts in northern or montane species, than for latitudinal shifts at southern range margins. An excellent example can be found in the highland cloud forest of Costa Rica, where lowland species are colonising higher altitudes as air temperatures and the cloud bank rise, whilst high altitude species are rapidly decreasing in abundance (Pounds *et al.* 1999). Another example of an altitudinal shift in the whole biome has been documented in the Montseny Mountains of north-east Spain, where beech forest and heather heathland have shifted attitudinally by 70m since 1945, and at lower altitudes are being replaced by holm oak forest (Penuelas & Boada 2003).

4.2.3: General aims of this chapter

Here, I use the extensive data held by the Biological Records Centre (BRC) to determine if, for groups that contain both northern and southern species in the UK, the northern species have retracted at their southern range margin to the same extent that southern species have expanded at their northern range margin. I also examine altitudinal shifts in these species and compare my findings with previous literature. The same methods are applied as in Chapter 3.

i) Latitudinal shifts at the southern range margin

For UK groups where enough data / species are available for analysis, are species retracting northwards at their southern range margin, as would be predicted if they were responding solely to climate change?

ii) Comparison between northern and southern species

Within taxonomic groups, are northern species shifting at their range margin to the same extent as their southern counterparts?

iii) Altitudinal shifts of northern species

Are northern species retracting uphill, and is the magnitude of the shift comparable with previous literature?

4.3: Methods

4.3.1: Species selection

i) Taxonomic groups chosen

I analysed distribution datasets at a 10km grid square resolution for five taxonomic groups that occur in terrestrial environments in Great Britain. The groups analysed were butterflies (Rhopalocera), spiders (Araneae), ground beetles (Carabidae), birds (Aves) and vascular plants. These groups were selected because they were the only groups in the BRC database where enough species (> 3 species) of both northern and southern species were available for comparison, and where enough data for analysis existed for those species. In the UK there are far fewer northern than southern species, and where records do exist for northern species they are often very patchy due to the difficultly of recording in the north of Britain. This is why such a small number of groups were suitable for this analysis.

ii) Inclusion of vascular plants

Vascular plants were included as a group in this analysis, but were not included in Chapter 3. This is because the first plant atlas, and therefore the bulk of early recording, occurred in the 1950s, and to use this as the first time period would have made comparison with other groups in Chapter 3 very difficult, as all other time periods were after 1960. This problem was augmented by the fact that the 1950s were actually slightly warmer than the 1960s, so not only would the comparison between groups have been difficult due to differences in time, it would also have been hindered by differences in the starting temperatures of the analysis.

However, in this chapter the emphasis is on within group comparisons of northern and southern species, rather than between group comparisons. Also plants are one of the few groups in Britain for which there are a large number of northern species available for analysis. Therefore vascular plants were included as a group in this chapter.

iii) Exclusion of bryophytes

Bryophytes were not included in the analysis, despite there being a large number of northern species in Britain, with large amounts of recording throughout time periods in some localities. This group was excluded because, despite excellent long-term recording in some areas, such records tend to be highly localised around recorders' homes, and often if recorders move house, the recording moves with them, leading to many geographical biases in the dataset which could not be accounted for using the large, cross-taxon methodology of Chapters 2 and 3. In order to study range shifts in bryophytes using the British dataset, a specific analysis would need to be designed to suit the geographical bias in the data.

iv) Criteria for inclusion / exclusion of species

As in Chapter 3, species were excluded from analyses if they were found only on the Channel Islands, were migratory, were clearly synanthropic, were introduced, if their taxonomy was still under debate, or if, after squares had been excluded by recorder effort and date, the species occupied fewer than 20 10km grid squares across the two time periods.

v) Distribution of species

For each group, species were only included in analyses if they were southern/low elevation species or northern/high elevation species. Ubiquitous species were excluded for this analysis, because they do not reach their climatic limits in Britain and therefore do not have distinct range margins with which to track distributional changes. A ubiquitous species was defined, as in previous chapters, as found throughout Britain and not reaching a range limit to its European range in Great Britain. Where possible, species classifications (northern, southern or ubiquitous) were checked by an expert. Spiders were checked by Peter Harvey (Spider Recording Scheme National Organiser), carabids were checked by Mark Telfer (Carabid National Recorder), and birds were checked by Shelley Hinsley (CEH Ornithologist). Classification of butterfly range margins was not in doubt and was therefore not checked by an expert, and classification of plant range margins was not checked by an expert due to the large numbers of species involved.

4.3.2: Selection of time periods

For each taxonomic group, as in previous chapters, two distinct time periods within the past 70 years (coincident with global (IPCC 2001) and regional (CIP 2005) warming) were selected. The time periods for each group were chosen so as to maximise the number of records available for analysis whilst still maintaining a substantial time interval between recording periods (Table 4.1). For butterflies, spiders, carabids and birds, these time periods were the same as in Chapter 3.

For plants, the selected time periods were 1930-1970 and 1987-1999, as used in the New Atlas of the British and Irish Flora (Preston *et al.* 2002). The earlier time period was particularly long to incorporate as many records as possible, since over this time period collection of records was less intensive. The later time period was relatively short, as this was a period of very intensive recording. This gives the plant group a particularly long period of 43 years (calculated from the mid-points of both time periods) over which range shifts could occur. Whilst this does not fit particularly closely with the time periods chosen for the other four groups, it was necessary in order to include sufficient records from the earlier period of recording.

Table 4.1: Time periods chosen for analysis for five taxonomic groups. Overall time period in which range shifts could occur was calculated as the number of years between the midpoints of the first and second time periods.

Taxonomic Group	First Time Period	Second Time Period	Overall Time Period (years)
Birds	1968-1972	1988-1991	21
Butterflies	1970-1982	1995-1999	25
Spiders	1965-1975	1990-2000	25
Carabids	1965-1975	1990-2000	19.5
Plants	1930-1970	1987-1999	43

4.3.3: Analysis of range shifts

As in previous chapters, in each time period, the location of the range margin of a species was defined as the mean latitude of the 10 most northerly or southerly occupied 10km grid squares (depending on whether the northern or southern range margin was being calculated). The shift of the range margin was calculated as the difference in these mean latitudes between the second and the first time period. Shift in altitude was calculated in a similar way to latitudinal shift. The mean altitude of the 10 highest elevation occupied 10km grid squares was calculated in the two time periods. The altitudinal shift was calculated as the difference in the mean altitude between the second and the first time period. The 95% confidence limits of the mean values for each group were calculated, and used to determine if shifts were significantly different from zero.

Differences between latitudinal and altitudinal shifts were compared for northern and southern species within each group, and significance was assessed by Mann-Whitney U-test and adjusted for tied values.

4.3.4: Subsampling of data

To take account of changes in recorder effort over time, all calculations were first made for a subset of 10km grid squares for which at least one species of a given taxonomic group was recorded present in both time periods (subsequently termed 'recorded' squares). Analyses were repeated by selecting only those grid squares with higher levels of recording, defined as grid squares with at least 10% (subsequently termed 'well-recorded' squares) and 25% ('heavily-recorded' squares) of species for a particular taxonomic group recorded present in both time periods.

4.4: Results

4.4.1: Latitudinal shifts of northern species

Out of a total of 166 northern species analysed across five taxa, 78 species shifted northwards at their range margin, 85 species shifted southwards, and three species' range margins did not move, with an average southwards shift across all species of 9 to 17 km (depending on level of sub-sampling of data). Only ground-beetles showed a significant ($p < 0.05$) northwards shift (Figure 4.1A). Birds showed a significant southward shift. Taking account of recording effort had little qualitative impact on our findings (Table 4.2; Figure 4.1).

4.4.2: Altitudinal shifts of northern species

Differing results were obtained with respect to elevation shifts: 89 northern species shifted to higher altitude, 61 species shifted to lower altitude and 16 species did not shift in altitude, resulting in a mean increase of 2m overall. Spiders and plants showed a significant shift to higher elevation (Figure 4.1B).

4.4.3: Comparison between northern and southern species

There was no significant difference in latitudinal shifts of northern and southern species (Figure 4.2) except for birds, where southern birds shifted northwards by 29km, but northern birds shifted southwards by 72km (Mann-Whitney U-test $n_1 = 22$ $n_2 = 16$, $W =$

499.5, $p = 0.0384$). There was no significant difference in altitudinal shifts of northern and southern species except for carabids, where southern carabids shifted uphill by 13m, but northern carabids shifted downhill by 57m (Mann-Whitney U-test ('recorded' squares) $n_1 = 59$ $n_2 = 7$, $W = 2095$, $p = 0.014$).

4.5: Discussion

4.5.1: Latitudinal shifts at the southern range margin

On average, northern species shifted southwards at their southern range margin between the time periods of study. This is the opposite of what would be expected if species were responding to climate warming. However, this average is driven by the birds. All three insect groups showed the expected northward retraction at their southern range margin, and given the differing ecological characteristics of these groups, it is quite possible that these northward shifts are driven primarily by a warming climate. On the other hand, plants showed a small but non-significant southward shift.

Whilst previous studies of invertebrates failed to detect a latitudinal shift at the southern range margin, we did detect a shift in the range margins of northern species. This may be due to variation in methodology or species selection. Previous studies of UK moths have concluded that climate change may be playing a role in the decline of ubiquitous species in the south of their range and the increase of southerly distributed species (Conrad *et al.* 2004), so both butterflies and moths may be responding to warming temperatures in similar ways. Northward retractions were also detected for northern spiders and carabids, which suggests that a variety of insect groups may be responding to climate change at their southern range margin.

Table 4.2: Number of northern (N) and southern (S) species available for analysis, mean northward shift at the range margin (km), and altitudinal shift (m), for five taxonomic groups, analysing 'recorded', 'well-recorded' and 'heavily recorded' grid squares. Asterisks indicate $p < 0.05$. SE signifies Standard Error.

	Recorded squares					
	Number of species		Mean northward shift at the range margin, km (SE)		Mean altitudinal shift, m (SE)	
Taxonomic group	**S**	**N**	**S**	**N**	**S**	**N**
Butterflies	29	5	37 (9.7)*	42 (57.7)	11.1 (6.75)	14.4 (19.60)
Spiders	85	6	84 (8.0)*	45 (60.6)	24.3 (4.97)*	63.9 (25.56)*
Ground beetles	59	7	55 (8.4)*	60 (25.1)*	12.7 (6.31)*	-56.6 (29.76)
Birds	22	16	29 (20.0)	-72 (35.2)*	-2.1 (13.14)	-13.4 (12.89)
Plants	215	127	4 (4.3)	-11 (6.5)	12.5 (2.78)*	6.3 (3.34)

	Well-recorded squares					
	Number of species		Mean northward shift at the range margin, km (SE)		Mean altitudinal shift, m (SE)	
Taxonomic group	**S**	**N**	**S**	**N**	**S**	**N**
Butterflies	29	5	35 (9.6)*	44 (58.0)	7.4 (5.71)	29.6 (21.67)
Spiders	54	2	59 (7.2)*	-	15.5 (4.92)*	-
Ground beetles	28	1	47 (12.4)*	-	7.3 (8.04)	-
Birds	22	16	29 (20.0)	-72 (35.2)*	-2.1 (13.14)	-13.1 (12.91)
Plants	215	127	3 (4.3)	-11 (6.5)	12.6 (2.77)*	7.9 (3.36)*

Table 4.2: continued.

	Heavily-recorded squares					
	Number of species		Mean northward shift at the range margin, km (SE)		Mean altitudinal shift, m (SE)	
Taxonomic group	**S**	**N**	**S**	**N**	**S**	**N**
Butterflies	29	3	30 (9.0)*	-8 (22.4)	-1.2 (6.06)	1.8 (5.39)
Spiders	15	0	68 (10.5)*	-	-0.9 (7.54)	-
Ground beetles	6	0	0 (28.6)	-	0.2 (28.55)	-
Birds	22	16	28 (20.0)	-73 (35.2)*	-2.1 (13.14)	-19.1 (18.24)
Plants	215	127	4 (4.4)	-10 (6.0)	12.9 (2.75)*	7.8 (3.31)*

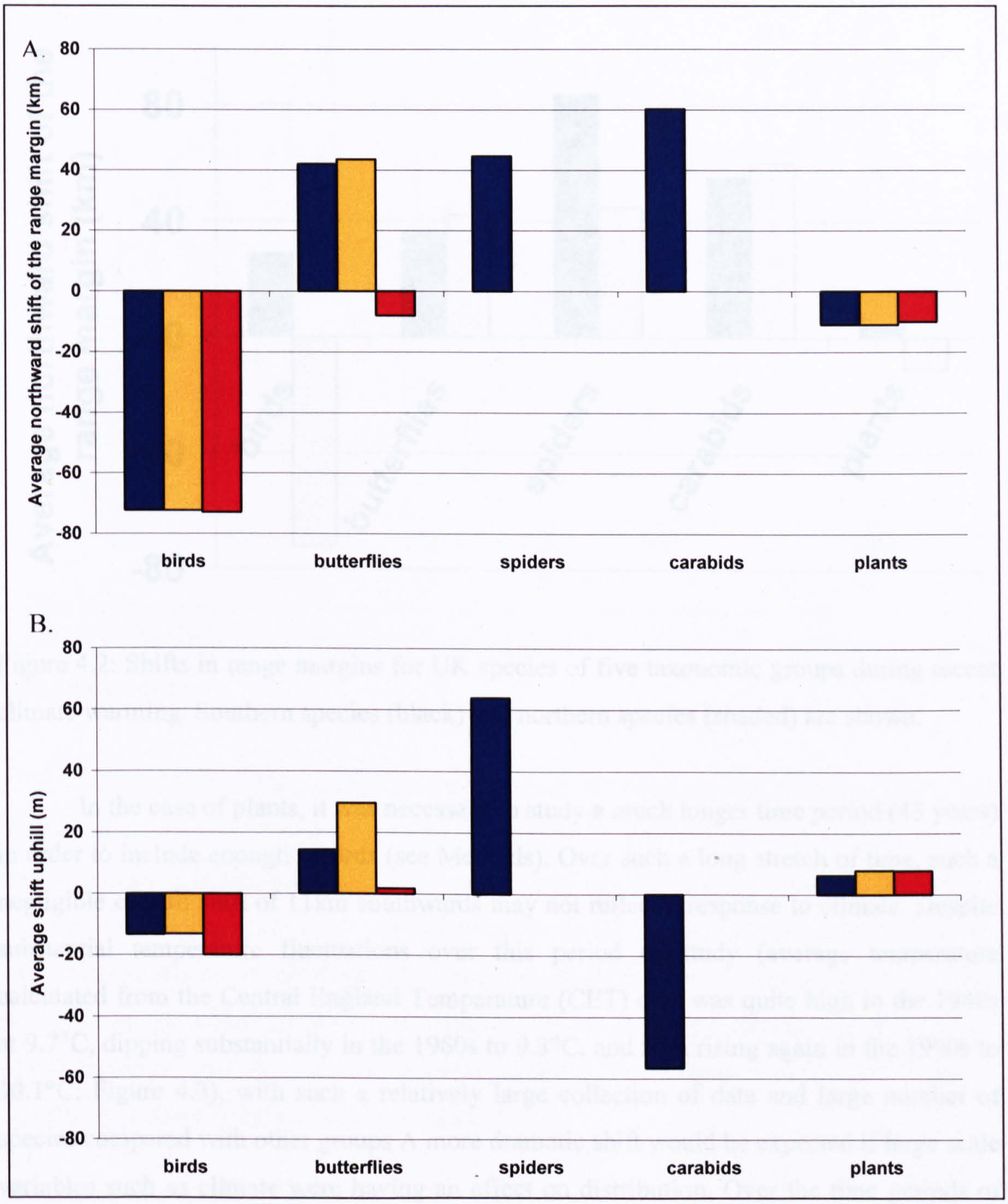

Figure 4.1: Shifts in range margins for northern species of five taxonomic groups during recent climate warming in relation to (A) latitude and (B) altitude. Results are given for three levels of sub-sampling of data ('recorded' = blue, 'well-recorded' = yellow, 'heavily-recorded' = red). Only species occupying more than twenty 10km grid squares across the two time periods are included. A positive northward and uphill shift would be expected for all species if they were responding solely to climate warming. Asterisks indicate where the shift is significantly different from zero ($p < 0.05$).

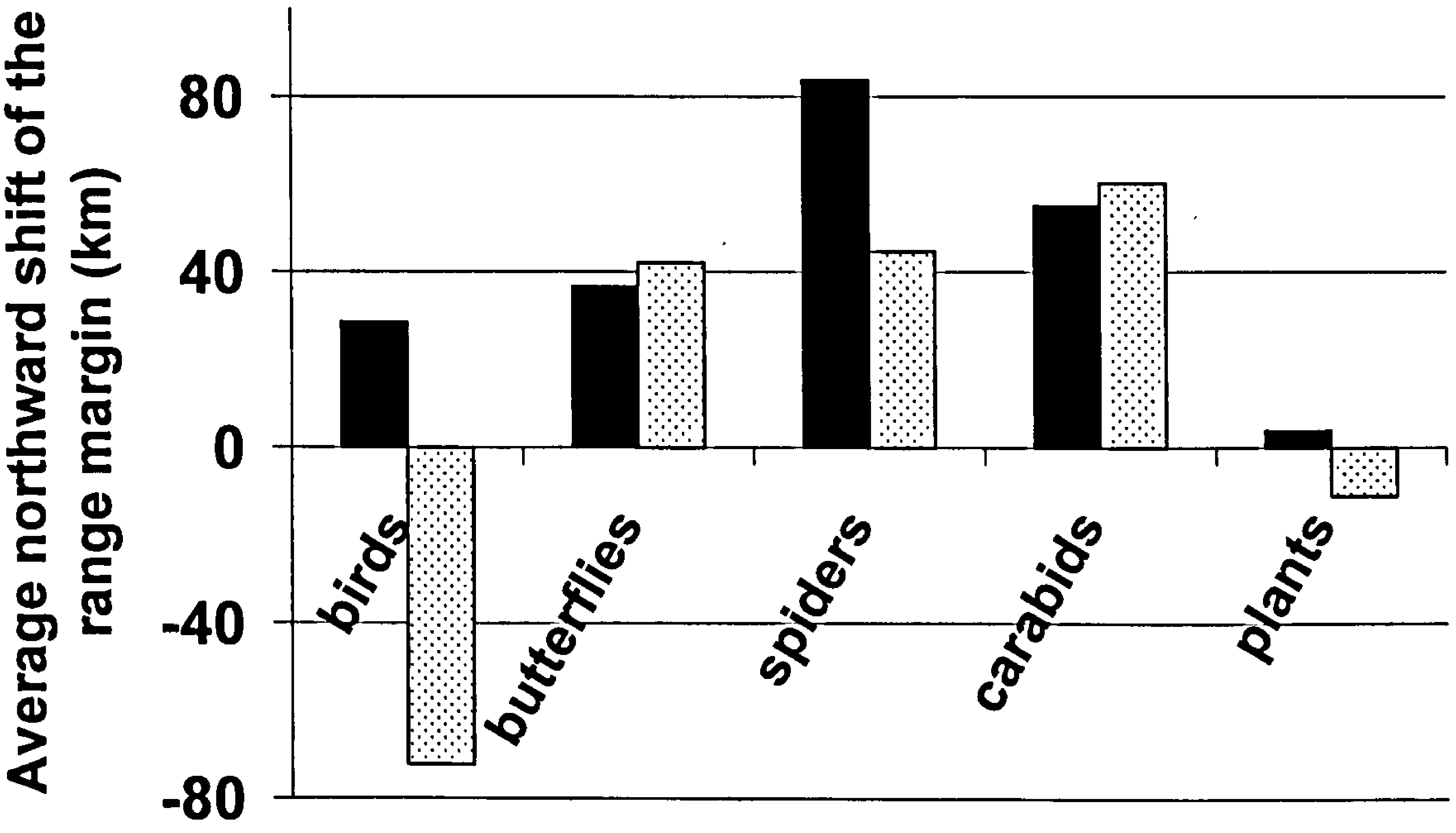

Figure 4.2: Shifts in range margins for UK species of five taxonomic groups during recent climate warming. Southern species (black) and northern species (shaded) are shown.

In the case of plants, it was necessary to study a much longer time period (43 years) in order to include enough records (see Methods). Over such a long stretch of time, such a negligible overall shift of 11km southwards may not reflect a response to climate. Despite substantial temperature fluctuations over this period of study (average temperature calculated from the Central England Temperature (CET) data was quite high in the 1940s at 9.7°C, dipping substantially in the 1960s to 9.3°C, and then rising again in the 1990s to 10.1°C; Figure 4.3), with such a relatively large collection of data and large number of species compared with other groups A more dramatic shift would be expected if large scale variables such as climate were having an effect on distribution. Over the time periods of study, the isotherm shifted northwards in the UK by approximately 76km (calculated using CET data), which is quite a large distance, and if plants were responding to climate change by shifting their distributions, some degree of corresponding northward shift would be expected as they tracked this rapidly shifting isotherm. A shift of 11km south could occur quite easily due to changes in habitat or dispersal by man, as the north of England becomes more heavily populated.

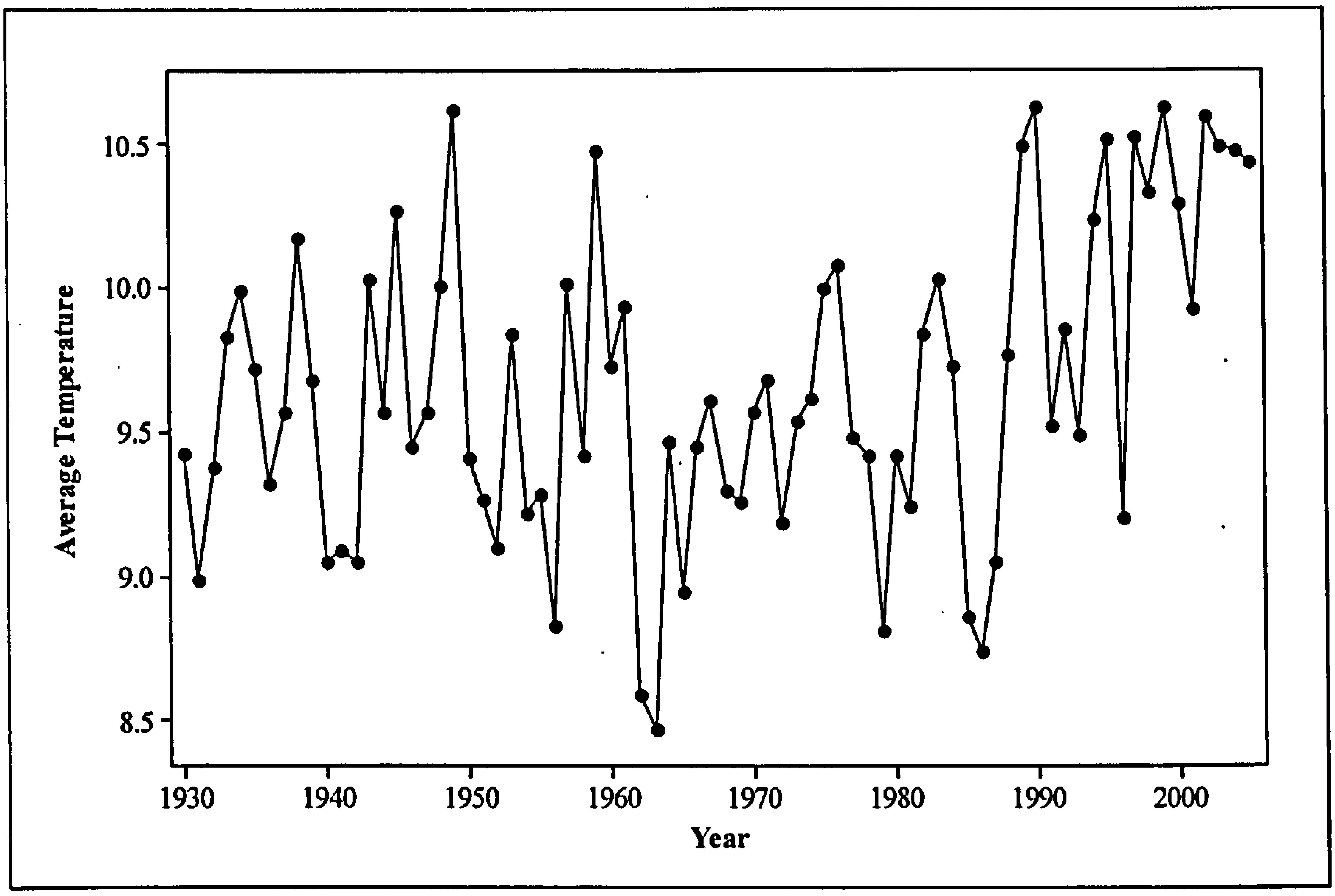

Figure 4.3: Variability in average yearly temperature (°C) calculated from Central England Temperature data.

Results from other studies of British plant distributions are variable. Whilst the New Atlas of the British and Irish Flora (Preston *et al.* 2002) found that northern species are in decline, it is likely that this is related to loss of habitat more than climate change, and therefore whilst species may be occurring in fewer 10km grid squares, a shift at the range margin would not necessarily be expected. This hypothesis is supported by a report of the Botanical Society of the British Isles Local Change survey (Braithwaite *et al.* 2006), which indicates that the northern species suffering the largest declines are found in threatened northern habitats such as moorland.

Other studies which have failed to detect the predicted latitudinal shifts in response to climate change have noted that some species are unable to colonize new sites in fragmented habitats, and many have very low dispersal and migration rates (Honnay *et al.* 2002). These species may be unable to track climate change even if habitat corridors are maintained. Therefore it is possible that plants will not show a distributional change in response to climate, or if they do, that change will occur over hundreds of years rather than decades.

If this is the case, it has strong implications for ecological interactions, particularly in temperate regions of the globe where climate warming will lead to a more rapid shift in isotherms. For example, species such as insects have already been shown to be responding quite rapidly to climate change by shifting their distribution northwards. The distributions of insects can sometimes be strongly constrained by the distribution of their host plants (Gutierrez & Thomas 2000), although other factors such as climate and weather can also limit insect distribution (Quinn *et al.* 1998). If plants do not track climate change latitudinally, these rapidly shifting insect species may soon be limited by a lack of host plants, or may be forced to adapt to using new host plants, which in turn could have a strong impact on other species historically found in that area.

The southward shift in the range margin of northern bird species was the opposite of what would be expected if they were responding to climate change. This may be because many of the northern bird species selected for analysis have suffered in the past from persecution such as poisoning, and work in recent decades to increase population sizes may have encouraged recolonisation of more southerly and low altitude sites, which, historically, have been well within the species' natural distribution. Previous studies of birds failed to find a northward retraction of the southern range margin (Thomas & Lennon 1999), but with such a varied avifauna in the UK, species selection is likely to have a strong effect on the result.

4.5.2: Altitudinal shifts of northern species

The results for altitudinal shift in northern species are more variable between groups than for latitude. The average shift across all species was just 2m uphill. However, 89 individual species shifted uphill compared with only 61 shifting downhill. This variety of response may be because altitudinal shifts can cover a smaller geographic area than equivalent latitudinal shifts, so distributions can shift up or downhill more rapidly as climate fluctuates. The UK also has a very diverse topography, and in some cases, observed shifts may simply be a result of latitudinal shifts to higher or lower areas of the country, but in many cases they may represent a genuine response of the population distribution to climate change.

Butterflies and spiders both shifted uphill between the two time periods, and this is comparable with previous findings (Hill *et al.* 2002, Konvicka *et al.* 2003, Wilson *et al.* 2005). This may reflect the fact that they also retracted northwards, so on average they occupied higher sites in the second time period, or it may reflect a genuine response as lowland sites became unsuitably warm and highland sites became milder. Given that other studies from both the UK (Hill *et al.* 2002) and from other European countries (Konvicka *et al.* 2003, Wilson *et al.* 2005) have found a similar trend of butterfly distributions shifting uphill, it seems most likely that this is a genuine and widespread response to climate change.

Carabids showed a northward retraction latitudinally, and yet a downhill shift. This could be explained if these species were colonising more grid squares in north-east Scotland, which has a lower altitude than the west. However, this is difficult to confirm without more specific data for that area. A targeted survey of carabid distributions in Scotland would help to answer this question, as well as help to inform the recording community about an area of general interest.

Whilst only a very small latitudinal shift was detected, and in the opposite direction to that predicted, a small but significant uphill shift was detected within northern plant species. Previous studies have found an altitudinal shift in plants from other countries (Kullman 2002; Penuelas & Boada 2003) so this may be the first sign of a response to climate change. As previously stated in the Introduction, altitudinal shifts are often easier to identify because they do not require such large geographic movements to occur in distributions in order for analysis to detect them. If plants are responding to climate change over a longer time scale than animals, then the more frequently reported altitudinal shifts may be the first stage of that response.

Despite northern bird species showing a large expansion south, possibly more due to habitat changes than climate, birds showed only a small shift downhill. Given that southern areas of Britain tend to be less mountainous than northern areas, a larger downhill shift would be expected to fit with the large southward shift. The fact that the downhill shift is comparatively small suggests that bird species may be selecting higher altitude habitats as they move south, further strengthening the hypothesis that the southward shift of bird species in recent years is only a temporary response to improved habitat, and suggesting that climate may yet be seen to affect this taxonomic group directly.

4.5.3: Comparison between northern and southern species

The results show that the response of northern species to climate change is not as clear as for southern species. Whereas most southern species in the UK shifted northwards at their northern range margin during the most recent period of climate warming, only just under half of northern species showed a comparable northward retraction at their southern boundary over the time period and temperature change. However, within three out of five groups studied, northern species showed, on average, a comparable northward shift to their southern counterparts. Only within birds and plants was this not the case.

In each of the three invertebrate groups studied, northern and southern species both showed a northward shift at the range margin. For all these groups, there was no significant difference between the degree of range margin shift in northern and southern species. This suggests that both northern and southern invertebrate species are highly responsive to climate warming and are able to colonise new areas quickly, but are also susceptible to quite rapid extinctions of populations at southern range margins. This conclusion contrasts with some of the previous literature (Hill *et al.* 2002) where systematic shifts northwards were not detected in invertebrates. However, the ecological characteristics of the specific species chosen for study and the methods employed to detect changes in distribution or abundance clearly have a strong outcome on the result. For example, more recent studies have detected a response to climate change at southern range margins (Wilson *et al.* 2005; Franco *et al.* 2006; Thomas *et al.* 2006).

There was no significant difference between northern and southern plant species, both groups shifting very little in either direction at their range margins. However, both northern and southern species did shift uphill very slightly, and this may indicate the beginning of a large scale distributional response to climate warming, as discussed previously.

Whilst most studies have failed to detect any latitudinal shifts in vascular plant distributions, some studies have found comparable indications of change. For example, lichens have been found to be responding to climate change. In this case boreo-montane and arctic-alpine species have decreased in abundance compared with warm-temperate and sub-tropical species (van Hark *et al.* 2002). Vascular plants and lichens may be expected to show different speeds of response to climate warming, as lichens tend to be more dispersive than plants due to their small spore size (Gilbert 2000), and this may explain why responses have been detected in lichens more than in plants.

If vascular plants do show a similar response to lichens in years to come, it would be expected that northern and montane species will fare less well than temperate or tropical species in a warming climate. On the other hand, some studies have demonstrated that Antarctic plant species are currently thriving in milder temperatures (Smith 1994) so the response of plants may depend very strongly on their habitat, competition with other species, interactions with herbivores and parasites, and the climatic conditions to which they are exposed. Ecological characteristics may also play an important role in whether or not plant species shift their distributions. For example, seed regenerating species have been shown to track climate more rapidly than vegetative species (Kullman 2002), and similar differences may apply to annual and perennial species, or generalist and specialist species, as has already been demonstrated for butterflies (Warren *et al.* 2001).

There are some differences in habitat requirement and ecological characteristics between the northern and southern bird species selected in this analysis. These differences have come about purely as coincidence during the process of species selection outlined in the methods section, and described more fully in Chapter 3. Southern species comprised a large number of insectivores and granivores, whilst northern species comprised large numbers of carnivores, and also upland and wading species.

There are three possibilities which can explain the distribution changes in UK birds. The first possibility is that both northern and southern species are indeed responding to climate change, and as previously stated, the unexpected southwards expansion of northern bird species may be a strong response to improved habitat conditions, which is obscuring any underlying response to climate.

The second possibility is that southern species are responding to climate by shifting northwards, because their overriding characteristics are to be small, and feeding on seeds or insects, making them particularly sensitive to temperature changes. Larger northern species which are predominantly carnivores and wetland birds may be less sensitive to climate changes.

The third possibility is that the northwards expansion in southern species is driven entirely by improved habitat in the north of the country and a reduction in persecution of certain species, and that birds are not responding to climate change. Without further investigation it is not possible to be certain which of these scenarios is actually occurring.

4.5.4: Possible explanations where northward retractions are not detected

Whilst I have demonstrated that many northern species, and particularly invertebrate species, are retracting at their southern range margin, possibly due to climate change, there are also many cases where this expected shift has not been detected. Where retractions at southern range margins have not been detected, either here or in previous studies, there are several possible explanations, as described in a number of papers (Davies *et al.* 1998; Davies *et al.* 2005). It is possible, particularly in Northern England and Scotland, that not enough data have been collected yet for most groups, in order to pick up any shifts at the range margin. Due to the difficulty in these areas of reaching some sites, data can often be quite patchy. Where high quality data are available, studies have detected northward retractions (Wilson *et al.* 2005; Franco *et al.* 2006; Thomas *et al.* 2006).

Another explanation is that not enough time may yet have passed for extinctions to occur, as every individual from a population must go extinct before it is recorded as an extinction. How rapidly populations respond to climate may therefore depend strongly upon ecological aspects such as how many generations can be produced per year and brood size, natural mortality and fecundity, longevity and dispersal. It may be supposed that responses to climate will be documented sooner in species with a rapid turnover of generations.

A similar explanation is that, due to the relatively coarse sampling level of 10km squares, extinctions have not yet been recorded as such, because every population in a 10km square must go extinct before the entire square is recorded as an extinction. A solution to this it to record data at a higher resolution suitable to the species of study. For example, range shifts at southern boundaries due to extinctions, in species with geographically small populations, may benefit from more intensive recording at a finer scale in order to detect range shifts more quickly. However, recorders frequently find such studies difficult due to time constraints and geographical restrictions. Where a small number of recorders are available, a specifically designed survey such as that used by Franco *et al.* (2006) may detect declines or extinctions more efficiently than a large-scale recording scheme. In the case of Franco *et al.* (2006), specific sites along the southern range margin where populations had been recorded historically were revisited, reducing the amount of effort required to detect changes in abundance at individual sites.

It is also possible that species at their southern range margin are able to survive in small areas where the climate has not so far changed much. Alternatively these species may not be limited by climate, but by competition with other southerly species (Darwin 1859), or by vegetation structure, and would therefore not be expected to shift at their southern range margin as climates warm in the short to medium-term.

4.5.5: Wider Implications

In Britain a larger proportion of northern species are naturally scarce compared with southern species, and some may have great difficulty in colonising new land masses further north as global warming makes them more climatically suitable. Therefore, where northern species are retracting at their range margins due to climate change they are becoming increasingly limited in habitat availability, and could become seriously threatened as climate warming continues. A further threat to these vulnerable northern species is encroachment upon their habitat by rapidly colonising southern species. Understanding fully the mechanisms behind distribution changes at southern range margins is essential if we are to preserve our rare northern species, both in the UK and in other countries.

Whilst the UK has an excellent history of collecting biological data, the nature of species distributions in the north of the country, and their scarcity, makes the UK less than ideal for studying range shifts at southern boundaries. Where long term data exist in other European countries, these may prove more useful for this type of study. Wherever possible, long term biological monitoring should be encouraged. Until suitably long term datasets have been established for study, analysis of altitudinal shifts, which can occur over a relatively short time period, may prove very useful in determining how much effect climate change may be having on species at their southern range margin.

4.6: Conclusion

Within insects and spiders, northern species are, on average, showing a similar response to climate change as their southern counterparts. However, fewer northern species have shifted northwards than southern species. The reasons for this may be varied, and further study is required, possibly in other countries where southern ranges are not so confounded by geographic variation and scarcity of species.

Chapter 5

The relationship between phenological and distributional change.

5.1: Abstract

Evidence is accumulating of changes in the size and position of species' distributions during recent climate warming. Changes in the timing of life cycle events have also been shown for a wide variety of different species. However, it is not known whether or not these two distinct measures of a species' response to climate warming are related to one another. Here, results indicate that a (weak) relationship exists between distribution and phenology changes amongst British butterflies (N = 35 species), once numbers of generations per year and habitat breadth are accounted for. However, distribution and phenology changes were not significantly related in either plants (N = 351 species) or birds (N = 60 species), even after accounting for ecological traits. It is possible, however, that such relationships might emerge in the future.

5.2: Introduction

During recent global climate warming (IPCC 2001), many studies (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003) have shown that species have exhibited changes in abundance (Roy *et al.* 2001; Conrad *et al.* 2006; Fox *et al.* 2006a) and distribution size (Warren *et al.* 2001; Fox *et al.* 2006a), or have shifted their distributions polewards (Parmesan *et al.* 1999; Hill *et al.* 2002; Hickling *et al.* 2006) or to higher altitude (Hill *et al.* 2002; Konvicka *et al.* 2003; Wilson *et al.* 2005; Franco *et al.* 2006). In other cases, the timing of species' life cycle events has been shown to be changing (Crick & Sparks 1999; Menzel & Fabian 1999; Roy & Sparks 2000; Fitter & Fitter 2002). Generally, studies have considered distributional and phenological changes as separate phenomena when carrying out meta-analyses of ecological impacts of climate warming (e.g., Hughes 2000; Parmesan & Yohe 2003), but it is not known whether distribution and phenology changes are related to one another.

5.2.1: Relationship between distributional and phenological change

It could be argued that distributional and phenological changes could be positively or negatively associated with one another, or that there might be no relationship. Positive relationships might be expected if highly temperature-sensitive species show both strong phenological responses to climate change and rapid distributional changes. Negative relationships may occur for species that show a strong phenological response because they have been able to adjust sufficiently to the new conditions *in situ* such that distributional responses do not occur. Alternatively, some species may change distribution partly because they have failed to adapt their phenology (e.g. species returning to their breeding grounds too late in the year for their food resources might move further north to find locations where their breeding would be synchronised with food availability). Finally, it is possible that phenological and distributional responses are not directly related to each other. This might occur, for example, if changes in the timing of the life cycle does not result in any net change in population growth, or if phenological disjunction between a species and its food supply (Visser *et al.* 1998; Crick & Sparks 2006) might lead to population decline and hence lack of distributional change, or even range contraction.

5.2.2: Differences between taxa

A further complication is that the relationship between phenology and distribution change might vary among different taxonomic or functional groups within a particular set of organisms. For example, distributional responses of species to climate warming have been shown to vary in relation to habitat associations (Warren *et al.* 2001) and both distributional and phenological responses have been related to generation time (Fitter & Fitter 2002; Perry *et al.* 2005).

5.2.3: General aims of this chapter

Here, data is analysed for British birds, butterflies and plants. Data are taken directly or derived from published studies of phenological and distributional changes associated with climate warming. The relationship between measures of phenology and distributional changes, and whether relationships vary according to species' ecological traits, are investigated. Where possible ecological traits that were comparable across taxa were used in analyses; for example the importance of generation time (and thus population growth rate) was examined by including into analyses either number of generations per year (butterflies), number of broods per year (birds) or annual, biennial or perennial lifecycle (plants). Taxon-specific traits that have been shown to affect responses to climate were also investigated; these included mode of pollination for plants (Fitter & Fitter 2002), and habitat associations of butterflies (Warren *et al.* 2001). In addition, other ecological traits and life history elements that are likely to affect species' sensitivity to climate were examined. These were body size and feeding guild in birds: Stevenson & Bryant (2000) predicted, on the basis of energetics studies, that the impacts of climate warming should be more evident in smaller-bodied species than larger bodied ones and they showed, using data in Crick & Sparks (1999), that the degree of phenological advancement for a species, per °C warming, was inversely correlated to body mass. Certain feeding guilds such as omnivores might be expected to respond more flexibly to changes in climate (Crick 2004). Overwintering form in butterflies and life form in plants were also investigated because the sensitivity to climate of different stages in the life cycle might affect the species' response to climate (Roy *et al.* 2001; Conrad *et al.* 2004).

5.3: Methods

For each taxonomic group, two measures of distribution change were calculated, in the same way as in Chapter 2: first, the change in the number of 10km grid squares occupied in Britain (subsequently termed 'distribution change') and second, the mean change in the latitude of the ten most northern (for southerly-distributed species) or southern (for northerly-distributed species) 10x10km grid squares (subsequently termed 'latitudinal change'; Hickling *et al.* 2006). For all three taxonomic groups, the number of species reaching a range limit in Britain is only a sub-set of all species and so sample sizes in analyses of latitudinal changes are reduced. Nonetheless, latitudinal change was analysed as this may be a more sensitive measure of species responsiveness to climate compared with my other measure of distribution changes. Phenology measures differed among taxa and were date of first sighting of adult butterflies, date of egg-laying in birds, and flowering date of plants (see below).

5.3.1: Sources of data

i) Butterflies

For 35 species, rates of changes in the date of first appearance of adults between 1976 and 1998 were obtained from Roy & Sparks (2000). These data are calculated from Butterfly Monitoring Scheme transect data (Pollard & Yates 1993). For each species, phenological change was calculated from the slope of the regression of date of first appearance (mean across monitored sites; data for the first generation for multivoltine species) against year (see Roy & Sparks (2000) for details). Change in distribution size between 1970-82 and 1995-99 was calculated from data in Thomas *et al.* (2004). These data are derived from intensive surveys prior to the publication of national atlases (Heath *et al.* 1984, Asher *et al.* 2001) and record presence of species at 10km grid resolution. Recorder effort increased over time and so distribution changes were estimated from data that had been sub-sampled to produce similar sampling effort in the two time periods (Thomas *et al.* 2004). Latitudinal shifts were estimated for 18 species that reach a northern range limit in Britain (according to Methods above) using data from Hickling *et al.* (2006). Number of generations (one or more than one), generalist or specialist species (based on number of habitats and habitat availability), and overwintering form (egg, larvae, pupa or adult) were defined following Pollard & Yates (1993).

ii) Birds

For each species, rates of change in mean egg-laying date were calculated for 60 species using data from Crick & Sparks (1999). Phenological change was estimated from the slope of the regression of first-egg-laying date (mean across monitored sites; data for the first generation for multi-brooded species) against year (weighted by number of sites recorded each year) over the period 1968-1991 (corresponding with the recording periods of distribution changes (Gibbons *et al.* 1993)). For some species in some years, laying dates were available from fewer than 10 nests and so analyses were carried out either including or excluding data for these years. However, this made no qualitative difference to the overall results, and so the full dataset was used in all subsequent analyses in order to incorporate as many data as possible.

Change in distribution size was the percentage change in distribution extent at a 10km grid resolution between 1968-72 and 1988-91 in Britain, as stated in Gibbons *et al.* (1993). For those species reaching a range limit in Britain, latitudinal changes were taken from Hickling *et al.* (2006; northern species' data from Chapter 4). Due to the selection of species used in Hickling *et al.* (2006), only a very small number of species (n = 7) were the same across datasets. Therefore this analysis was repeated using data from Thomas & Lennon (1999). These authors used identical methods for estimating latitudinal changes, but were much less stringent in selecting which species reached a range limit in Britain and so enabled the incorporation of more species into analyses (n = 34). Data on number of broods per year (one, two, or three or more), body size (small (<24cm) or large (>24cm)) and feeding guild (omnivore, carnivore, insectivore, granivore) were obtained from Cramp & Perrins (1993).

iii) Plants

For 385 species, rates of change in mean flowering date were calculated using data from Fitter & Fitter (2002); phenological change was calculated for each species from the slope of the regression of first flowering date against year over the period 1954–2000. Distribution changes over the same time period were estimated from the Change Index (Telfer *et al.* 2002). This index measures the change in frequency of species in 10km squares between 1930-69 and 1970-99 relative to the average change of frequency of all species. Latitudinal changes were calculated using the same methods as for butterflies and birds, for the period 1930-70 to 1987-99 from data in Preston *et al.* (2002). Data on life cycle (perennial, biennial or annual) were from Hill *et al.* (2004), Raunkiaer life form (classifies species according to the height of the resting buds in winter) and pollination vector (insect or wind) were derived from the EcoFlora database (Fitter & Peat 1994; www.ecoflora.co.uk).

5.3.2: Analysis

For each taxon, the relationships between phenological change and distributional change, and phenological change and latitudinal change were examined using regression analysis. These analyses were extended using general linear models with distribution/latitudinal change as the response variable and phenology as the covariate and including the effects of life history elements and ecological traits as fixed factors. For butterflies, life history elements chosen were number of generations per year, habitat associations and over-wintering form. For birds, life history elements chosen were number of broods per year, body size and feeding guild. For plants, life history elements chosen were life cycle, life form, and mode of pollination. Family was included as a random factor in these analyses to investigate the importance of phylogenetic effects, and to allow for these effects in significance tests.

5.4: Results

5.4.1: Distribution changes and phenology

Of the three taxonomic groups studied, butterflies were the most sensitive to climate changes over time and showed the greatest overall advancement in phenology, the greatest distribution changes, and the greatest latitudinal shift northwards (Table 5.1).

Across all three taxonomic groups, there was no significant relationship between distribution change and phenology (regression; butterflies, n = 35 species, R^2 = 9.8%, slope = -0.159, $p = 0.068$; birds n = 60 species, R^2 = 0.4%, slope = 5.09, $p = 0.619$; plants n = 351 species, R^2= 0.8%, slope = -0.316, $p = 0.103$). When life history elements, ecological traits and phylogeny were incorporated into generalized linear models, these results were not changed qualitatively for plants and birds, but were changed for butterflies (Table 5.2, Figures 5.1, 5.2).

For butterflies, when number of generations (univoltine or multivoltine) was accounted for, a significant negative relationship between distribution and phenological change was found (Generalized Linear Model; $F_{1,30} = 5.22$, $p = 0.030$), showing that species exhibiting the greatest phenological changes also showed the greatest increases in distribution size, with phenology accounting for 14% of the variation in the dataset. There was no significant effects of phylogeny (family identity, $F_{3,28} = 0.42$, $p = 0.741$).

Similar results were obtained for butterflies when habitat association (generalist or specialist) was included in analyses, instead of number of generations, when there was also a significant negative relationship between phenology and distribution change (Table 5.2). Habitat association was included in the study because it is commonly used to categorize

Table 5.1: Summary data showing phenological change, distributional change, and latitudinal change, for three taxonomic groups, and split by different life history traits. See text for details of methods for calculating change variables (means and standard errors are shown). Negative values indicate phenological advancement, decline in distribution size, and latitudinal shift southwards. Bird species selected for analysis of latitudinal change follow Thomas & Lennon (1999).

	Phenological Change (days)			Distribution change (% change or relative change)			Latitudinal change (km)		
	No. of species analysed	Arithmetic Mean	S.E.	No. of species analysed	Arithmetic Mean	S.E.	No. of species analysed	Arithmetic Mean	S.E.
All Butterflies	35	-0.37	0.079	35	-6.3%	4.00	18	46	13.9
Univoltine Butterflies	22	-0.46	0.085	22	-10.1%	4.74	13	44	9.4
Multivoltine Butterflies	13	-0.23	0.151	13	0.2%	7.08	5	51	47.7
Generalist Butterflies	24	-0.37	0.105	24	3.7%	4.07	12	53	15.5
Specialist Butterflies	11	-0.38	0.105	11	-28.2%	4.47	6	31	18.0
All Birds	60	-0.04	0.034	60	-4.0%	2.66	34	-7	8.4
Single Brood Birds	18	-0.01	0.085	18	-0.3%	7.25	9	6	10.3
Double Brood Birds	22	-0.05	0.047	22	-6.1%	3.68	14	-8	14.0
Many Brood Birds	20	-0.04	0.049	20	-6.2%	2.49	11	-16	17.6
All Plants	351	-0.11	0.012	351	0.09	0.044	26	-3	7.8
Annual Plants	54	-0.19	0.037	54	0.09	0.124	0	n/a	n/a
Biennial Plants	29	-0.07	0.032	29	-0.03	0.086	3	-2	3.1
Perennial Plants	268	-0.10	0.014	268	0.10	0.052	23	-3	24.3

Table 5.2: Results of Generalized Linear Models examining the effects of different life history elements, ecological traits and phylogeny on the relationship between changes in phenology and distribution. A = relationship between phenology and distribution change, B = difference between groups (ecological traits and life history elements), C = effect of Family.

Taxonomic Group	Life History Element	Results A	 B	 C
Butterflies	Number of generations	$F_{1,30} = 5.22, p = 0.030$	$F_{1,31} = 1.84, p = 0.185$	$F_{3,28} = 0.42, p = 0.741$
	Generalists v Specialists	$F_{1,30} = 6.61, p = 0.015$	$F_{1,31} = 25.91, p < 0.001$	$F_{3,28} = 1.49, p = 0.239$
	Overwintering form	$F_{1,26} = 1.00, p = 0.327$	$F_{3,14} = 1.11, p = 0.379$	$F_{3,24} = 0.90, p = 0.457$
Birds	Number of broods	$F_{1,49} = 0.19, p = 0.665$	$F_{2,22} = 0.35, p = 0.710$	$F_{24,30} = 1.83, p = 0.058$
	Feeding Guild	$F_{1,47} = 0.04, p = 0.841$	$F_{3,12} = 1.35, p = 0.308$	$F_{24,28} = 1.39, p = 0.202$
	Body size	$F_{1,55} = 0.08, p = 0.784$	$F_{1,17} = 0.70, p = 0.414$	$F_{24,32} = 1.65, p = 0.092$
Plants	Perennial, Biannual, Annual	$F_{1,343} = 2.64, p = 0.105$	$F_{2,175} = 0.26, p = 0.770$	$F_{69,276} = 1.36, p = 0.043$
	Pollination strategy	$F_{1,343} = 2.71, p = 0.101$	$F_{2,30} = 1.66, p = 0.207$	$F_{69,276} = 1.31, p = 0.068$
	Life Form	$F_{1,328} = 3.03, p = 0.083$	$F_{3,65} = 1.93, p = 0.133$	$F_{69,274} = 1.48, p = 0.014$

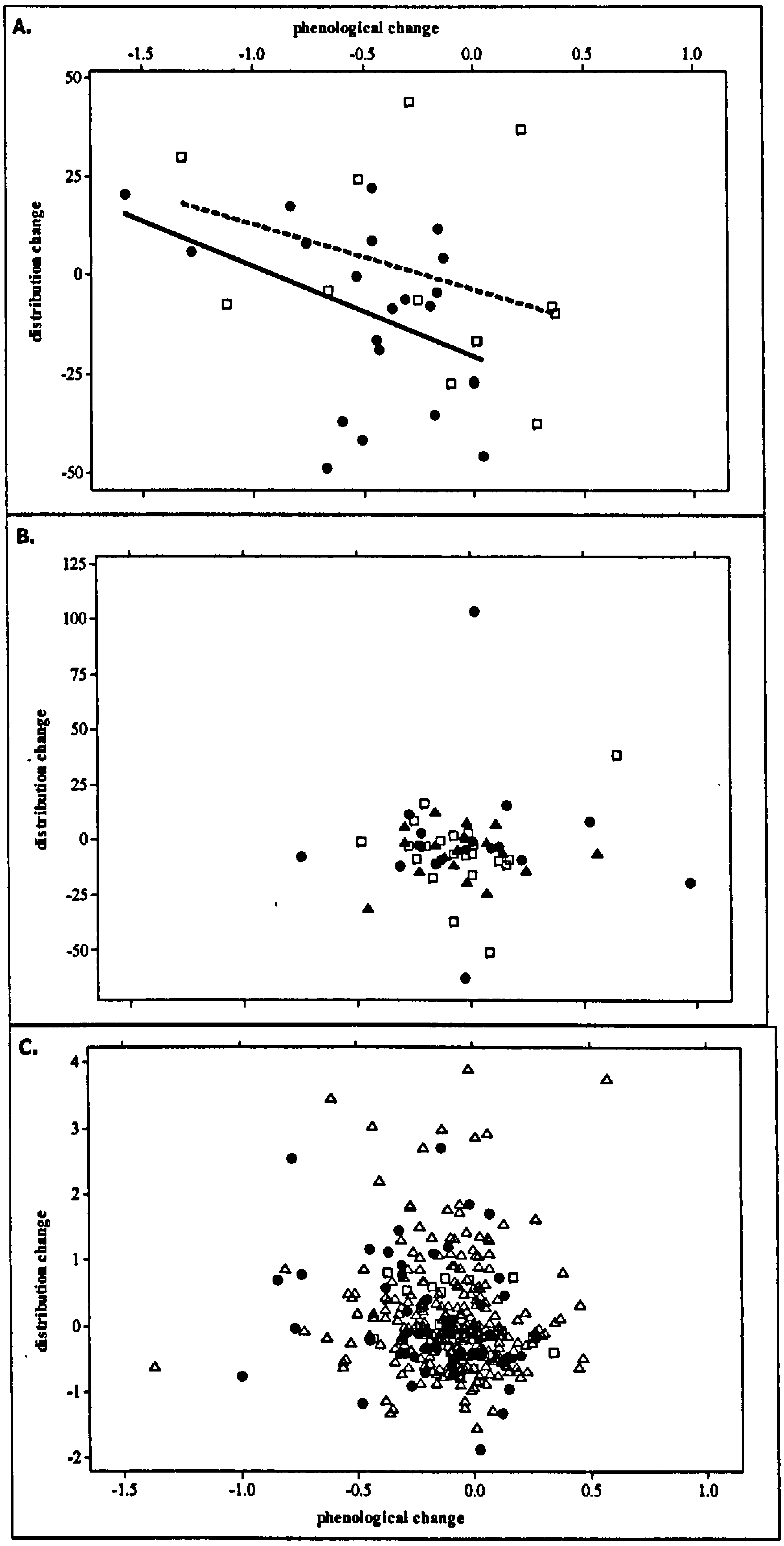

Figure 5.1: The relationship between phenological and distributional change in relation to number of generations per year. [A] – butterflies, solid circles and lines = univoltine, hollow squares and dotted lines = multivoltine; [B] – birds, solid circles = one brood possible, hollow squares = two broods possible, solid triangles = three or more broods possible; [C] – plants, solid circles = annual, hollow squares = biannual, hollow triangles = perennial. The regression line is shown where significant, fitted separately for each group. See text for methods of calculating phenological and distribution change for each taxon.

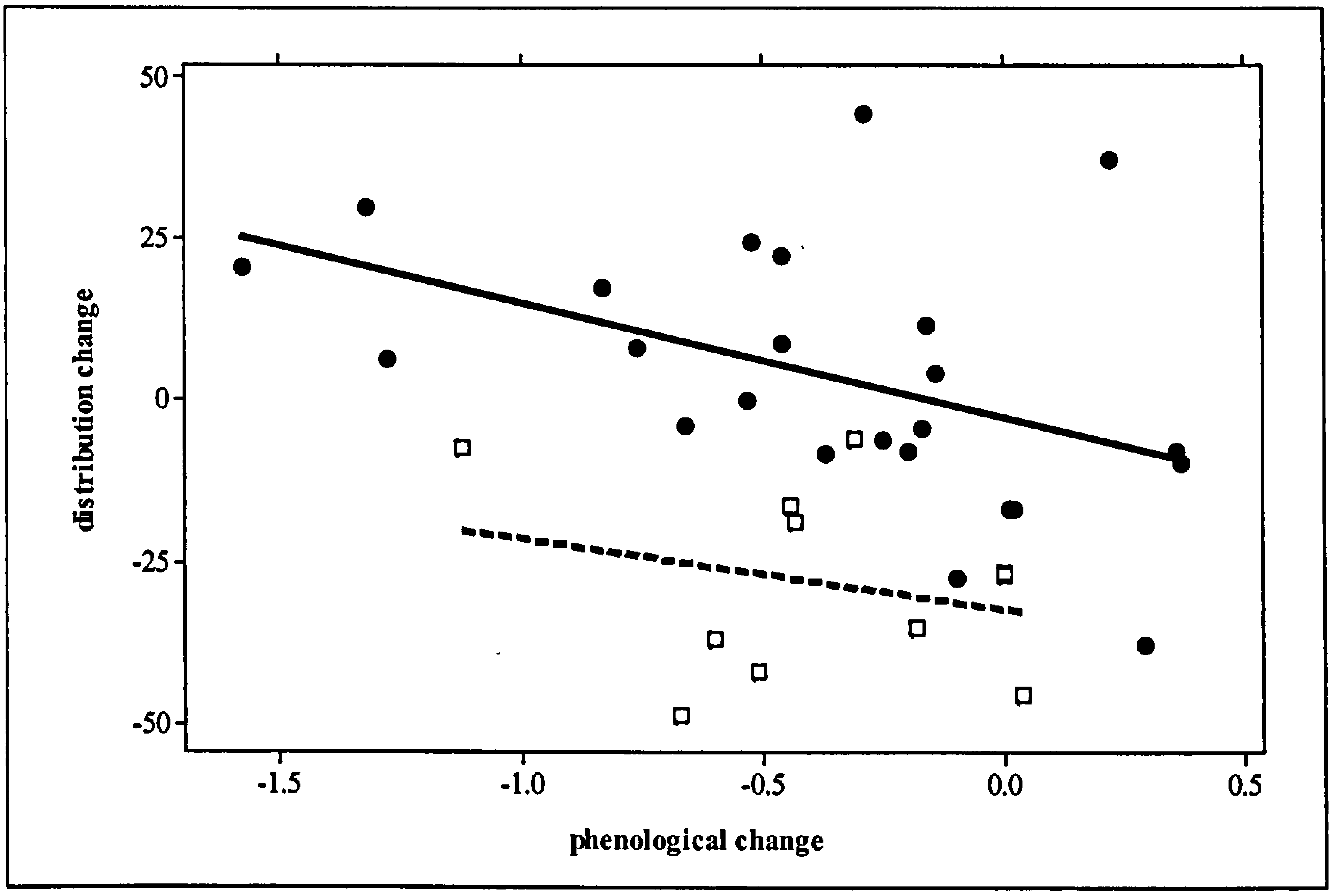

Figure 5.2: The relationship for butterflies between phenological and distributional change in relation to habitat associations. Solid circles and lines = generalists, hollow squares and dotted lines = specialists (an increase on the y axis indicates an increase in percentage distribution size). Regression lines are shown fitted separately for each group.

butterfly species (Warren *et al.* 2001), even though it is a somewhat arbitrary measure. In this analysis, there was a significant difference between generalists and specialists in the elevation of the regression line (habitat association factor, $F_{1,31} = 25.91, p < 0.001$; Figure 5.2), showing that many generalist species had maintained their distribution size whereas specialists had declined, but the slope of the regression was not significantly different between habitat groups (interaction effect, $F_{1,21} = 0.15, p = 0.705$). Again, there was no significant effect of phylogeny (family identity, $F_{3,28} = 1.49, p = 0.239$) in this analysis, and no significant effect of over-wintering form in any analyses.

There was still no significant relationship between distributional and phenological changes for either birds or plants in any analyses, regardless of whether life history elements, ecological traits, or phylogeny were included in the model (Table 5.2, Figure 5.1B, 5.1C).

5.4.2: Latitude changes and phenology

Relatively few species in any taxon reach their range limits in Britain and so sample sizes for latitude change analyses were lower than in analyses of distribution changes. For butterflies, there was a significant negative relationship between phenology and latitudinal change (regression; n = 18 southern species, $R^2 = 24.2\%$, slope = -71.89, $p = 0.038$): butterfly species with the greatest tendency to fly earlier in the year have also tended to move northwards the most. When species were analysed according to number of generations, overall significance of the relationship between phenological and distribution change was marginal (Table 5.3; $p = 0.055$). When habitat association was considered instead of number of generations, a significant negative relationship between phenology and latitudinal change was also found (Table 5.3; $p = 0.017$). In this case 29% of the variation was accounted for by phenology (calculated from the Generalized Linear Model including family as a random factor).

For birds and plants, there was no relationship between phenology and latitudinal change (regression; birds, n = 7 species, $R^2 = 0.1\%$, slope = -2.45, $p = 0.939$; plants, n = 26 species, $R^2 = 6.3\%$, slope = -41.41, $p = 0.217$). For birds, this finding was qualitatively similar regardless of whether data from Hickling *et al.* (2006) were analysed (as above), or data from Thomas & Lennon (1999), for which more species were available (regression; n = 34 species, $R^2 = 0.3\%$, slope = -8.38, $p = 0.771$). Incorporation of life history elements, ecological traits and phylogeny into a Generalized Linear Model did not qualitatively change these findings for any of the taxa (Table 5.3).

5.5: Discussion

5.5.1: Relationship between phenology and distribution in butterflies

Phenological and distributional change (both distribution size and latitudinal margin) were correlated with one another in butterflies (Figure 5.1A, 5.2). This indicates that species that have responded strongly to climate change by flying earlier in the year have also increased in distribution size and moved northwards the most. Equally, those species that have not undergone any phenological change, or, for a few species, are flying later in the year, have generally decreased in distribution size. However, there are some

Table 5.3: Results of Generalized Linear Models examining the effects of different life history elements, ecological traits and phylogeny on the relationship between changes in phenology and changes in latitude. A = relationship between phenology and latitudinal change, B = difference between groups (ecological trait, life history element), C = effect of Family.

Taxonomic Group	Life History Element	Results A	 B	 C
Butterflies	Number of generations	$F_{1,12} = 4.51, p = 0.055$	$F_{1,14} = 0.06, p = 0.808$	$F_{3,11} = 0.55, p = 0.656$
	Generalists v Specialists	$F_{1,12} = 7.65, p = 0.017$	$F_{1,12} = 0.92, p = 0.357$	$F_{3,11} = 0.54, p = 0.663$
	Overwintering form	$F_{1,7} = 1.61, p = 0.245$	$F_{3,10} = 3.74, p = 0.050$	$F_{3,7} = 0.40, p = 0.756$
Birds	Number of broods	$F_{1,28} = 0.07, p = 0.799$	$F_{2,14} = 0.44, p = 0.650$	$F_{18,10} = 1.19, p = 0.401$
	Feeding Guild	$F_{1,26} = 0.14, p = 0.712$	$F_{3,26} = 0.89, p = 0.460$	insufficient data
	Body size	$F_{1,30} = 0.01, p = 0.920$	$F_{1,11} = 1.27, p = 0.284$	$F_{18,12} = 1.34, p = 0.308$
Plants	Perennial, Biannual, Annual	$F_{1,22} = 1.48, p = 0.236$	$F_{1,22} = 0.02, p = 0.879$	insufficient data
	Pollination strategy	$F_{1,21} = 1.49, p = 0.235$	$F_{1,8} = 0.20, p = 0.666$	$F_{12,10} = 0.65, p = 0.764$
	Life Form	$F_{1,22} = 1.58, p = 0.222$	$F_{1,22} = 0.20, p = 0.659$	insufficient data

differences among butterfly species, depending on the number of generations per year, and the types of habitat they inhabit. On the whole, species with a single generation per year (univoltine) have decreased in distribution size and shown greater phenological advancement, whereas multivoltine species have shown little overall change in distribution size (some have expanded, others have declined) and less phenological advancement (Table 5.1), leading to a difference between the two groups (Figure 5.1A). Species capable of multiple generations per year are able to increase more in abundance during climate warming compared with univoltine species (Roy *et al.* 2001), and might therefore also be expected to expand their ranges more through increased propagule pressure.

The classification of butterfly species into generalists and specialists could be considered to be somewhat arbitrary, reflecting the availability of habitats in the landscape, as well as basic attributes of the biology of the species (Pollard & Yates 1993; Warren *et al.* 2001). However, this classification was included in this study because it is so commonly used in other studies and is therefore useful for comparison. Significant negative relationships between phenology and distribution size/latitude were maintained in butterflies when habitat association was incorporated in analyses (Figure 5.2; Table 5.3). Generalists are able to survive in existing habitats and spread more rapidly across fragmented landscapes, so distribution changes have been much more positive than for specialists (Hill *et al.* 1999b; Thomas *et al.* 2001; Warren *et al.*, 2001).

5.5.2: No relationship for birds or plants

No relationship was detected between phenological and distributional change for either birds or plants, even though more species were available for analysis in these groups and so these analyses might be expected to have more statistical power (Table 5.2, Figure 5.1B, 5.1C). The life history categories were chosen to reflect characteristics of species that were as similar as possible across groups. For example, possible number of broods in birds and perennial versus annual plants are the equivalent of number of generations per year in butterflies, yet controlling for this did not reveal any relationships between phenology and distribution change. Feeding guild in birds is comparable with generalists and specialists in butterflies to some extent, as both attributes consider food and habitat flexibility, which could affect rate of response to climate change, yet relationships were significant only in butterflies. Alternatively, it is possible that the lack of correlation between distribution change and phenology in plants and birds is that the time periods for which data were available in these groups do not reflect as great a period of climate change as for butterflies. Thus, it is possible that relationships between distribution change and phenology will emerge with subsequent data.

My conclusion therefore is that relationships between phenology and distribution or latitude changes for plants and birds were weak or absent. Given the sample sizes analysed in these groups, I would have expected to detect significant relationships for birds and plants had they been as strong as those for butterflies, where up to 29% of the variation was explained. Of course, it is possible that relationships might have been revealed had I incorporated other measures of life history variation. Nonetheless, the life history elements chosen were comparable across groups and included the commonly analysed traits.

5.5.3: Differences between butterflies and birds and plants

Assuming the results reflect reality, other possible reasons why these results for butterflies should differ from those for birds and plants must be examined. It is possible that birds and plants are not as sensitive to climate change as butterflies, and that a relationship may emerge over a longer time period. Some studies of distribution change in plants have come to the conclusion that plants may be slow to respond to changes in climate, due to low dispersal rates (Honnay *et al.* 2002). Likewise, whilst some studies of birds have identified climate-driven distributional changes in recent years (Thomas & Lennon 1999; Hickling *et al.* 2006), habitat changes may have a stronger effect upon distribution change in this group of homeothermic animals, and so the link between climate and distribution change in birds may not be as strong as it is for butterflies.

I suggest that phenology and distribution changes are linked in butterflies because they are short-lived poikilotherms, with weather-related population growth rates (especially in species with flexible numbers of generations per year), that are sufficiently mobile for at least some of the changes in population growth rates to be translated into distribution changes. By contrast, the failure of most plants to express climate-related range changes due to dispersal limitation, and more complex linkages between phenology shifts and population growth rates in homeothermic birds (Both & Visser 2005) may have obscured any overall relationships; although it is possible that they might emerge in the future.

5.5.4: Wider implications

My analysis clearly identifies a relationship between phenological and distributional changes in butterflies, and this has consequences for future ecological research. In some cases, focusing on phenology may be preferable, because phenological data may be easier to collect over long periods of time compared with distributional data. However, phenological data should not be used in isolation because, whilst the relationship with distribution change is statistically significant, there is considerable variation in the data, and so monitoring of distribution change is also essential to our understanding of how butterflies are responding to climate change. In addition, we still have no information on the relationship between phenological and distribution change in biotas where most species are retreating. In Britain, the majority of species have relatively southerly distributions, and should in principle be able to expand northwards. In regions where the majority of species are retreating in response to climate change, the relationship between phenology and distribution change could be quite different.

My results have wider implications for researchers assessing the impacts of climate change. Much of the evidence for the impacts of climate change on wildlife comes from phenology studies (Parmesan & Yohe 2003; Root *et al.* 2003; Root *et al.* 2005), but for birds and plants in Britain, phenology changes were not linked to distribution changes over the time period considered. However, distribution and abundance changes are ultimately the important responses of species to climate change as these measures drive conservation policy and are the variables used to measure the status of species. Therefore, it is important that the impacts of climate change on species are not assessed solely by phenological responses.

5.6: Conclusion

There was a significant relationship between phenological and distributional changes in butterflies, but phenology only explained 14% and 24% of the variation in distribution and latitudinal changes, respectively (after accounting for whether species were univoltine or multivoltine). This suggests that both phenological and distribution measures are needed when interpreting recent responses to climate change, and when predicting possible future responses. No relationships between phenological and distributional changes were detected for birds or plants, but it is possible that a similar relationship to that of butterflies will emerge over time.

Chapter 6

Abundance changes in birds and insects as a response to climate change.

6.1: Abstract

There are few studies of changes in abundance in relation to climate change, particularly across different taxonomic groups and for northern species, for which data are often scarce. This is an important aspect of ecology to study, because a decline in northern species would be expected if climate primarily determines population size, as temperatures increase and become less suitable for cold-loving species. Here, abundance datasets from the Rothamsted Insect Survey, the Common Bird Census, and the Butterfly Monitoring Scheme were analysed in two different ways, in order to establish how climate change is affecting abundance of British species. The first method examined changes in abundance between northern and ubiquitous moth species at the same sites. Moth data showed little evidence of greater abundance declines over time in northern species compared with ubiquitous species, although northern moth species were present at much lower abundance levels overall. The second method examined changes in the proportions of in northern and ubiquitous species of moths, birds and butterflies, in hot, warm and cool regions of Britain. There was also no difference between abundance changes of northern and ubiquitous moths and butterflies, although northern bird species did appear to decline to a greater degree than their ubiquitous counterparts, particularly in the hottest parts of their range. Lack of significant results may have reflected lack of sensitivity in the data; study periods may not have been long enough, and few northern species were available for analysis. Relative declines in abundance of northern bird species may have been detected because birds show less year to year variation compared with insects.

6.2: Introduction

6.2.1: The predicted relationship between abundance and climate change

Changes in abundance of individuals within a population have been documented frequently over recent years, and in many cases these changes in abundance have been linked to climate change. Parmesan & Yohe (2003) demonstrated via meta-analysis that, in 81% of cases of abundance change, change was in accord with what would be expected if climate change were responsible. The most common response predicted in European studies, and what has been most commonly observed, is that as global temperatures increase, the abundance of northern or montane species will decrease. By contrast the abundance of southern species will increase, as those species which are warm-loving, and whose northern boundaries are limited by cold climates, will be most favoured by a warming climate. This has been predicted or documented in a wide range of taxa, including lichens in the Netherlands (van Hark *et al.* 2002), butterflies in Britain (Roy *et al.* 2001), marine fish (Perry *et al.* 2005), and copepods in the North Sea (Beaugrand *et al.* 2002).

However, in some cases, studies have found conflicting examples of abundance change in response to climate. In the UK, a study of abundance trends over time in moth species (Conrad *et al.* 2004) found that species with populations across the whole country (ubiquitous species) tended to be decreasing in abundance at southerly sites and increasing at northerly sites: the opposite to that predicted if climate change was a major factor affecting decline. However, this study also found that southern species reaching a northern range margin in Britain were, on average, increasing in abundance: the predicted response to climate change. The authors concluded that, for British moths, both habitat and climate change were having a strong effect on population sizes. For example, the decrease in grassland specialist species may be a response to loss of grassland habitats in recent decades, as has already been noted in studies of butterflies (Thomas & Abery 1995; Asher *et al.* 2001). The increase in southern species, on the other hand, was attributed more to climate warming than to habitat change, with milder winters favouring species which overwinter as adults. Another interesting point of note was that species which overwintered at the egg stage of development showed a sharp population decline, suggesting that milder winters may reduce hardiness, or increase susceptibility to pathogens in these species

(Conrad *et al.* 2004). This is an excellent example of the complex relationships between abundance, climate and habitat change in insect species.

6.2.2: Patterns of decline and variability

If predictions are based on theory rather than previous studies, it could be surmised that a northern species at its southern range margin will have more variability in abundance. This is based on observations by Thomas *et al.* (1994) who found that, in nine out of 24 species of butterfly, populations showed more variability in abundance towards their northern range margins. Increased variability in abundance is likely towards all range margins, regardless of whether they form a northern or southern range limit, and thus the observed pattern of increased variability is likely to be the same for species at their southern range margins. This would lead to an increased sensitivity to climatic changes and overall decline in abundance (McLaughlin *et al.* 2002) at range margins. Both unusually hot and unusually cold years would be expected to fall within the species' tolerance zones in the centre of the species' distribution, whereas at range margins extreme years could cause individuals to experience conditions beyond their physiological tolerances, leading to extreme mortality or reduced fecundity.

6.2.3: The potential importance of abundance changes

In some cases, quantifying the shift of the southern range margin, as I did in Chapter 3, may not be a sensitive measure of the response to climate warming of northern species. This is because, at the southern range margin, extinctions may occur patchily, throughout the southern part of a species' distribution, rather than along the edge of the range margin, because at some sites populations may persist in favourable microclimates (Thomas *et al.* 2001; Davies *et al.* 2006). This would not necessarily lead to any latitudinal shift in the range margin, despite potentially large decreases in abundance at these occupied sites. In such cases, analysis of abundance data may illustrate responses to climate change more reliably than distribution data because decreases in abundance within sites could potentially be detected at a much earlier stage than range margin shifts. Furthermore, relatively small decreases in distribution size can sometimes be accompanied by large decreases in abundance (Shoo *et al.* 2005), and in such cases studies focusing on distribution change will give very conservative estimates of the extinction risk to a species.

As with many studies of ecological processes, scale is very important when studying abundance changes. For example, in a study of butterflies (Cowley *et al.* 2001), the abundance changes detected at a small scale (1km x 1km) were much greater than those detected at a larger scale (10km x 10km). This is one of the primary reasons why my first method analysed abundance data at a small scale, by analysing moth data from individual sites.

6.2.4: Availability of data

As is so often the case, even with large biological datasets, there are few datasets with abundance data that span more than a couple of decades. When investigating the effect of climate change, it is particularly important to have datasets which span as long a period of time as possible during which climate warming has taken place, in order to detect changes which are a response to the increase in temperature over the time period. Datasets of a shorter period may not cover sufficiently large temperature changes for species' responses to be detected. In the UK, suitable data are available only for butterflies, moths and birds, from the Butterfly Monitoring Scheme (1976-2004), Rothamsted Insect Survey (1968-2003), and the Common Bird Census (1966-2002), respectively.

6.2.5: General predictions and aims of this chapter

In this chapter I use two different methods to analyse existing long-term datasets for birds, moths and butterflies. I examine the success of each method and compare results obtained from different methods and between species groups. Specifically, I examine the following questions:

i) Changes in abundance of northern species

Have northern species of butterflies, moths and birds decreased in abundance in recent years in the UK, and is the decline more pronounced at lower latitudes; ie. towards the southern edge of the range?

ii) Comparison with southern species

At the same sites and over the same time periods, have species with southern or ubiquitous distributions increased in abundance, compared with northerly distributed species, which would be expected to decline?

iii) Comparison between taxonomic groups

Do butterflies, moths and birds differ in the patterns of abundance changes of northern species, and if so what possible reasons could explain such differences?

6.3: Methods

I developed two different methods (see below) for analysing abundance data. The first method was developed and applied only to the moth dataset. However, this method required data for specific species and sites to be collected intensively over time, and data for butterflies and birds were not suited to this method. Therefore, a second method was developed and applied to all three datasets. The advantage of this second method is that it allowed less intensively-collected data to be analysed.

6.3.1: Datasets

i) Moths

Data on abundances of British moths were obtained from the Rothamsted Insect Survey. These data were assembled from standardised tungsten filament light traps at sites across the country, and over approximately three decades. Sites were usually studied for several years, but only very few sites (31 out of 114) were continuously studied without breaks, as the availability of suitable sites and recorders was a limiting factor. Data were first collected from a single site in 1933, but organised recording across a large number of sites (24 sites) did not begin until 1968. Only five sites were monitored for the whole period of the survey (1968-2003). Other sites were added to the initial 24 sites as years passed. In many cases recording at a site was erratic, with several years missed, or recording in a particular year did not continue for the full year. In the majority of cases, recording at a site ceased several years before 2003. In total, 115 sites across the country were studied for 10 years or more, although not necessarily continuously.

In total, data were collected on 1889 species of moth. The vast majority of these species (74%) were micromoths (some of which are difficult to identify), immigrant species, or rare species of macromoths, and were excluded from subsequent analyses. For the purposes of this study I defined a rare species as one having fewer than 20 records per year on average, and fewer than 200 individual records across the whole survey in total. All species from the pug group (within the subfamily Larentiinae) were also excluded from the analysis due to difficulties in identifying these species. Thus only well-recorded species and species that can be identified reliably were included in the analysis. A lower threshold for species inclusion would have selected data for analysis where abundance numbers were frequently very low (eg. only one individual recorded per year), so making detection of trends over time difficult, whilst a higher threshold for species selection would have excluded most species, making it difficult to compare results across genera. Moth species were identified as mostly northerly distributed, mostly southerly distributed, or ubiquitous, using books (Waring & Townsend 2003), distribution maps (created from Rothamsted moth survey data), and expert advice (Nick Greatorex-Davies, Biological Records Centre, CEH Monks Wood). In total, 91 southern species, 276 ubiquitous species and nine northern species were available for analysis.

ii) Butterflies

Butterfly data were obtained from the Butterfly Monitoring Scheme. These data have been assembled from studies of fixed transects, across the country over approximately three decades. Transects of approximately 2-4km length were walked weekly during the season (first week in April to last week in September) and a standard recording procedure was applied following Pollard & Yates (1993). All individuals within 5m of the walker were recorded. As with the Rothamsted Insect Survey, sites were usually studied for several years, but very few sites were continuously studied throughout the survey. Data were available from the beginning of organised recording in 1976 (36 sites). Other sites were added over time. In total, 203 sites across the country were available for analysis. Data were collected on 76 species of British butterfly. Of these, 33% (25 species) were identified as either particularly scarce or rare, or migrants in Britain, and were therefore excluded from analyses. This left 30 southern species, 16 ubiquitous species, and five northern species available for analysis. For the purposes of this analysis, the Chequered Skipper was included as a northern species in my analyses. In the UK, this species is confined to Scotland, but occurs at low elevation further south in Europe. As it occurs on few transects, inclusion or exclusion of this species did not affect my overall conclusions, but its inclusion gave slightly more power to the analysis.

iii) Birds

Bird data were obtained from the Common Bird Census. These data were from over 1,000 different sites in a range of habitats, across Britain. Transects of variable length were walked 10 times between March and July, and numbers of individuals were identified from visual sightings and calls. As with the other surveys, sites were usually studied for several years, but very few sites were continuously studied throughout the survey. The earliest records dated back to 1966, with recording at only five sites continuing right through to the end of recording in 2002. A total of 299 bird species were available for analysis. Once migrant, rare, and non-native species were excluded (60% of species), 22 southern species, 82 ubiquitous species, and 16 northern species were selected for analysis.

6.3.2: Analyses

I analysed data using two methods. The first method (subsequently termed 'site-based' method) analysed pairs of species at individual sites. It examined the abundance trend over time of a single northern species and a single ubiquitous partner species, of close taxonomic relation and similar life history, at each site where they were found together in reasonably high abundance (geometric mean of the species at the site ≥ 1.5). The second method combined data across sites. It compared the change over time in the proportion of all individuals that were from northern species and the analysis involved combining data from all sites within a given area. This second method allowed for the analysis of more species, for species with relatively patchy data (where abundance varied greatly from year to year or between sites), as well as species occurring at low abundances.

i) Method 1 - Site-based method for moths

This analysis was applied only to moth data from the Rothamsted Insect Survey, following the data selection procedure described above. Sites were included only if they had data for at least 10 years, although not necessarily for consecutive years. Species were included only if they were present at the site for at least ten years, but not necessarily for 10 consecutive years. Species were paired for analyses so that changes in abundance of northern and ubiquitous species could be compared at the same site and over similar time periods. Nine northern species were available for analysis, and these were paired with nine ubiquitous, or 'partner', species. Species were matched as closely as possible, based on family, genus, habitat requirements, flight periods, and abundance. By pairing species, I was able to control for inter-annual and between-site variation in environmental conditions, that might be expected to affect both species in a similar way, and so such variation could be accounted for when examining results.

For each species, sites were only included in analyses if the geometric mean number of individuals over the entire time period was greater than 1.5. At these suitable sites, data from some years were excluded to produce a continuous run of data, subsequently termed the 'study run' (see Figure 6.1 for an example). At each site and for each species, the longest continuous run of data was identified. Data from other years were excluded if there was a gap of more than one year with no data between runs of data, resulting in a single data set from each site. Preliminary examination of data indicated that this was appropriate as, without such selection, very small numbers of individuals recorded either side of the study run would make it difficult to detect trends in abundance. At most sites and for most species, few data were excluded (only one or two individual records). The longest study run from all study species and sites was 27 years, and the shortest study run analysed for a species was seven years. Shorter study runs (four years or less) were obtained using this technique, but were not analysed because reliable trend data could not be calculated from such a short run of data.

Once the final 25 sites were selected (Figure 6.2), data from northern and partner species were compared where both species occurred at the same site. Data from partner species were matched as closely as possible in time with northern species, but this was not always an exact match, as in many cases one or the other species would have some years where it was absent from records. However, in most cases there was a high degree of overlap, as can be seen in Figure 6.3, which shows yearly occurrence of the raw data

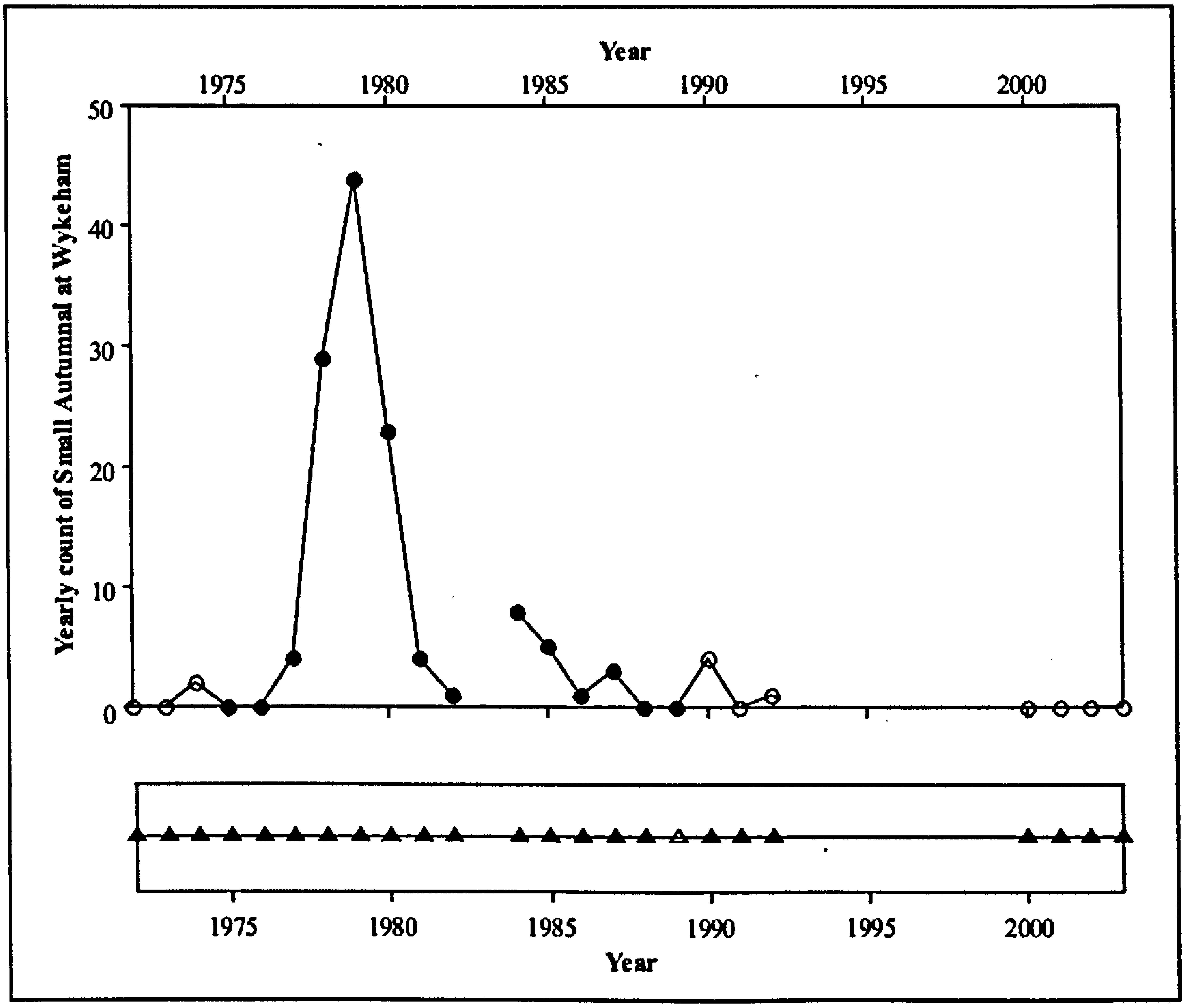

Figure 6.1: Example of data selection for a single species of moth at a single site. Data were excluded from analysis (hollow circles) if more than one year consecutively had a zero count. Underneath the main graph, the recording period at the site is shown, with years where recording continued for the full season (black triangles), years where recording did not continue for the full season (hollow triangles) and years where recording did not take place at all (absence of triangles).

analysed for the Grey Mountain Carpet (a northern species), and its partner species the Common Marbled Carpet, at each site. For each species at each site, geometric mean abundance over the study run (subsequently termed 'mean'), coefficient of variation (%, calculated as standard deviation over abundance log transformed count (Moss and Pollard 1993); subsequently termed 'variation') and linear trend in $\log_{10}$ transformed count

Figure 6.2: Final sites used in the moth 'Site-based method' abundance analysis.

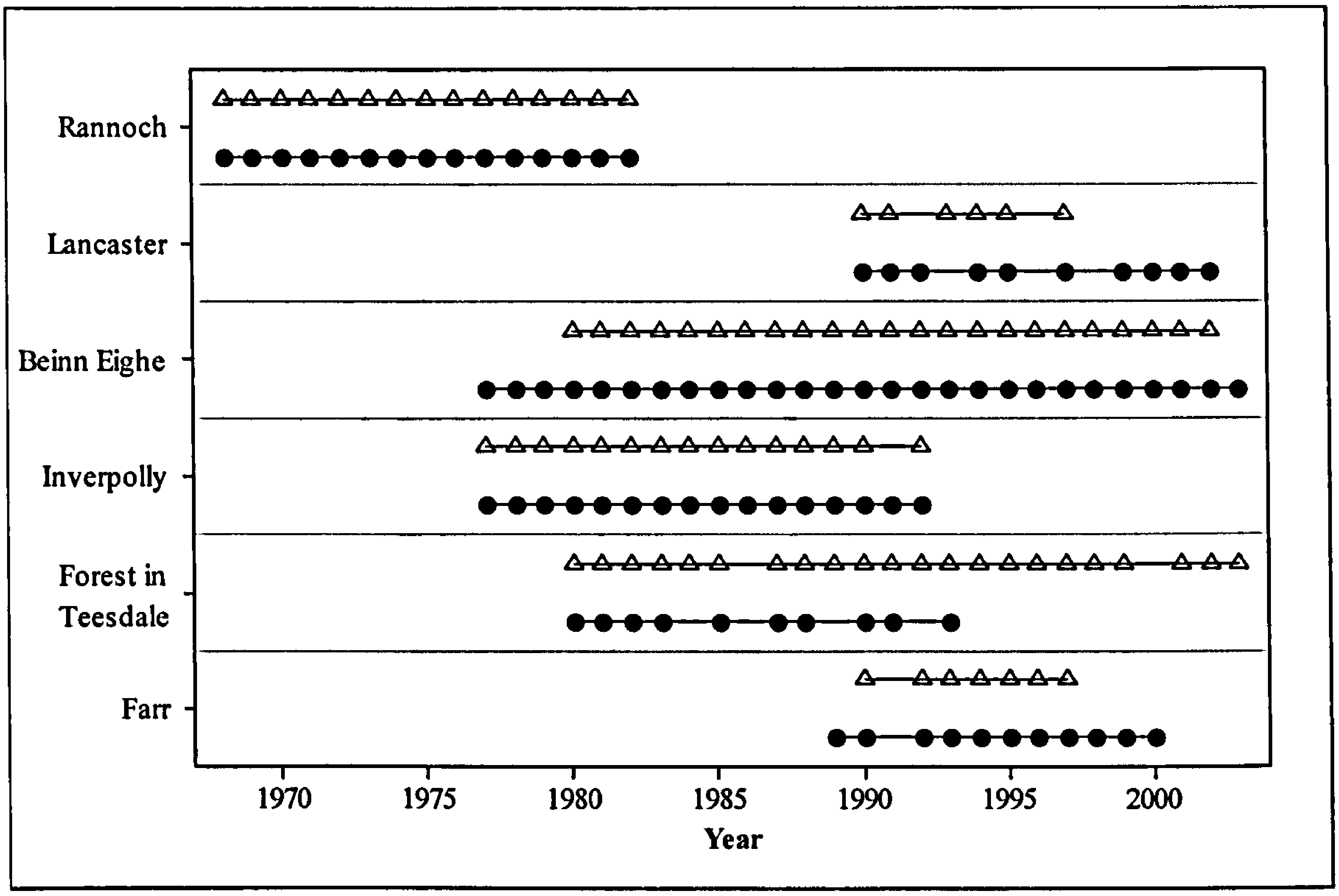

Figure 6.3: Presence or absence of data for analysis, for the Grey Mountain Carpet (*Entephria caesiata*; hollow triangles) and its partner species the Common Marbled Carpet (*Chloroclysta truncate*; solid circles) at each site over time. Absence of a symbol indicates an absence of data in that year.

('trend') were calculated. The continuous data for the trend were also put into two categories ('category') based on whether the trend was positive or negative, and regardless of whether the trend was significant. A regression was used to test for relationships between the distance north of the site and the four abundance variables (mean, variation, trend and category). A two-sample T-test was used to compare mean, variation, trend and category between northern and partner species.

iii) Method 2 – Proportional method for moths, butterflies and birds

This analysis was applied in the same way to each taxonomic group (moths, butterflies and birds), following the initial data selection procedures described previously (Section 6.3.1). For each Ordnance Survey 10km grid square in Britain, the mean yearly temperature was calculated (using data from the Climate Impacts Programme; see

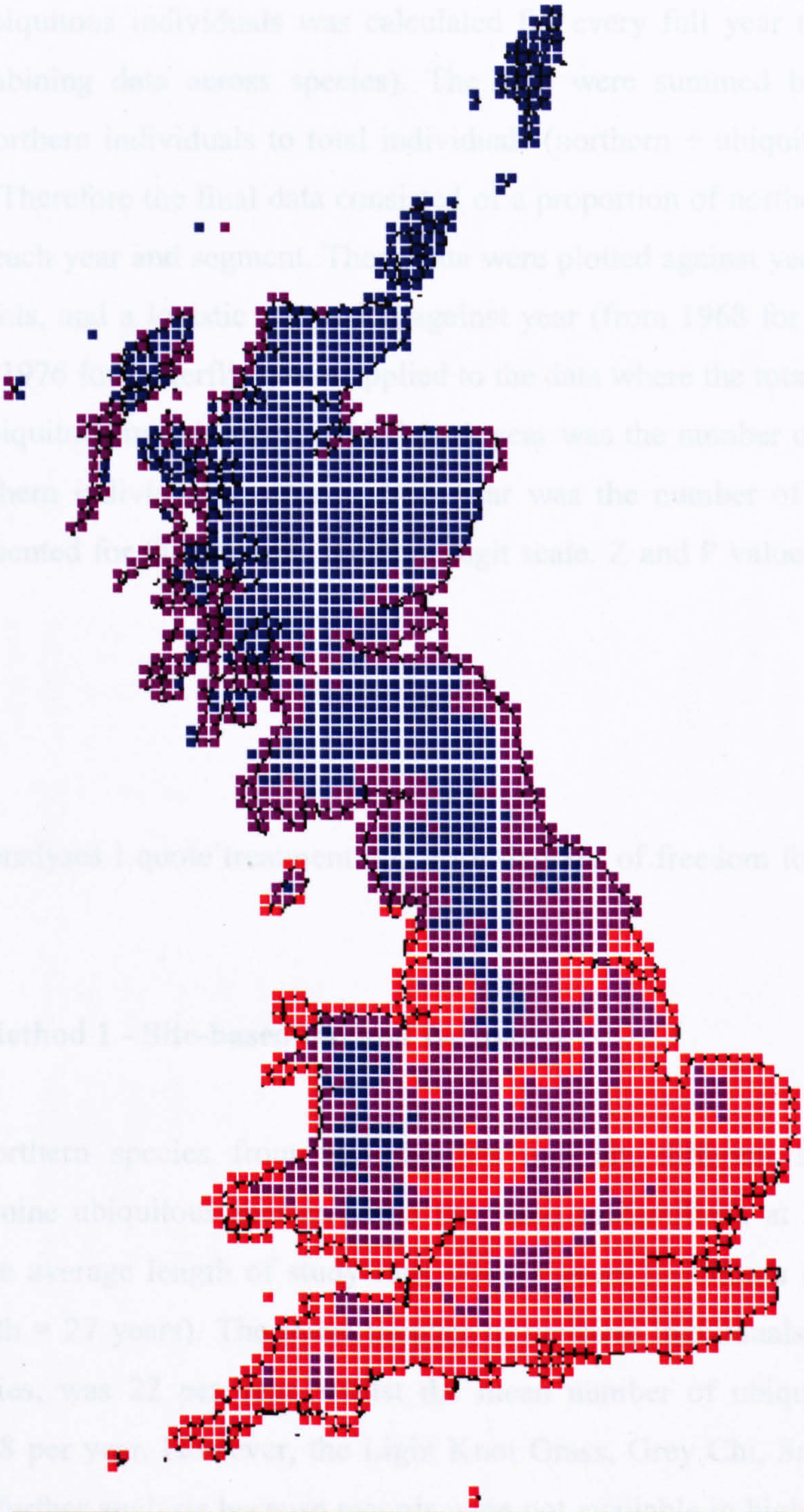

Figure 6.4: Hot (red), warm (purple) and cool (blue) segments in the UK, based upon mean annual temperature (hot 9.28-11.61°C; warm 7.97-9.27°C; cool 2.71-7.96°C).

Declaration), and these data were split into three equally-sized geographical regions, subsequently termed 'segments' (hot, warm and cool; Figure 6.4) based upon the mean annual temperature at each site. The mean temperature of the hot segment was 9.79°C, the mean temperature of the warm segment was 8.63°C, and the mean temperature of the cool segment was 6.89°C. At each site where a northern species was recorded, the number of northern and ubiquitous individuals was calculated for every full year that the site was monitored (combining data across species). The data were summed by year, and the proportion of northern individuals to total individuals (northern + ubiquitous individuals) was calculated. Therefore the final data consisted of a proportion of northern to ubiquitous individuals for each year and segment. These data were plotted against year, for hot, warm and cool segments, and a logistic regression against year (from 1968 for moths, 1975 for birds, and from 1976 for butterflies) was applied to the data where the total number of both northern and ubiquitous individuals recorded each year was the number of 'trials' and the number of northern individuals recorded each year was the number of 'successes'. All coefficients presented for this analysis are on a logit scale. Z and P values allow for over-dispersion.

6.4: Results

For all analyses I quote treatment and error degrees of freedom for the appropriate statistical test.

6.4.1: Method 1 - Site-based method for moths

Nine northern species from two families and six different subfamilies were partnered with nine ubiquitous species (from the same subfamilies), at 25 different sites (Table 6.1). The average length of study runs was 15 years (minimum length = 7 years, maximum length = 27 years). The mean number of northern individuals recorded yearly, across all species, was 22 per year, whilst the mean number of ubiquitous individuals recorded was 48 per year. However, the Light Knot Grass, Grey Chi, Smoky Wave were excluded from further analysis because records were not available in high enough numbers for their partner species, leading to too few available sites (< 3) for subsequent analyses. All further results thus refer only to the six remaining northern species. Data for mean (geometric mean abundance over the 'study run'), variation (coefficient of variation), trend (linear trend) and category (positive or negative trend) for each species and site are presented in Table 6.1.

Table 6.1: Data for each species and each site, with corresponding latitude and the number of years analysed in the study run, for the four data values mean (geometric mean abundance over the 'study run'), variation (coefficient of variation), trend (linear trend – asterisks indicate a trend was significantly different from zero) and category (positive or negative trend).

Site	Northing (km)	Northern Species	No. of years	Mean	Variation	Trend	Category	Partner Species	No. of years	Mean	Variation	Trend	Category
Lancaster	467	Small Autumnal - *Epirrita filigrammaria*	11	9.6	123.4	-0.09	0	November Moth - *Epirrita dilutata*	13	61.7	64.3	-0.04	0
Wykeham	488		11	6.7	109.5	-0.08	0		20	24.7	104.5	-0.02	0
Stainton	519		11	8.6	92.4	-0.07	0		12	6.2	87.4	-0.05	0
Shildon	526		9	4.7	82.1	-0.08	0		8	3.3	33.8	0.01	1
Hamsterley	531		13	14.5	120	-0.07	0		16	141.6	97.9	-0.07 *	0
Chester-le-Street	551		9	2.7	70.2	0.01	1		10	2.2	43.8	-0.04 *	0
Kielder	594		15	29.8	180.6	-0.13 *	0		18	21.3	81.6	0.01	1
Embleton	623		10	3	53.9	-0.04	0		14	5.8	98.9	-0.03	0
Belford	633		11	1.5	32.2	-0.01	0		12	10.3	65.2	-0.03	0
Brodick	638		17	10.5	135.4	0.02	1		18	71.8	68.5	-0.03 *	0
Rowardenna	696		10	3.2	76.8	-0.03	0		12	565.3	33.8	0	1
Kindrogen	763		14	21.6	88.4	0.06 *	1		20	42.8	83.6	-0.01	0
Lancaster	467	Grey Mountain Carpet - *Entephria caesiata*	8	2.7	66.9	0.05	1	Common Marbled Carpet - *Chloroclysta truncata*	13	7.5	121.6	-0.07	0
Forest-in-Teesdale	531		24	6	89.5	0.01	1		14	1.6	46.5	-0.02	0
Rannoch	756		15	72.9	73.9	0.02	1		15	66.8	81.8	-0.03	0
Farr	834		8	2.6	63.6	-0.02	0		12	20.9	79.7	-0.01	0
Beinn Eighe	863		23	3.5	61.1	0.01	1		27	23.7	92	-0.02	0
Inverpolly	914		16	4.7	97.1	0.01	1		16	17.1	67.5	0	1

Table 6.1: continued.

Site	Northing (km)	Northern Species	No. of years	Mean	Variation	Trend	Category	Partner Species	No. of years	Mean	Variation	Trend	Category
Hamsterley	531	Beech-Green Carpet - *Colostygia olivata*	16	14.2	157.1	0.11 *	1	Mottled Grey - *Colostygia multistrigaria*	7	164.6	60.8	-0.02	0
Rowardenna	696		9	8	71.1	-0.01	0		12	18.4	51.2	0.07 *	1
Kindrogan	763		11	2.1	53.3	-0.02	0		26	25	64.1	0	0
Monymusk	819		10	9.2	53.4	-0.01	0		10	54.7	79.9	-0.01	0
Beinn Eighe	863		17	2.7	59.7	0.01	1		27	43.5	72.6	-0.01	0
Forest-in-Teesdale	531	Red Carpet - *Xanthorhoe decoloraria*	24	24.4	66.6	-0.01	0	Flame Carpet - *Xanthorhoe designata*	24	4	82.7	-0.02	0
Kirkwhelpington	585		12	2.2	53.6	-0.02	0		12	7.6	97.9	0.08 *	1
Sourhope	620		11	7.5	83.3	-0.04	0		11	5.9	51.2	0.05 *	1
Rannoch	756		15	19.5	42.3	-0.01	0		15	18.5	65.5	-0.02	0
Kindrogan	763		20	9.8	87.4	-0.02	0		20	13.4	79.9	0.02	1
Farr	834		12	10	101.1	-0.09 *	0		12	15.4	72.2	0.03	1
Beinn Eighe	863		14	3.6	55.1	0.03	1		27	12.2	75.6	0.02 *	1
Yarner Wood	79	Smoky Wave - *Scopula ternata*	22	3.4	73.4	-0.01	0	Cream Wave - *Scopula floslactata*	27	110.7	60.9	0	0
Embleton	623	Grey Chi - *Antitype chi*	15	4.9	69.7	0	0	Black Rustic - *Aporophyla nigra*	12	3	49.6	0.01	1
Tregaron	262	Light Knot Grass - *Acronicta menyanthidis*	26	30.9	99	-0.01	0	Knot Grass - *Acronicta rumicis*	26	11	66.7	-0.02 *	0
Sourhope	620	Crinan Ear - *Amphipoea crinanensis*	11	4	50.1	0.01	1	Ear Moth - *Amphipoea oculea*	7	1.8	38	0.03	1
Kindrogan	763		20	4	70.1	-0.02	0		16	3	56.5	-0.01	0
Farr	834		12	17.8	40.7	0	1		12	14.9	54.6	-0.06 *	0

Table 6.1: continued.

Site	Northing (km)	Northern Species	No. of years	Mean	Variation	Trend	Category	Partner Species	No. of years	Mean	Variation	Trend	Category
Kindrogan	763	Plain Clay - *Eugnorisma depuncta*	20	6.8	71.1	0.02	1	Autumnal Rustic - *Paradiarsia glareosa*	14	2.6	51.9	-0.02	0
Farr	834		12	24.9	33.7	0.02	1		12	14.3	85.7	-0.05	0
Cromarty	867		19	5	66.6	0.01	1		23	4.1	82.7	-0.01	0

i) Single pairs of species

First, patterns of abundance change in each pair of species were examined separately. The relationship between abundance and latitude for each species (with separate regressions of mean, variation and trend at each site against the latitude of the sites). This gave 36 separate tests for six species (three species were not present at enough sites for this analysis). Most of these regressions were non-significant for both northern and partner species. The values used in each regression can be seen in Table 6.1. Only two northern and one ubiquitous species showed a significant relationship with latitude for any abundance variable (mean, variation, or trend). The ubiquitous species Flame Carpet showed an increase in mean abundance with latitude, the northern species Beech-Green Carpet showed a decrease in variation with latitude, and the trend of the northern Small Autumnal became less negative with increasing latitude.

The mean, variation and trend in abundance were then compared between pairs of species. For one pair (Red Carpet and Flame Carpet) the northern species showed a more negative trend over time compared with the ubiquitous species (two-sample T-test; t_{12} = -2.53, p = 0.026), as would be predicted if climate change were having a more negative effect upon northern species. For two pairs, there was no significant difference between abundance trends for northern and partner species. Finally, for two pairs (Plain Clay and Autumnal Rustic, Grey Mountain Carpet and Common Marbled Carpet), northern species showed a significantly more positive trend over time than partner species, the opposite of what would be predicted due to climate change.

ii) *All northern species compared with all ubiquitous species*

Second, I analysed data by considering data from each site and species as a separate data point, and analysing data in a single Generalized Linear Model – GLM (n = 39 paired sites and species, Table 6.1). A problem with this approach is that by considering each site as an independent data value, it led to pseudo-replication, inflating the degrees of freedom, e.g. sites with data for more years had more data points, and therefore more weight, in the analysis. Therefore all results using this technique must be considered with this in mind. When all northern species were compared with all ubiquitous species, different patterns in the data were detected. At most sites, there was no significant trend in abundance change for either ubiquitous or northern species (Figure 6.5). When abundance variables (mean, variation and trend) were regressed with latitude, northern species showed a significant negative relationship between variation in abundance and latitude (n = 39 sites, coef. = -0.006, R^2 = 10.7%, $F_{1,37}$ = 4.42, p = 0.042). Thus northern species at sites at higher latitudes showed less variation in abundance compared with sites at lower latitude. Ubiquitous species showed no relationships between any measures of abundance and latitude ($p > 0.4$ in all cases).

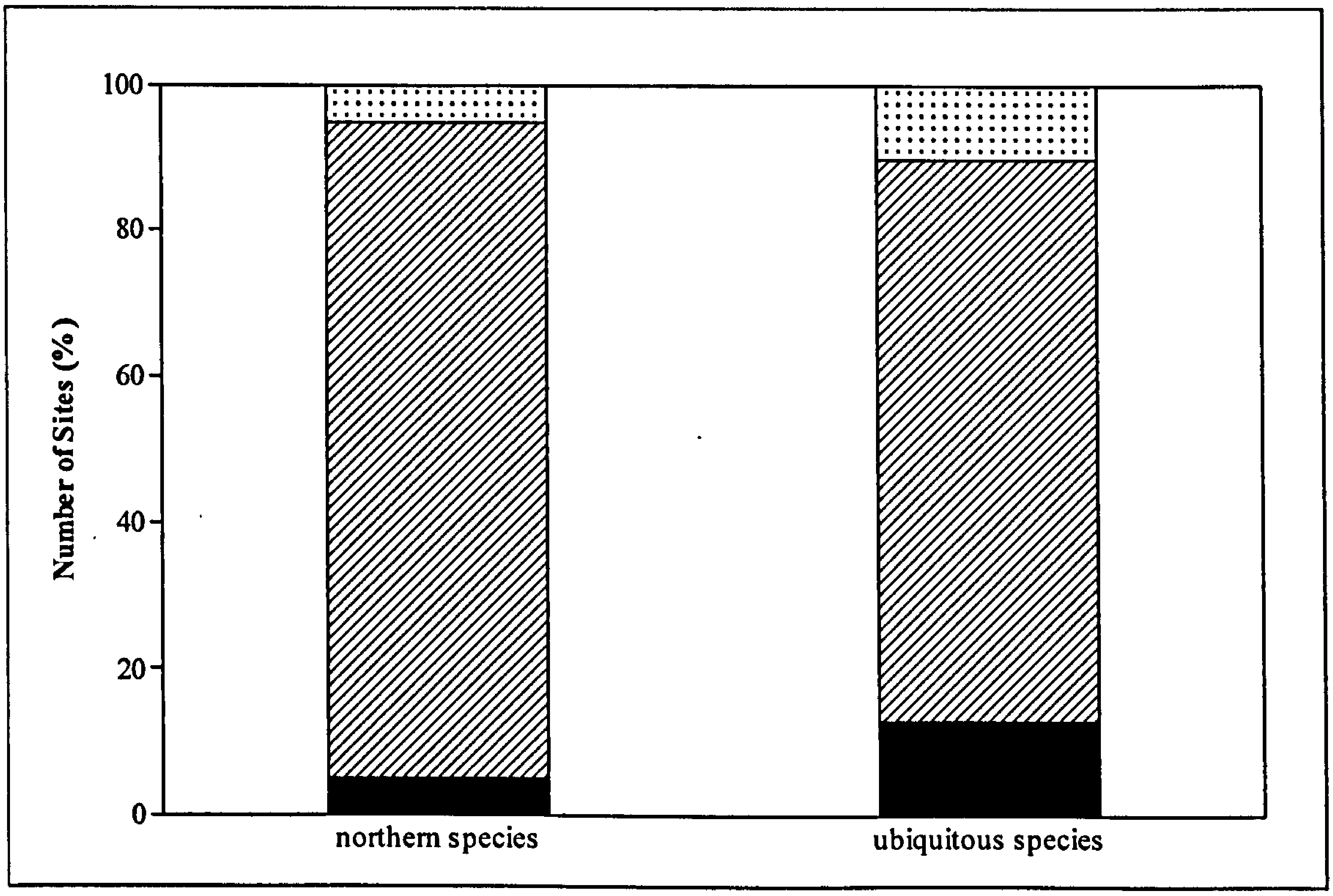

Figure 6.5: Percentage of sites where northern and ubiquitous species of moth have shown a significant increase (white speckled), no significant trend in abundance (grey striped) or a significant decrease (solid black).

Overall, ubiquitous species had a significantly higher abundance across sites than did northern species (two-sample t-test: n = 39 sites, t_{76} = -2.06, p = 0.043). For both northern and ubiquitous species, sites at which species increased in abundance were at a higher latitude (mean northing = 729km) than sites where species decreased in abundance (mean northing = 609km): this difference of 120km implies that for all species, more northerly sites provided a more suitable environment in recent decades (Figure 6.6; General Linear Model: $F_{1,74}$ = 4.64, p = 0.034). However, there was no difference between northern and ubiquitous species in this respect (Generalized Linear Model: $F_{1,74}$ = 0.92, p = 0.341;

northern species, mean difference in latitude = 120km; ubiquitous species = 53km). However, when abundance changes were analysed by 'trend', a continuous variable, rather than 'category', no relationship between latitude and abundance was detected for either northern or ubiquitous species (Generalized Linear Model: $F_{1,74} = 1.87, p = 0.175$).

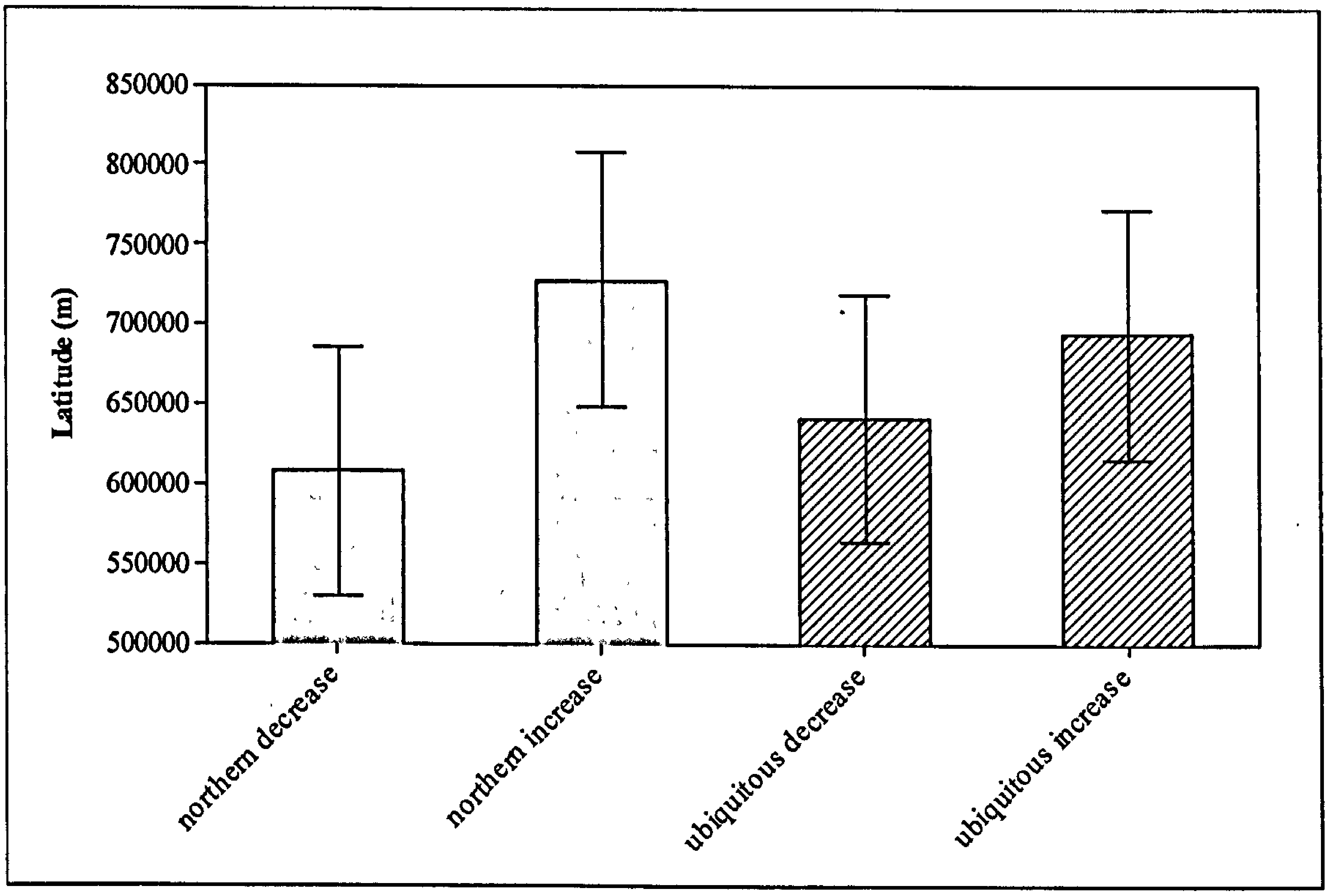

Figure 6.6: Average latitude of sites where northern and ubiquitous species of moth have shown an increase or decrease in abundance.

6.4.2: Method 2 - Proportional method for moths, butterflies and birds

For birds, 659 northern individuals and 28,192 ubiquitous individuals were analysed, from 76 sites. The average number of individuals recorded per site, per year, was three northern and 149 ubiquitous individuals. For butterflies, a total of 49,813 northern individuals and 307,434 ubiquitous individuals was analysed from 31 sites. The average number of individuals recorded per site, per year, was 147 northern and 910 ubiquitous. For moths, a total of 44,223 northern individuals and 4,577,593 ubiquitous individuals were analysed, from 194 sites. The average number of individuals recorded per site, per year, was 26 northern and 2669 ubiquitous individuals. (Figure 6.7)

Figure 6.7: Sites included in the proportional analysis for birds (A), butterflies (B), and moths (C).

For moths, there was very little consistent change in the population of northern individuals over time (Figure 6.8A; logistic regression; coef. = -0.25, Z = -2.140, p = 0.32). However, numbers of northern individuals were much lower than those of ubiquitous individuals, and therefore variations in abundance of northern individuals may not have been detected. Only one peak in abundance of northern individuals was noted, during 1974-1988. Interestingly, this peak in northern individuals was observed only in the cooler regions of Britain. As a result of this peak, there was a higher proportion of northern individuals at cool sites (mean proportion = 0.022) than at hot sites (mean proportion = 0.001; Z = 3.776, p < 0.001). However, logistic regression analysis may not be an appropriate analysis in the case where there is so little change in abundance over time (P. Rothery, CEH Monks Wood, personal communication), and so these data may warrant further analysis using other methods.

In butterflies, the total numbers of northern and ubiquitous individuals recorded were more similar than in moths. For butterflies, the proportion of northern individuals increased over time in all three segments (Figure 6.8B; coef. = 0.076, Z = 3.390, p =

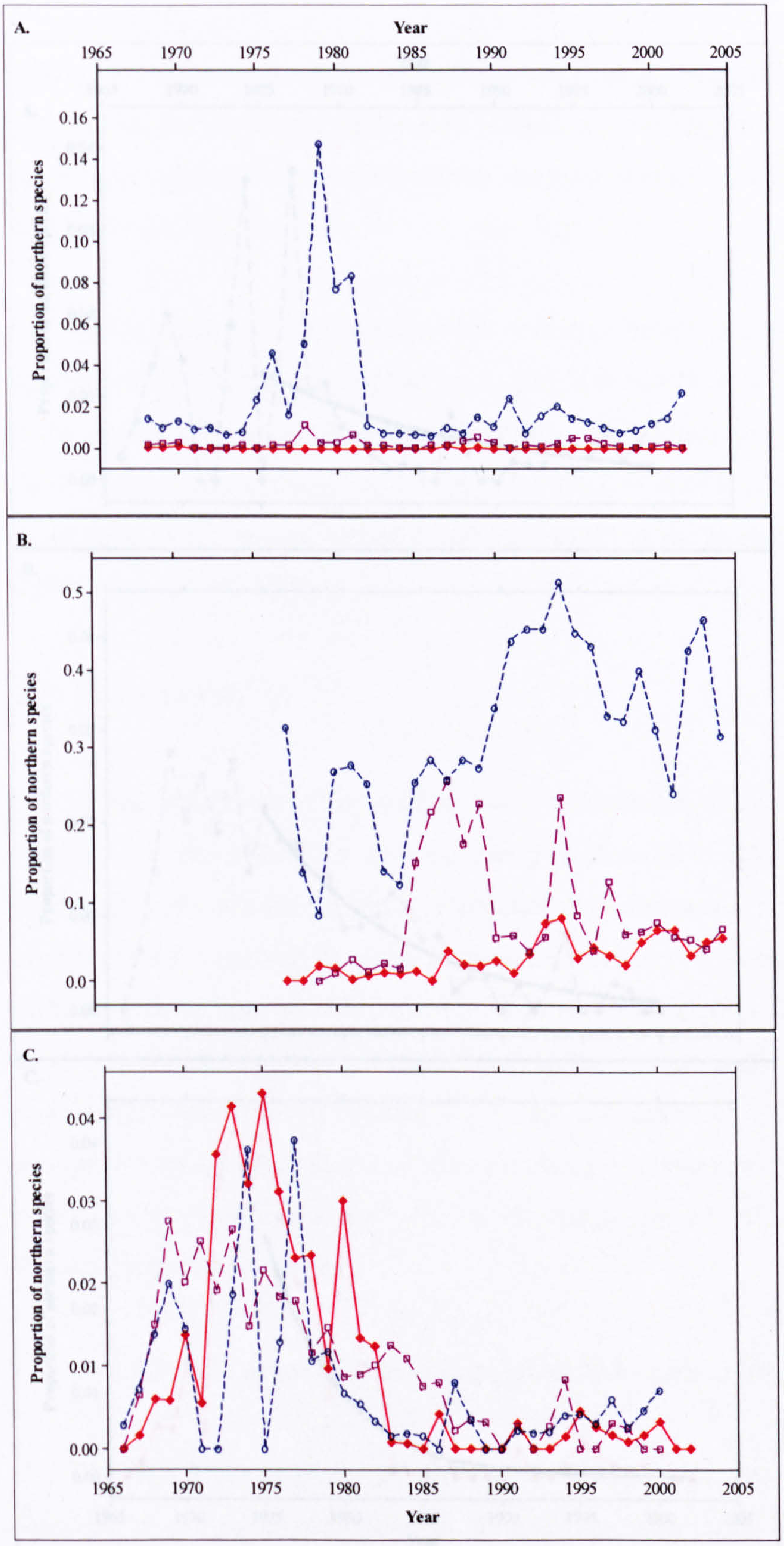

Figure 6.8: Change in the proportion of northern to ubiquitous individuals over time for moths (A), butterflies (B), and birds (C). Data for hot (solid red diamonds), warm (hollow purple squares) and cool (hollow blue circles) segments of Britain are shown, using data from the Met Office. Note that scales on each panel vary.

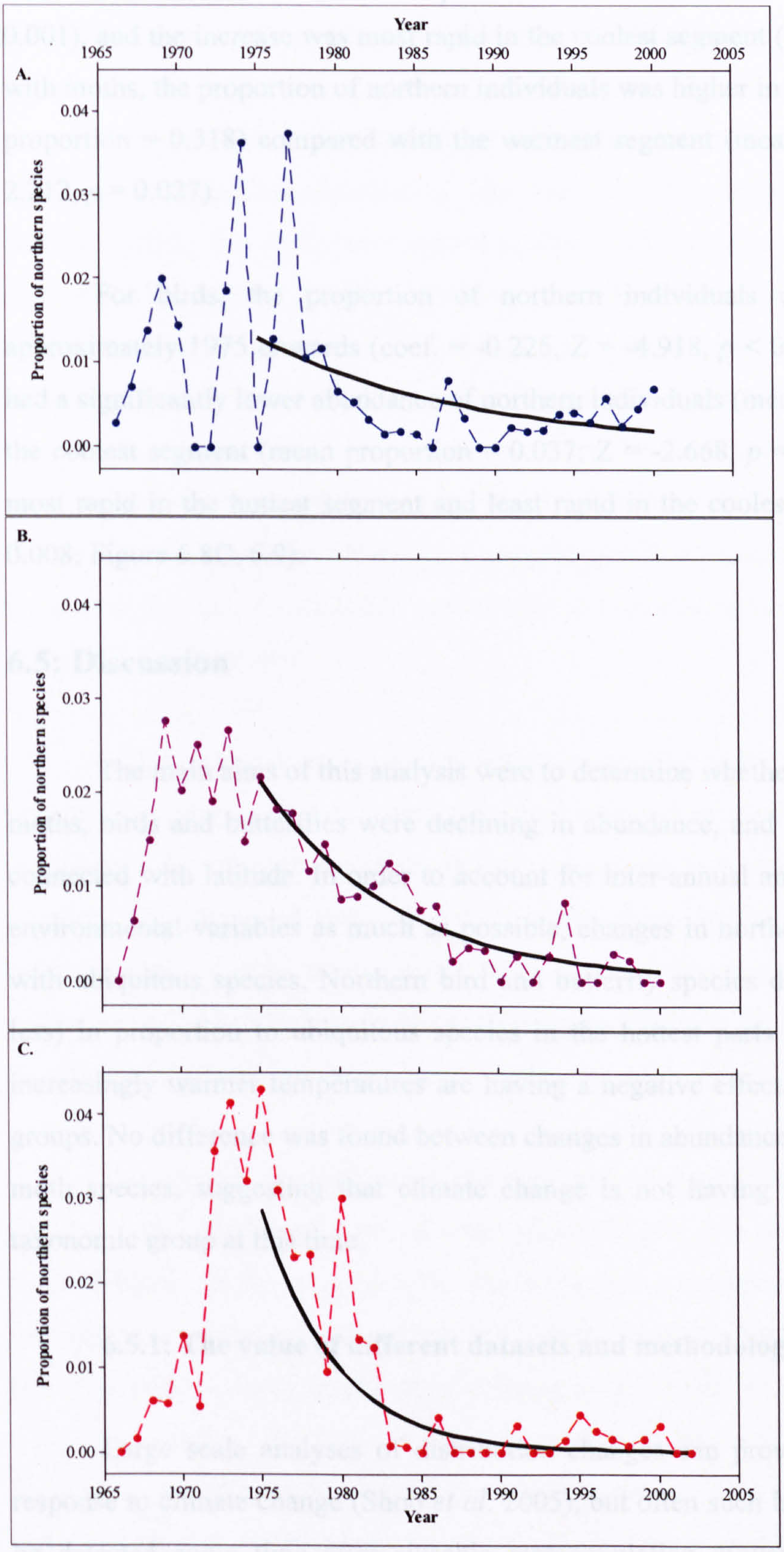

Figure 6.9: Changes in the proportion of northern to ubiquitous UK bird species over time for cool (A blue symbols), warm (B purple) and hot (C red) segments (Figure 6.8C extended). Proportional data are shown with dashed lines, fitted logistic regression lines are shown as solid lines, calculated from the time of decline (1975).

0.001), and the increase was most rapid in the coolest segment (Z = -2.155, p = 0.031). As with moths, the proportion of northern individuals was higher in the coolest segment (mean proportion = 0.318) compared with the warmest segment (mean proportion = 0.030; Z = 2.212, p = 0.027).

For birds, the proportion of northern individuals declined over time from approximately 1975 onwards (coef. = -0.225, Z = -4.918, $p < 0.001$). The hottest segment had a significantly lower abundance of northern individuals (mean proportion = 0.019) than the coolest segment (mean proportion = 0.037; Z = -2.668, p = 0.008). The decrease was most rapid in the hottest segment and least rapid in the coolest segment (Z = 2.668, p = 0.008; Figure 6.8C, 6.9).

6.5: Discussion

The main aims of this analysis were to determine whether or not northern species of moths, birds and butterflies were declining in abundance, and whether any declines were connected with latitude. In order to account for inter-annual and between-site variation in environmental variables as much as possible, changes in northern species were compared with ubiquitous species. Northern bird and butterfly species declined more (or increased less) in proportion to ubiquitous species in the hottest parts of Britain, suggesting that increasingly warmer temperatures are having a negative effect on the abundance of these groups. No difference was found between changes in abundance of ubiquitous and northern moth species, suggesting that climate change is not having a detectable effect on this taxonomic group at this time.

6.5.1: The value of different datasets and methodologies

Large scale analyses of distribution changes can provide evidence of a species' response to climate change (Shoo *et al.* 2005), but often such large-scale changes can only be detected some time after sizeable metapopulation movement has already occurred (Hanski & Ovaskainen 2002). Thus study of distribution change, particularly at a 10km resolution, may not always be a suitable method to detect change, especially where rare species may be at risk of extinction. Site-based abundance datasets can be very useful in helping detect subtle or population-specific changes at a much earlier stage in the extinction (or colonisation) process (Franco *et al.* 2006; Thomas *et al.* 2006).

Thus we might expect abundance data to be a more sensitive measure of responses to climate change than distribution data. However, several elements of the abundance datasets used in this study have caused problems with analyses. The primary dilemma is that, whilst the number of species, sites and records in an entire dataset may look detailed and comprehensive, at a single site and species level, the data are still remarkably sparse, with often only a few individuals recorded each year, usually from the most common species. At such low levels of abundance, it can be very difficult to extract a long-term trend, as year-by-year variability in a population with so few individuals is naturally very high and masks long-term trends. Even partnering with ubiquitous species can only account for a small amount of variability, particularly as such ubiquitous species are often recorded in much higher numbers.

In this study, the site-based method was applied to the moth dataset. This method was highly selective of data, using only data from the most-recorded sites over the most consistently recorded time periods. In this way, trends over time were detected for a small number of species and sites, and such trends could be compared across species and between sites. In most cases, trends were detected where reasonably large numbers of northern species had been recorded each year, emphasizing the need for abundance data to be collected for large numbers of individuals.

The second, proportional, method of analysis was found to have advantages over Method 1 (the site-based method) when analysing bird data, because even where data for an individual species at a specific site were poor, the species and site could still be included, hence increasing the number of data available for analysis. However, this method is a less-sensitive study of abundance change as it is based on proportions of northern and ubiquitous species, although it allows more data to be included in the analysis than in Method 1, and thus may uncover patterns not detected by the site-based method. This second method was particularly suitable for birds, where numbers of ubiquitous individuals recorded at sites changed little over time, but was less suitable for moths, where pronounced changes in the large number of ubiquitous species skewed proportional values, and may have obscured any underlying patterns in northern species.

I would therefore suggest that where many more ubiquitous individuals are recorded in comparison with northern individuals, as in the case of the moths, the site-based method may be more appropriate. In the case of birds and butterflies, where the numbers of ubiquitous and northern individuals are less disproportionate, the proportional method may be able detect large-scale changes that would be unreported at the site-based level. In my study, using the proportional method for birds produced results which could not have been derived from a site-based method, as the data were so patchy.

6.5.2: Moths

The majority of UK moth species are decreasing in abundance, as already documented (Fox *et al.* 2006b). I found little evidence for any relationship between trend in abundance and latitude, although there was a relationship between variability and latitude for northern species: northern species were more variable at lower latitudes, indicating that warmer sites may have larger fluctuations in abundance that could lead to increased probability of extinction at low latitude sites. An alternative interpretation of these results is that species may have a lower abundance at lower latitudes, making populations more variable and making it difficult to detect any effect of latitude on abundance.

There was no difference between the abundance changes of northern and ubiquitous species, suggesting that climate change has not had a detectable disproportionate effect upon northern moth species over the period of study. This result was supported by the proportional analysis, which also failed to detect any strong trend in abundance over time, or between climatic regions. It is possible that habitat deterioration is as important as climate warming in causing population decreases (Conrad *et al.* 2004; Fox *et al.* 2006b). It may be that whilst changes in abundance are quite site specific due to the individual habitat changes at a site, distributional changes will eventually occur at range margins as a response to climate warming. Species-specific studies in Europe have found a shift both northwards and uphill in moths, and this has been attributed to warming winter temperatures (Battisti *et al.* 2005). Therefore, I conclude that whilst northern moth species may not currently be exhibiting a detectable widespread response to climate warming, such responses as have been documented in other countries will eventually also be found in northern British moths.

Despite the abundance dataset used here seeming large and comprehensive, at a species level, the data are quite sparse, and lack of data may have inhibited my ability to pick up long term trends. In the case of the site-based method of analysis, with only 9 northern species, at only 23 different sites across the north of the UK, natural variation between sites and years may have confounded the data to such an extent that reliable comparison between species and sites is impossible. This lack of power is a common problem with large datasets comprising many species, where specific analysis of individual species is difficult. When studying insects in general, problems with too few northern species (in Britain) and too much year to year variation are particularly notable.

6.5.3: Birds and butterflies

Northern butterfly species increased in abundance over time compared with ubiquitous species at the same sites. However, it is my opinion that this result reflects more a decrease in the abundance of ubiquitous species, rather than an increase in northern species. This could be tested in the future by analysing trends for northern and ubiquitous species separately, rather than as proportions (but time constraints prevented this analysis here). The most recent report from the Butterfly Monitoring Scheme (Greatorex-Davies & Roy 2004) shows that six out of the 16 butterfly species I have identified as ubiquitous are significantly decreasing in abundance, compared with only two significantly increasing. Whilst information for calculating these trends was scarce from the north of Britain, it seems likely that a species declining in general will also be showing the same trend in the north of the country. Therefore, whilst northern species may be apparently faring better than ubiquitous species, they are not necessarily increasing in abundance. Until Butterfly Monitoring Scheme sites from the north of Britain have accumulated sufficient data for abundance trends to be calculated for individual northern species, the long-term trend in these species cannot be confirmed.

The increase in abundance of northern butterfly species was least pronounced in the warmest segment (Figure 6.8B), suggesting that either fecundity of these species is inhibited or mortality increased in the warmest areas of the country. Therefore, it may be that climate change is having some negative effects on these species. I would predict that abundance changes as a response to climate change would occur before large distributional shifts. Northern butterfly species have already been shown to be retracting northwards at their southern range margin (see Chapter 4; Wilson *et al.* 2005; Franco *et al.* 2006), and so the possibility that northern butterflies are increasing less in the hottest compared with coldest parts of Britain (Fig 6.8B) may provide some support for this group responding to climate change. In order to fully understand a species' response to climate change, both changes in distribution and abundance should be studied in conjunction. Whilst abundance changes may start to occur as a response to climate change before distribution changes (Brown 1984), the natural variation in many abundance datasets may restrict the detection of these changes. It is also possible that habitat changes affecting butterflies have been more extreme in lowland, warmer sites. However, this factor would be expected to affect both ubiquitous and northern species to a similar degree, as there is little evidence for increased specialisation in northern species, and therefore is accounted for in this proportional analysis.

The results for birds generally were comparable with butterflies, and as predicted if climate is affecting abundance. The rapid increase in the proportion of northern species recorded in the late 1960s is almost certainly due to an increase in recording effort, picking out more scarce species at each site. For this reason, logistic regression analysis was only applied to the data after this initial period. After this initial increase, northern species were decreasing more than ubiquitous species in all regions, but the decrease was most rapid in the hottest region. This contrasts with my results showing that northern bird species are shifting southwards at their range margin (see Chapter 4), and underlines the point that changes in abundance and changes at range margins may tell us very different things. Current analysis of distribution data indicates that northern bird species are shifting southwards, implying that they are 'doing well', whereas analysis of abundance data has indicated that in hotter (more southerly) areas of the country, northern species are faring poorly compared with their ubiquitous counterparts. A similar pattern has been documented for butterflies, where little regional distribution change was documented even though there were huge local declines in abundance (Cowley *et al.* 1999). This contrasts with the generally assumed hypothesis that there is a positive relationship between distribution and abundance (Hanski 1982; Brown 1984; Gaston & Lawton 1990; Gaston & Blackburn 1999). However, whilst this theoretical relationship has often been described in the field, it is sometimes the case that several different mechanisms can operate simultaneously in nature to give a variety of different results (Russell *et al.* 2005).

One explanation of this apparent inconsistency between abundance and distribution changes in birds is that the southward latitudinal shift in birds may be due to improved habitat and a reduction in persecution, allowing these species to re-colonise their natural range. For example, goldeneye have rapidly colonised new areas to the south, partly due to nest-boxes being provided, and persecution of goosander and birds of prey has been reduced in recent years. In general, moorland habitat which many northern species of bird favour has received increased protection over the time period of study. However, within these species' natural range, increases in temperature at specific 'hot' sites may lead to decreases in abundance and eventual extinction, ahead of an eventual widespread retraction north.

Another explanation relates to the 'proportional' nature of this analysis. It may be that northern species are indeed faring quite well across all parts of the country, but their ubiquitous partners are increasing much more rapidly in abundance in the hotter areas. This would lead to the same proportional decrease in northern species that has been detected here. It is my opinion that this is a more likely explanation, but in order to confirm this, further work would be required on abundance changes in both ubiquitous and northern bird species, calculating trends over time for both groups in the different climatic segments. Further discussion of the relationship between distribution, phenology and abundance changes can be found in Chapter 7.

6.6: Conclusion

There does not appear to be a significant difference between the abundance changes of northern and ubiquitous moth species in the UK. However, lack of data and natural variation between sites and years is likely to have confounded results. As abundance datasets continue to grow, it is possible that further studies will be able to demonstrate a link between changes in insect abundance and climate warming. Northern bird species appear to be showing a decrease in abundance, particularly in the hottest regions of the country. Northern butterfly species are increasing compared with ubiquitous species, but the rate of this increase is much reduced in the hottest regions of the country. This suggests that for northern birds and butterflies, climate may be having a negative effect upon abundance.

Chapter 7

General Discussion

The overall aim of my thesis was to study distribution, abundance and phenology changes in British plants and animals, in relation to climate change. I aimed to examine the relationships between these factors, and to focus on any differences in the responses of southern and northern species.

- In Chapter 2, I studied distribution shifts in British dragonflies and damselflies, and used this study group to design a robust yet simple method of analysis, which could then be applied to a wider range of taxonomic groups. I discovered that southern species of Odonata are shifting northwards at their northern range margin, whilst the southern range margin of northern species has remained relatively static.
- In Chapter 3, I applied my method of analysis devised in Chapter 2, and applied it to southern species from a wide variety of taxonomic groups. I found that 84% of species studied had shifted northwards at their range margin over recent decades.
- In Chapter 4, I applied the method from the previous two chapters to taxonomic groups with relatively large numbers of northern species in Britain. I compared the rate of range margin shift in northern and southern species. I found that in invertebrate groups, northern species are retracting at their southern range margin to a similar degree as southern species are expanding at their northern range margin.
- In Chapter 5, I compared distribution and phenological change for three, well-studied British groups. I found that there is a weak relationship between distribution and phenological change in butterflies, with species that appear earlier in the year also shifting northwards to a greater degree. However, there was no relationship detected between distribution change and phenology for birds or plants.
- In Chapter 6, I examined changes in abundance of birds, moths and butterflies, using two different statistical techniques to compare northern species with

ubiquitous species. I found that there was little difference between changes in abundance of northern and ubiquitous moth or butterfly species, but northern bird species are decreasing in abundance compared with ubiquitous species, particularly at the warmest sites in Britain.

Whilst some of my results, particularly in Chapters 2-4, support the existing literature well, some results are less conclusive, and in some cases they conflict with existing literature, or what I found in other chapters, using different analyses. Here I examine my main results and, where conflicts exist, suggest what might explain unusual results. Finally, I summarise what appears to be happening to British plants and animals as climate warming increases, and what further work needs to be done to enhance our understanding of how climate change will affect species' biodiversity.

7.1: Distribution changes

In general I have shown that most terrestrial animal species (84%) are shifting northwards at their range margins in Britain, probably as a result of climate change (see Chapter 3). The methods I used produced results for southern species of birds and butterflies which were comparable with previous studies (Parmesan *et al.* 1999; Thomas & Lennon 1999; Warren *et al.* 2001). My study found that butterfly species in Britain have shift northwards by an average of 37km; Parmesan *et al.* (1999) found that 65% of European butterfly species had shifted northwards by 35-240km this century. My study found that southern British bird species had shifted northwards by 29km; Thomas & Lennon (1999) found that southern British breeding bird species had shifted northward by 19km. In this case the discrepancy in results is probably due to small differences in the selection of species for analysis.

By applying this simple methodology of calculating shift at the range margin between two time periods to a variety of other, less well-recorded groups, a direct comparison can be made of range shifts across groups. Whilst the distributions of some individual species within different taxa may be particularly affected by habitat change or pollution, the fact that so many species with an assortment of different ecological characteristics and life histories showed a similar northward shift suggests that, broadly speaking, climate change is probably a key factor influencing distribution change for the majority of British species. In some cases, for example dragonflies, damselflies and soldier beetles, the rate of northward shift (on average 4km per year) was substantially higher than for well-studied groups such as butterflies and birds (on average 1-2km per year). It is my opinion that the simple methods I used in this analysis, which compared change in latitude of the 10 most northerly 10km grid squares, may not detect subtle changes, so results for all taxa may be conservative. For example, recent work (Franco *et al.* 2006; Thomas *et al.* 2006) has shown that species have apparently shifted their ranges over much greater distances when data are analysed at a 1km rather than a 10km grid resolution. It is therefore important that future assessments of the effect of climate change, such as the IPCC report, which base their conclusions on studies of well-recorded groups, acknowledge that other species may potentially be showing much greater degrees of distribution change than have currently been documented.

My analysis has also shown that many species (69%) are shifting their distributions to higher altitudes. Altitudinal shifts have been documented across the globe, and particularly in montane regions (Kullman 2002; Konvicka *et al.* 2003; Penuelas & Boada 2003). It is likely that in some cases, altitudinal shifts will be detected as a response to climate change before, or instead of, latitudinal shifts, particularly in topographically diverse habitats. In many cases, habitat may already be too fragmented to allow a species to shift latitudinally (Warren *et al.* 2001, Hill *et al.* 2002), and only an uphill shift will be possible. In places where recording is limited, focusing efforts on identifying altitudinal shifts may produce more conclusive results of distribution change.

When the same methodology from Chapter 3 was applied to northern species reaching their southern range margin in Britain (Chapter 4), I found that 72% of invertebrate species (groups analysed here were butterflies, spiders and ground beetles) retracted north at their southern range margin. This retraction was at a similar rate to which their southern counterparts were expanding northwards. Whilst only a few studies have previously documented retraction at southern range margins (Parmesan *et al.* 1999; Parmesan & Yohe 2003; Wilson *et al.* 2005; Franco *et al.* 2006), this widespread response across a variety of different species suggests that, for invertebrates at least, climate change is negatively affecting populations at the southern and low-elevation limit of their species' distribution. This has obvious consequences for the conservation of such species, particularly in a northerly island such as Britain, where many northern species may find it difficult to colonise new climatically suitable areas closer to the North pole. The overall distribution of biodiversity across Europe will also change, as northern species decrease in the extent of their distributions, whilst southern species increase (Hill *et al.* 2002).

My figures of 84% of southern species shifting northwards and 72% of northern invertebrate species retracting northwards are comparable with a meta-analysis by Parmesan & Yohe (2003) who found that 81% of species were expanding at their northern range margin, whilst 75% of species were retracting northwards at their southern range margin. However, they calculated that species were shifting 6.1km per decade polewards (or uphill) whereas my calculations of range margin shift per decade (12.5 – 24.8km decade^{-1}) are larger. Parmesan & Yohe analysed different groups over different geographical regions to my analysis. This may account for some differences in the magnitude of range shifts, whilst similarities in our results are all the more impressive.

My analysis suggests that plant range margins have not changed very much over recent decades. Some studies have found northern plant species in Britain to be in decline (Preston *et al.* 2002) and some southern species (particularly those favoured by warm winter temperatures such as the Bee Orchid (*Ophrys apifera*) and the Hart's-tongue Fern (*Phyllitis scolopendrium*), or those with highly dispersive seeds or spores) to be increasing in distribution size (Braithwaite *et al.* 2006). However, in most cases it is changes in land management and habitat availability which may be primarily responsible for recent changes in individual species' distributions (Braithwaite *et al.* 2006), with no firm evidence that climate change is affecting the distribution of British plants at a 10km resolution.

In Britain, recording of vascular plants has been organised differently from animals, with more project-based recording. For example, two national atlas surveys were carried out in the 1950s and the 1990s, with more detailed county flora surveys in between, whereas animal recording has typically been more continuous (except for birds). Analysing changes in plant distribution therefore may require a different strategy from that used here: some British plant researchers aim to overcome variability in recording (Preston *et al.* 2002), or chose to collect new empirical data entirely (Braithwaite *et al.*

2006). However, because data collection methods vary so greatly, it can be difficult to compare plant research directly with studies of distribution change in animals.

Extinction debt (Tilman *et al.* 1994) may be another reason why changes in plant distributions have not been detected on a widespread basis. Longer-lived organisms, particularly woody plants and trees, may take a long time to die off, if climate changes are having a negative effect upon them. This could mean that large-scale distribution changes in these species will not be detected for many years (Hanski & Ovaskainen 2002; Helm *et al.* 2006). Other studies of European plants have found altitudinal shifts occurring (Kullman 2002; Penuelas & Boada 2003; Huntley 1991), possibly because any delay in detection of extinctions is less pronounced when studying altitudinal distribution change. Alternatively it may be because these specific studies are based in climates where recent warming has been much greater than in Britain, suggesting that similar distribution changes may be detected in British plants in future years.

Whilst my results of latitudinal shifts in southern British bird species are comparable with previous studies using the same data (Thomas & Lennon 1999), I found an average southward shift in northern bird species, whereas Thomas & Lennon (1999) detected no change in the southern range margin of northern species. Inspection of results on an individual species basis proves that neither analysis was flawed, but that selection of species for inclusion in analysis can have a profound effect on the quantification of shift. Some of the species I included in my study which were not included by Thomas & Lennon (1999), such as goldeneye (*Bucephala clangula*) and goosander (*Mergus merganser*), showed a large southward shift over the time periods of study, but this is almost certainly due to increased protection of habitats and a reduction in persecution, allowing such species to re-colonise areas within their historically natural distribution. Such large-scale improvements to habitats over the time period of study may mask some species' responses (not only birds) to climate change, and this fact should be taken into account when considering my results. However, not all species are experiencing widespread improvement in habitat. For example, despite some efforts from conservationists, the habitat of red and black grouse is in decline, and it should be noted that these species also show a marked retraction at their southern range margin.

7.2: Phenological changes

In Chapter 5, there was a relationship between phenological and distributional change in butterflies, when the number of generations per year (and hence the rate at which populations increase and the species can respond to change) were taken into account. Butterfly species which have responded to climate change by flying earlier in the year are also the species which have shifted northwards at their southern range margin to the greatest extent. However, this relationship between phenology and distribution change was fairly weak in butterflies and there was no relationship between these two measures in either birds or plants, despite a clear indication that both birds (Crick & Sparks 1999) and plants (Fitter & Fitter 2000) are responding to climate change by engaging in reproduction earlier in the year. In the case of plants, my previous analysis (Chapter 4) indicated that neither southern nor northern species of British vascular plants have shifted their range margins much over recent decades. Therefore a relationship with phenology might not be expected for this group. However, in the case of British birds, both distribution change (Chapter 3; Thomas & Lennon 1999) and phenological change (Crick & Sparks 1999) have been well documented using the same datasets as I used, yet I found no relationship between the two measures. It may be that birds are not as sensitive to climate change as insects, and that a relationship between distribution and phenology will become apparent over a longer period of time. Alternatively, it may be that the mechanisms controlling birds' phenological response to climate warming are in no way linked to the process of colonising new areas (leading to distribution change), and that no link will ever appear between the two measures of response to climate.

7.3: Abundance changes

In Chapter 6, I found that, in invertebrates, changes in the abundance of northern species over time was very similar to their ubiquitous counterparts, and there was little evidence that northern species had declined more during recent climate warming. For some species there was a negative relationship between abundance and latitude, although many results were not statistically significant. In general, northern moth species were less abundant overall and showed greater variability in abundance at lower latitudes compared with ubiquitous species. This pattern of increased variability at range margins has also been documented for southern butterfly species (Thomas *et al.* 1994) and may illustrate the first patterns of a species being negatively impacted by climate change, before a large scale shift at the range margin occurs. In ubiquitous moth species, there was no relationship between abundance and latitude, and in this case habitat change may to be responsible for many changes in abundance (Conrad *et al.* 2004).

In butterflies, the abundance of northern species also appeared to be relatively stable (or possibly even increasing) compared with ubiquitous counterparts. In this case it may be that climate change is not yet having a discernable effect upon the abundance of northern species, and that habitat changes are having a strong negative impacts upon the abundance of ubiquitous species in the same areas (Fox *et al.* 2006a). Alternatively, it may be that the sensitivity of the data available for the analysis was not sufficient to detect any decreases in the abundance of northern species. In both moths and butterflies, year to year variability in abundance was quite high, with some species recording only a few individuals present at a site in one year, and several hundred the following year. This high degree of natural variability may have inhibited my ability to detect a response to climate change in these species. Also, the spatial coverage of monitoring sites may be too small. Nonetheless, I did detect a difference in the abundance of northern and ubiquitous bird species, which also showed less year to year variation in abundance, providing further support for the idea that the signal-to-noise ratio is important for the detection of abundance trends. In birds, there was a clear decline in the abundance of northern species compared with their ubiquitous counterparts, particularly in the hottest regions of Britain.

7.4: The relationship between distribution, phenology and abundance

The general principal of population dynamics is that, under favourable conditions, the abundance of a population will increase due to higher fecundity/immigration or lower mortality/emigration. As the population size increases, the number of individuals ranging further from the hub of the population will increase, and so the chance of colonisation of new areas is increased. Under less favourable conditions, lower fecundity or higher mortality at a site may lead to a decrease in abundance, and eventual local extinction. However, sometimes a population may go extinct without any preceding decrease in abundance (Franco *et al.* 2006). In other cases, a population may be close to extinction for many years, with just a few individuals continuing to breed in favourable microclimates, such as particularly sheltered areas, or particularly sunny areas (Thomas *et al.* 2001;

Davies *et al.* 2006). At a large spatial scales (often 10km squares or larger), colonisations usually appear as a front expanding from an established population. On the other hand, extinctions rarely occur as a front, but are generally more patchily distributed, with increasing numbers of extinct populations towards the edge of the range (Wilson *et al.* 2004). At larger spatial scales, extinctions may not be identified for many years, as it is difficult to confirm extinctions by comparison with colonisations.

As I have shown in Chapter 5, there is not always a relationship between phenology and distribution change. However, for some species, for example in butterflies, a relationship between the two does exist. Where this is the case, it may be that by flying earlier in the year, a species can take advantage of a longer reproductive season. This might lead to an immediate increase in abundance at a site, and hence the potential number of migrants able to colonise new sites (increase in distribution). For species where there appears to be no relationship between phenology and distribution, such as birds, it may be that beginning reproductive processes earlier in the year has less effect on the number of new individuals produced, and therefore less effect on a species' potential to colonise new areas (Visser *et al.* 1998). Alternatively, it may be that in groups where no relationship between distribution and phenology has so far been detected, it is simply that any benefit from beginning reproduction earlier in the year has not yet translated into an increased chance for colonisation. In longer lived species, such as birds, where fewer individuals are produced each year (compared with insects, for example) it may take many more years with an increased opportunity to produce extra offspring before any corresponding shift in distribution is seen.

It is generally agreed that there is a positive relationship between the abundance of a species and the occupancy of a species at a site (Hanski 1982, Brown 1984, Gaston & Lawton 1990, Gaston & Blackburn 1999). For the majority of species this may be the case, and my results broadly support this hypothesis. However, by applying the same methodologies across a wide variety of different taxonomic groups, and by investigating different aspects of population ecology, my findings illustrate the complex nature of abundance-occupancy relationships, and how changes in habitat and interactions with other species may lead to unexpected, and sometimes even contradictory results. For example, I have shown that, on average, northern bird species are expanding their ranges southwards, but in comparison with ubiquitous species, they are also declining in abundance.

Table 7.1 shows summary information for each taxonomic group covered in more than one chapter of this thesis (butterflies, birds and plants). General trends in distribution, abundance, phenology and habitat availability are shown for both northern and southern species. Plants and southern species of butterflies and birds are all showing changes that would be predicted from abundance-occupancy relationships. In these groups, increasing abundance is generally accompanied by range expansion, whilst decreasing abundance is accompanied by range retraction. In the case of plants, distribution changes in Britain have not been documented in a wide variety of species, but it is likely that abundance changes will occur and will be detected before any distribution changes (Helm *et al.* 2006; Brown 1984).

Northern butterflies and birds do not follow the typical pattern expected from abundance-occupancy relationships. In the case of butterflies, abundance at specific sites appears to be stable or increasing when compared with ubiquitous species, but distributions are nonetheless retracting northwards at the range margin (Franco *et al.* 2006). This suggests that even large populations may go extinct quite rapidly if environmental conditions become unsuitable. This combination of climate and habitat effects could lead to the patterns of change I detected in Chapters 4 and 6 using different datasets and methodologies. In northern bird species, the opposite pattern is seen, with abundance of northern bird species decreasing at specific sites, whilst the range margins shifts southwards. Again, I hypothesise that effects of improved habitat in the North of England, coupled with direct (physiological) or indirect (asynchrony of biotic interactions) effects of climate change at specific hot sites across the country, could explain this pattern.

Table 7.1: Summary of changes documented, either in this study (if no reference is given) or previous studies, for the taxonomic groups examined in more than one Chapter (butterflies, birds and plants). Where change is 'Unknown' it is due to a current lack of data, so no studies have documented that change.

	Butterflies		**Birds**		**Plants**	
	Northern	**Southern**	**Northern**	**Southern**	**Northern**	**Southern**
Distribution	Northward shift at the range margin. (2km year^{-1})	Northward shift at the range margin. (2km year^{-1})	Southward shift at the range margin. (4km year^{-1})	Northward shift at the range margin. (1km year^{-1})	No change.	No change
Phenological Change	Unknown.	Adults appear earlier. [1]	Unknown.	Egg-laying occurs earlier. [2]	Unknown.	Flowering occurs earlier. [3]
Abundance	Stable or increasing. [7]	Some generalists are increasing, specialists are decreasing. [4,7]	Decreasing.	Increasing for common species. [5]	Some species decreasing. [6]	Variable depending on species. [6]
Habitat Availability	Decreasing. [7]	Specialist habitat is decreasing. [4]	Increasing for some species. [8]	Increasing for common species. [5]	Many habitats specific to the north decreasing. [9]	Variable depending on habitat. [9]

[1] Roy & Sparks 2000

[2] Crick & Sparks 1999

[3] Fitter & Fitter 2000

[4] Warren *et al.* 2001

[5] R. Gregory pers. comm.

[6] Preston *et al.* 2002

[7] Fox *et al.* 2006a

[8] R. Gregory pers. comm.

[9] Braithwaite *et al.* 2006

7.5: The effects of climate and habitat change

In all groups (birds, butterflies and plants), climate change is probably having an effect on species, as responses are seen across taxa (Table 7.1). When examining the effects of climate change on biological systems, phenological change is currently one of the most commonly documented and accepted forms of evidence, as few other environmental changes could cause such a widespread response in the timing of biological events across different taxa. Widespread distribution change had also been documented for a variety of species, both in this thesis and in other studies, but as I have shown (Table 7.1), distribution change is often correlated with habitat change. It can be very difficult to determine how much distribution change is due to climate and how much is due to habitat.

For example, southern butterfly species have been shown to be responsive to climate by appearing earlier in the year (Roy & Sparks 2000). In mobile, habitat-generalist species, distribution size is increasing as abundance at specific sites is increasing, whilst in low mobility, habitat-specialist species the opposite is occurring (Warren *et al.* 2001). In this group, it is likely that the relative importance of habitat change and climate change differ among species. For southern generalist species which are not as constrained by the need for specific habitats, the negative effects of habitat loss are more than offset by the positive effects of climate change, allowing southern and ubiquitous species to fly earlier in the year, and allowing multivoltine species to fit in another brood (Roy *et al.* 2001). However, for specialist species, the effects of climate change do not compensate for loss of habitat, leading to declines in both abundance at sites and overall distribution size (Hill *et al.* 2002, Warren *et al.* 2001). In order for range expansion to occur in some of these species, habitat corridors could be constructed and the quantity of suitable habitat in the landscape increased, so that migrants could colonise new sites (Hill *et al.* 1999b).

Whilst I failed to detect any distribution change in plants, other studies (Preston *et al.* 2002; Braithwaite *et al.* 2006) have indicated that northern species and grassland species are declining in abundance and overall distribution size, whilst scrub species and those genera typical of roadside verges are increasing. Whilst there are some specific examples of species benefiting from climate change, in most cases, the availability of suitable habitat seems to be the main factor driving abundance changes (Braithwaite *et al.* 2006). The broad effect of climate change on the abundance and distribution of plants, if there is any, may not currently be detectable due to the more prevalent effect of habitat change. In general, plants have been slow to respond to change (Braithwaite *et al.* 2006) compared with other species, so if climate change is affecting the distribution or abundance of plants, it is likely that this signal will not become apparent for some years.

Insects and plants often share a close ecological relationship, with insects often relying on the presence of specific food-plants for larvae, or as sources of habitat. As I have demonstrated that many insect species are shifting northwards rapidly whilst the range margin of plant species is not changing to a large degree, it may be of concern that insect species will soon be limited by plant distributions. However, this is unlikely to be a problem in Britain for many decades. Only a very few British butterfly species are limited by the distribution of their host-plant (Guiterrez & Thomas 2000), and in most cases, larval host plants are common and widespread, and do not limit insect distributions. For example, in Britain, southerly butterfly distributions are mostly limited by climate rather than by habitat (Quinn *et al.* 1998), and so under climate warming scenarios these species would be expected to shift northwards until they have colonised the whole country. Only at this point, when a geographical barrier limits colonisation, or when climate change has progressed to such a degree that many interspecific interactions break down, would I expect to see a severe negative effect upon most southern generalist butterfly species.

7.6: Direct and indirect effects of climate change

The direct effect of increased temperature on species has received much study, particularly the responses of insects to temperature (since they are poikilothermic and therefore quite responsive as well as relatively easy to study). Of particular interest to my study is how northern and southern species differ in their response to temperature, and what effect an increase in temperature has on species at their southern range margin. A key question is how the activity of adults (and hence their reproductive success) is affected by temperature. If the assumption is that northern species are better adapted to lower temperatures, it would be expected that northern species would start flying at lower temperatures than their southern or ubiquitous counterpart at the same site, but would also stop flying at lower peak temperatures, as tolerance to high temperatures would be expected to be lower.

In preliminary field experiments I carried out on butterflies, this hypothesis was not supported. The number of flying individuals was recorded throughout a single day (11th July 2005) at a single site of unimproved grassland, as temperatures rose and fell. A transect of 618m was walked at half hourly intervals from 7:15am until 6:45pm. The northern species (Northern Brown Argus) started flying at higher temperatures than its ubiquitous counterparts (Common Blue, Small Heath, Dark Green Fritillary, Meadow Brown), and continued to increase activity rate as temperatures increased, compared with some ubiquitous counterparts which maintained a similar level of activity regardless of temperature. A logistic regression was applied to these data with temperature as the explanatory variable. The fitted lines of the logistic regression can be seen for each species against temperature (in the shade) in Figure 7.1. There was no clear difference between northern and ubiquitous species. All species were flying at 21°C, and the northern species (Northern Brown Argus) showed no decline in activity at high temperatures.

Another key question is whether eggs, larvae, or adults are most affected by temperature. Some studies have found larvae to be the most sensitive stage of the life cycle to temperature (Bryant *et al.* 1997). Given the above field observations, and the conclusions of Bryant *et al.* (1997), it seems more likely that the egg or larval stages are most likely to be negatively impacted by climate change, rather than adults. Phenological studies of butterflies also record date of first appearance of the adults, which may be more a measure of larval development than adult activity (apart from those species which overwinter as adults), again suggesting that the larval stage may be more sensitive to climate change. The adult stage in insects may be quite robust to climate warming, and responses to temperature at this point in development may be more related to taxonomy and evolution. This needs more study.

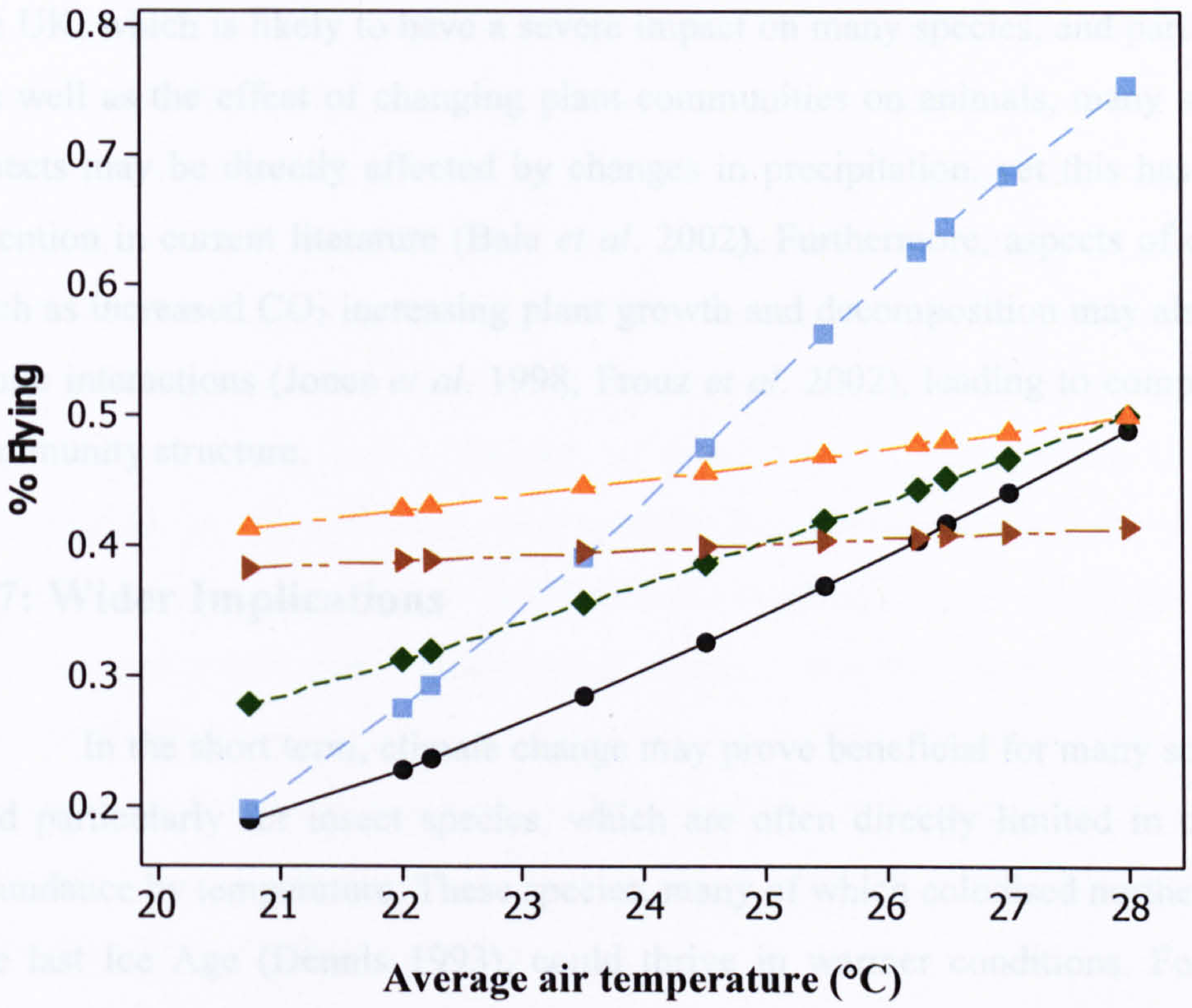

Figure 7.1: The activity of Northern Brown Argus (black), Common Blue (blue), Small Heath (orange), Meadow Brown (brown) and Dark Green Fritillary (green) at a single site at Bakewell, Peak District on a single day in 2005.

Whilst species may respond to consistently increasing temperatures year on year, many climate change scenarios predict that the variability in temperature will also increase as weather patterns become more erratic. For many species, variability or extremes of temperatures may have more effect on populations than a gradual increase. For example, some insect species have been shown to develop at faster or slower rates (depending on species) under variable temperatures compared with constant temperatures (Bryant *et al*. 1999). Extreme events such as drought may have a negative effect upon populations (Thomas *et al*. 1998; Morecroft *et al*. 2002; Roy & Thomas 2003), whilst unusually milder winters may allow species to rapidly colonise new areas (Battisti *et al*. 2006).

Most studies of climate change focus on the direct and indirect effect of temperature on species' physiology or populations (Bale *et al*. 2002). However, climate change scenarios predict more drought conditions for many parts of the planet including the UK, which is likely to have a severe impact on many species, and particularly plants. As well as the effect of changing plant communities on animals, many species such as insects may be directly affected by changes in precipitation, yet this has received little attention in current literature (Bale *et al.* 2002). Furthermore, aspects of climate change such as increased CO_2 increasing plant growth and decomposition may also impact upon biotic interactions (Jones *et al.* 1998; Frouz *et al.* 2002), leading to complex changes in community structure.

7.7: Wider Implications

In the short term, climate change may prove beneficial for many southern species, and particularly for insect species, which are often directly limited in distribution and abundance by temperature. These species, many of which colonised northern regions after the last Ice Age (Dennis 1993), could thrive in warmer conditions. For most groups, habitat change is likely to remain an important factor governing population dynamics for many years to come. For northern species, habitat change may also remain a threat, but climate change will add another stress which may push some species towards extinction (Thomas *et al.* 2004).

Predictions of climate change and how it will affect the UK become less precise as we predict further into the future, with different scenarios being predicted based on levels of pollution, the change in sea and air currents, and the rate and tipping point of various physical processes around the planet. Assuming that temperatures continue to rise at a steadily increasing rate, with milder winters and dryer summers in the UK, we can expect large-scale habitat changes in most plant communities, leaving much of southern Britain with a countryside more typical of the current Mediterranean region. Whilst some generalist species across all taxonomic groups may be able to respond to these new conditions, depending on the speed of change, the majority of native species may be unable to survive in these conditions. Many species present in Britain today have had to respond and adapt to past climate change. The concern is that these species may be unable to respond to such rapid climate change as is currently occurring, and that the fragmentation of natural habitats may limit a species' ability to adapt to new conditions.

Some southern species may be able to shift their distributions northwards and so persist in Scotland and Northern England. However, those species which already favour conditions in these areas (for example northern or cold-adapted species), or are unable to shift their distribution quickly enough (for example specialist southern species, or sedentary species), may be committed to eventual extinction. Against such large environmental changes, conservation efforts focused on these species may fail in the long term, as the preservation of existing landscapes may not provide sufficient habitat for distributions to shift and adaptation to occur rapidly. This bleak outlook is further complicated by the complex interspecific interactions which have developed over evolutionary time for many of Britain's most important and diverse habitats. It is so far unclear how much effect phenological changes, and the rapid rate of some southern species shifting northwards, will have on ecosystems. In some cases, asynchrony of seasonal events (Visser & Holleman 2001) and new competition for resources may push some species to local extinction, even in cases when there was little evidence for direct negative effects of climate change.

7.8: Future work

Over the course of my study, I was unable to carry out some investigations due to time constraints. Throughout my discussion of results in each chapter, other analyses that would help clarify or confirm hypotheses have been highlighted. Here, I suggest other studies or analyses which I feel would be most beneficial in taking the study of the effects of climate change on ecosystems further.

At all times throughout this study, I used what I deemed to be the best method of analysis, but it is likely that additional methods of analysis, when applied to the same datasets, could provide additional insights. In Chapter 2, I demonstrated how aspects of analyses such as whether to use median or mean values in calculations, or how many grid squares to define as marginal, can have major or minor effects on results, depending on the data. For example, I demonstrated how when the number of grid squares defining the range margin is increased from 10 to 40, estimates of range shift are decreased for southern species (from 88km to 73km) whereas estimates are increased for ubiquitous species (from 51km to 118km). Issues such as how the data were collected, how many sites and species were covered, how variable the data are, and how long the period of study was, are all very important when deciding how to analyse data. I was also constrained to some degree in my choice of analytical techniques, since throughout this study I have endeavoured to apply similar methods across taxa wherever possible. This limits analyses to relatively simple methods. However, if only single taxa are studied, or groups of closely related and similarly recorded taxa (e.g. beetles), then more specific analyses could be applied which might provide further insights. For example, the relative change in distribution size (as number of grid squares) for northern and southern bryophyte species could be examined, only for vice counties which have been thoroughly and consistently recorded through time.

Throughout this discussion I have emphasized that the effects of climate and habitat change are both important factors affecting most species, and that these factors can have similar or opposite impacts depending on the species being studied. However, whilst I have hypothesized from my results that in some cases habitat, and in some cases climate, are of more importance to a species' distribution, it is very difficult to prove this. Field and laboratory studies on the relative importance of habitat and climate for a variety of species groups would help to inform this debate, which is likely to only increase as climate change becomes a focal issue.

Throughout my study, I have assumed (as do most studies of this type) that latitude correlates with temperature in the UK. Whilst this is true to some extent, an east-west gradient also exists in Britain (Roy & Asher 2003). Furthermore, yearly temperatures are not necessarily relevant when examining species' responses to climate change, as yearly temperatures do not reflect seasonal temperatures or temperature variation. For example, many insect (Battisti *et al.* 2005; Battisti *et al.* 2006) species have been shown to be positively affected by milder winters, yet few analyses correlate changes in insect or plant abundance and distribution with mean temperature of the coolest month (Crozier 2003). Most analysis of large-scale distribution changes also assume all species' groups are equally sensitive to temperature when, for some species, moisture availability or other environmental variables may be more important factors in limiting distributions. As these types of environmental data become available at increasingly fine scales, I suggest that future studies include such variables in analyses of change. Species which do not appear to be responding to climate change by shifting their distributions latitudinally may be found to responding in a different way. One simple way is to repeat the analysis in Chapter 3, but to use other environmental variables instead of temperature. Where a species appeared to be shifting its range towards areas with more moisture or milder winters, but not latitudinally, it could be surmised that the species was still responding to climate change, but not necessarily in relation to temperature. If detailed data for historical environmental variables become available, this type of study could be taken further, by correlating grid squares with most colonisations across time with grid squares showing the most extreme changes in environmental variables (e.g. moisture, winter temperature). Such analyses of historical data could be complemented by laboratory tests, exposing common and rare species from a variety of taxonomic groups (e.g. plants, butterflies and moths) to different extremes of variables such as moisture and winter temperature, and measuring fecundity and mortality rates.

Dispersal ability is clearly a very important factor when studying distribution change. Whilst some species-specific analyses have used mark-recapture or related techniques to document dispersal distance, I found that most reports of species' dispersal ability were only anecdotal, and large-scale study of most species groups had never been undertaken. I would suggest that a clear understanding of the dispersal ability of all major species groups, at different stages in their life cycle, is essential if we are to understand differences in distribution change between groups. For example, I found millipedes and woodlice both shifting northwards to a surprisingly large degree (Chapter 3), but published reports did not specify how far these species might travel. For some species, simple mark-recapture techniques might illustrate how far an individual can travel. In the case of eggs, spores and seeds, molecular techniques could be used to examine how related populations are, therefore giving an indication of gene flow and dispersal distances.

Finally, it is important that we consider how the most rapidly expanding species might affect ecosystems. A great deal of attention is currently given to the problem of invasive species and the negative effects they may have on ecosystems (Williamson 1996). I suggest that southern species which are rapidly shifting northwards into areas to which they are not native may bring about equally marked changes as alien 'invasive' species. It is becoming clear that disproportional increases in generalist species due to climate warming are affecting patterns of species richness and consequently the biodiversity of many regions in Europe (Menendez *et al.* 2006).

7.9: Overall conclusions

The majority of species studied appear to be responding to climate change, both by changing the timing of their reproductive events, and by shifting their distributions polewards. In many cases, large-scale distribution shifts are accompanied or preceded by declines in abundance, but this is not always the case. Habitat change is also an important factor governing biodiversity in Britain, and this, coupled with potential changes in interspecific interactions due to climate change, may lead to local extinctions in some species in forthcoming years.

References

Asher J, Warren M, Fox R, Harding P, Jeffcoate G, Jeffcoate S (2001) *The millennium atlas of butterflies in Britain and Ireland.* Oxford University Press.

Askew RR (1988) *The Dragonflies of Europe.* Harley Books, Colchester, England.

Atkin OK *et al.* (2000) Leaf respiration of snow gum in the light and dark. Interactions between temperature and irradiance. *Plant Physiology*, **122**, 915–923.

Aukema B (2001) Recent changes in the Dutch Heteroptera fauna (Insecta: Hemiptera). In *Proceedings of the 13th International Colloquium of the European Invertebrate Survey* (ed M. Reemer, van Helsdingen, P.J., Kleukers, R.M.J.C.), European Invertebrate Survey, The Netherlands.

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1-16.

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications*, **15**, 2084-2096.

Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biology*, **12**, 662-671.

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science*, **296**, 1692-1693.

Beaumont LJ, Hughes L (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology*, **8**, 954-971.

Bennett AF, Lenski RE, Mittler JE (1992) Evolutionary adaptation to temperature. 1. Fitness responses of *Escherichia-coli* to changes in its thermal environment. *Evolution*, **46**, 16-30.

Benton MJ, Twitchett RJ (2003) How to kill (almost) all life: the end-Permian extinction event. *Trends in Ecology and Evolution*, **18**, 358-365.

Bergman P, Molau U, Holmgren B (1996) Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. *Arctic and Alpine Research*, **28**, 196-202.

Bezemer TM, Jones TH (1998) Plant-insect herbivore interactions in elevated atmospheric CO2: quantitaive analyses and guild effects. *Oikos*, **82**, 212-222.

Both C, Visser ME (2005) The effect of climate change on the correlation between avian life history traits. *Global Change Biology*, **11**, 1606-1613.

Braithwaite ME, Ellis RW, Preston CD (2006) *Change in the British Flora 1987-2004.* Botanical Society of the British Isles.

Bratton JH (1990) A review of the scarcer Ephemeroptera and Plecoptera of Great Britain. *Research and survey in nature conservation,* **29**, 39 pp.

Brooks SJ (2001) Dragonflies and damselflies. In *The Changing Wildlife of Great Britain and Ireland* (ed D.L. Hawksworth), pp. 340-354. Taylor & Francis, London.

Brooks SJ, Birks HJ (2001) Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews*, **20**, 1723-1741.

Brown JH (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.

Bryant SR, Thomas CD, Bale JS (1997) Nettle-feeding nymphalid butterflies: temperature, development and distribution. *Ecological Entomology*, **22**, 390-398.

Bryant SR, Bale JS, Thomas CD (1999) Comparison of development and growth of nettle-feeding larvae of Nymphalidae (Lepidoptera) under constant and alternating temperature regimes. *European Journal of Entomology*, **96**, 143-148.

Bryant SR, Thomas CD, Bale JS (2002) The influence of thermal ecology on the distribution of three nymphalid butterflies. *Journal of Applied Ecology*, **39**, 43-55.

Bryla DR *et al.* (2001) Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field. *Plant Cell Environment*, **24**, 781–790.

Buse A, Dury SJ, Woodburn RJW *et al.* (1999) Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, **13**, 74-82.

CIP (Climate Impacts Program) (2004; 2005) Last accessed on 28th July 2005 at URL: http://www.ukcip.org.uk

Conrad KF, Woiwod IP, Parsons M, Fox R, Warren MS (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119-136.

Conrad KF, Warren M, Fox R, Parsons M, Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279-291.

Covey-Crump EM (2002) Regulation of root respiration in two species of Plantago that differ in relative growth rate: the effect of short- and long-term changes in temperature. *Plant Cell Environment*, **25**, 1501–1513.

Cowley MJR, Thomas CD, Thomas JA, Warren MS (1999) Flight areas of British butterflies: assessing species status and decline. *Proceedings of the Royal Society of London B Series,* **266**, 1587-1592.

Cowley MJR, Thomas CD, Roy DB, Wilson RJ, Leon-Cortes JL, Gutierrez D, Bulman CR, Quinn RM, Moss D, Gaston KJ (2001) Density-distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology*, **70**, 410-425.

Cramp S, Perrins CM (1993) *The Birds of the Western Palearctic.* Oxford University Press.

Crick HQP (2004) The impacts of climate change on birds. In Rehfisch MM, Feare CJ, Jones NV, Spray C (eds) Climate Change and Coastal Birds. *Ibis*, **146**, 48-56.

Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. *Nature*, **399**, 23-424.

Crick HQP, Sparks TH (2006) Changes in the phenology of breeding and migration in relation to global climate change. *Acta Zoologica Sinica*, **52**, 154-157.

Crozier L (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris. Oecologia*, **135**, 648-656.

Darwin C (1859) *On the Origin of Species*. pp. 60-61 Watts & Co., London, England.

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783-785.

Davis R, Callahan JR (1992) Post-Pleistocene dispersal in the Mexican vole (*Microtus mexicanus*), an example of the apparent trend in the distribution of southwestern mammals. *Great Basin Naturalist*, **52**, 262-268.

Davies MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. *Ecology*, **86**, 1704-1714.

Davies ZG, Wilson RJ, Coles S, Thomas CD (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**, 247-256.

De Knijf G, Anselin A, Goffart P (2001) Trends in dragonfly occurence in Belgium (Odonata). In *Proceedings of the 13th International Colloquium of the European Invertebrate Survey* (ed M. Reemer, van Helsdingen, P.J., Kleukers, R.M.J.C.), European Invertebrate Survey, The Netherlands.

Dennis RLH (1993) *Butterflies and climate change*. Manchester University Press.

Ecoflora Database (2006) http://www.ecoflora.co.uk

Environment Agency (2004) *Environmental Facts and Figures*. Last accessed on 13th April 2004 at URL: http://www.environment-agency.gov.uk/yourenv/eff/water/?version=1&lang=_e

Epstein PR, Diaz HF, Elias S (1998) Biological and Physical Signs of Climate Change: Focus on Mosquito-borne Diseases. *Bulletin- American Meteorological Society*, **79**, 409-418.

Etterson JR, Shaw RG (2001) Constraint to adaptive evolution in response to global warming. *Science*, **294**, 151-154.

Fischer K, Eenhoorn E, Bot ANM, Brakefield PM, Zwaan BJ (2003) Cooler butterflies lay larger eggs: developmental plasticity versus acclimation. *Proceedings of the Royal Society of London B Series*, **270**, 2051-2056.

Fitter AH, Peat HJ (1994) The ecological flora database. *Journal of Ecology*, **82**, 415-425.

Fitter AH, Fitter RSR, Harris ITB, Williamson MH (1995) Relationships between 1st flowering date and temperature in the flora of a locality in central England. *Functional Ecology*, **9**, 55-60.

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

Fox R, Asher J, Brereton T, Roy D, Warren M (2006a). *The State of Butterflies in Britain and Ireland.* Pisces Publications, Newbury.

Fox R, Conrad KF, Parsons MS, Warren MS, Woiwod IP (2006b) *The state of Britain's larger moths.* Butterfly Conservation and Rothamsted Research, Dorset.

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B and Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545-1553.

Frouz J, Novakova A, Jones TH (2002) The potential effect of high atmospheric CO_2 on soil fungi-invertebrate interactions. *Global Change Biology*, **8**, 339-344.

Gaston KJ, Lawton JH (1990) Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos*, **58**, 329-335.

Gaston KJ, Blackburn TM (1999) A critique for macro-ecology. *Oikos*, **84**, 353-368.

Gibbons DW, Reid JB, Chapman RA (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991.* T & A D Poyser Ltd, London.

Gilbert O (2000) *Lichens (The New Naturalist).* Harper Collins.

Gonseth Y, Monnerat C (2001) Recent changes in distribution of dragonflies in Switzerland (Odonata). In *Proceedings of the 13th International Colloquium of the European Invertebrate Survey* (ed M. Reemer, van Helsdingen, P.J., Kleukers, R.M.J.C.), The Netherlands.

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature*, **369**, 448.

Greatorex-Davies JN, Roy DB (2004) Butterfly *Monitoring Scheme: Report to Recorders.* Centre for Ecology and Hydrology, Huntingdon.

Gutierrez D, Thomas CD (2000) Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni. Ecological Entomology*, **25**, 165-170.

Hanski I (1982) Dynamics of regional distribution: the core and satellite hypothesis. *Oikos*, **38**, 210-221.

Hanski I, Woiwod IP (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656-668.

Hanski I, Ovaskainen O (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666-673.

Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. *Trends in Ecology and Evolution*, **14**, 146-150.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.

Heath J, Pollard E, Thomas JA (1984) *Atlas of butterflies in Britain and Ireland.* Harmondsworth: Viking.

Helm A, Hanski I, Partel M (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, **9**, 72-77.

Hewitt GM (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, **68**, 87-112.

Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502-506.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450-455.

Higgs S, Snow K and Gould EA (2004) The potential for *West Nile virus* to establish outside of its natural range: a consideration of potential mosquito vectors in the United Kingdom. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **98**, 82-87.

Hill JK, Thomas CD, Blakeley DS (1999a) Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia*, **121**, 165-170.

Hill JK, Thomas CD, Huntley B (1999b) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B Series*, **266**, 1197-1206.

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D, Huntley B (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313-321.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London B*, **269**, 2163-2172.

Hill JK, Hughes CL, Dytham C, Searle JB (2006) Genetic diversity in butterflies: interactive effects of habitat fragmentation and climate-driven range expansion. *Biology Letters*, **2**, 152-154.

Hill MO, Preston CD, Roy DB (2004) *Plantatt.* Centre for Ecology and Hydrology, Cambridgeshire.

Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. *Journal of Applied Ecology*, **34**, 1484-1496.

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

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution,* **15**, 56-61.

Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature*, **418**, 313-316.

Huntley B, (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67**, 15-22.

IPCC (2001). *Climate Change 2001: the scientific basis.* Cambridge University Press.

Jones TH, Thompson LJ, Lawton JH, Bezemer TM, Bardgett RD, Blackburn TM, Bruce KD, Cannon PF, Hall GS, Hartley SE, Howson G, Jones CG, Kampichler C, Kandeler E, Ritchie DA (1998) Impacts of Rising Atmospheric Carbon Dioxide on Model Terrestrial Ecosystems. *Science*, **280**, 441-443.

Kirby P, Stewart AJA, Wilson MR (2001) True bugs, leaf- and planthoppers, and their allies. In *The Changing Wildlife of Great Britain and Ireland* (ed D.L. Hawksworth), pp. 262-299. Taylor & Francis, London.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography,* **12**, 403-410.

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology,* **90**, 68-77.

Kutzbach J, Gallimore R, Harrison S, Behling P, Selin R, Laarif F (1998) Climate and biome simulations for the past 21,000 years. *Quaternary Science Reviews*, **17**, 473-506.

Levey DJ, Bolker BM, Tewksbury JJ, Sargent S, Haddad NM (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146-148.

McClean CL, Lovett JC, Ku W, Hannah L, Sommer JH, Barthlott W, Termansen M, Smith GF, Tokumine S, James R, Taplin D (2005) African plant diversity and climate change. *Annals of the Missouri Botanical Garden*, **92**, 139–152.

McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 6070-6074.

Menendez R, Megias AG, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB, Thomas CD (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society of London B*, **273**, 1465-1470.

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

Merritt R, Moore NW, Eversham BC (1996) *Atlas of the dragonflies of Britain and Ireland*. London.

Miyazaki S, Kayukawa T, Chen B, Nomura M, Ishikawa Y (2006) Enhancement of cold hardiness by acclimation is stage-specific in the non-diapausing pupae of onion maggot Delia antiqua (Diptera : Anthomyiidae). *European Journal of Entomology*, **103**, 691-694.

Morecroft MD, Bealey CE, Howells O, Rennie S, Woiwod IP (2002) Effects of drought on contrasting insect and plant species in the UK in the mid-1990s. *Global Ecology and Biogeography*, **11**, 7-22.

Ott J (2001) Expansion of Mediterranean Odonata in Germany and Europe - consequences of climatic changes. In *"Fingerprints" of climate change* (eds G.R. Walther, C. Buga & P.J. Edwards), pp. 89-112. New York, Ascona, Switzerland.

Parmesan C, Ryrholm N, Stefanescu C, Hil, JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature,* **399,** 579-583.

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

Penuelas J, Flella I (2001) Responses to a warming world. *Science,* **294,** 793-795.

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology,* **9,** 131-140.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science,* **308,** 1912-1915.

Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature,* **416,** 626-628.

Peyron O, Begeot C, Brewer S, Heiri O, Magny M, Millet L, Ruffaldi P, Van Campo E, Yu G (2005) Late-Glacial climatic changes in Eastern France (Lake Lautrey) from pollen, lake-levels, and chironomids. *Quaternary Research,* **64,** 197-211.

Pollard E (1991) Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos,* **60,** 7-10.

Pollard E, Yates TJ (1993) *Monitoring butterflies for ecology and conservation.* Chapman and Hall, London.

Pollard E, Rothery P (1994) A simple stochastic model of resource-limited populations. *Oikos,* **69,** 287-294.

Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature,* **398,** 611-615.

Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL, Foster PN, La Marca E, Masters KL, Merino-Viteri A, Puschendorf R, Ron SR, Sanchez-Azofeifa GA, Still CJ, Young BE (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161-167.

Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature,* **365**, 335-337.

Preston CD, Pearman DA, Dines TD (2002) *New Atlas of the British and Irish Flora.* Oxford University Press.

Prop J, Black JM, Shimmings P, Owen M (1998) The spring range of barnacle geese *Branta leucopsis* in relation to changes in land management and climate. *Biological Conservation*, **86**, 339-346.

Quinn RM, Gaston KJ, Roy DB (1998) Coincidence in the distributions of butterflies and their foodplants. *Ecography*, **21**, 279-288.

Root TL (1988) Environmental factors associated with avian distributional boundaries. *Journal of Biogeography*, **15**, 489-505.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-59.

Root TL, MacMynowski DP, Mastrandrea MD, Schneider SH (2005) Human-modified temperatures induce species changes: Joint attribution. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 7465-7469.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407-416.

Roy DB, Rothery P, Moss D, Pollard E, Thomas JA (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201-217.

Roy DB, Asher J (2003) Spatial trends in the sighting dates of British butterflies. *International Journal of Biometeorology*, **47**, 188-192.

Roy DB, Thomas JA (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia*, **134**, 439-444.

Russell LK, Evans SJ, Smith L, Bevers CM, Luxford AP, Stubbs WJ, Wilson JB (2005) Distribution/abundance relations in a New Zealand grassland landscape. *New Zealand Journal of Ecology*, **29**, 61-68.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1773.

Shimada T, Saitoh T, Sasaki E *et al.* (2006) Role of tannin-binding salivary proteins and tannase-producing bacteria in the acclimation of the Japanese wood mouse to acorn tannins. *Journal of Chemical Ecology*, **32**, 1165-1180.

Shoo LP, Williams SE, Hero JM (2005) Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology*, **11**, 1469-1476.

Simmons AD, Thomas CD (2004) Changes in dispersal during species' range expansions. *American Naturalist*, **164**, 378-395.

Smith RIL (1994) Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia*, **99**, 322-328.

Sparks TH, Menzel A (2002) Observed changes in seasons: An overview. *International Journal of Climatology*, 22, 1715-1725.

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecology and Climatology: Ecological Effects of Climate Fluctuations. *Science*, 297, 1292-1298.

Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. *Nature*, 406, 366-367.

Sutcliffe OL, Thomas CD, Moss D (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, 65, 85-95.

Telfer MG, Preston CD, Rothery P (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation*, 107, 99-109.

Thomas CD, Abery JCG (1995) Estimating rates of butterfly decline from distribution maps: the effect of scale. *Biological Conservation*, 73, 59.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, 399, 213.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, 411, 577-581.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend-Peterson A, Phillips OL, Williams SE (2004) Extinction risk from climate change. *Nature*, 427, 145-148.

Thomas CD, Franco AM, Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, 21, 415-416.

Thomas JA, Moss D, Pollard E (1994) Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography*, 17, 215-220.

Thomas JA, Surrey R, Shreeves B, Steele C (1998) *New Atlas of Dorset Butterflies*. The Dorset Natural History & Archaeological Society, Dorchester.

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis. *Science,* **303**, 1879-1881.

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65-66.

Tjoelker MG *et al.* (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q10. *Global Change Biology*, **7**, 223–230.

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B*, **270**, 467-473.

Turner JRG, Gatehouse CM, Corey CA (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, **48**, 195-205.

Uvarov BP (1931) Insects and climate. *Transactions of the Entomological Society London*, **79**, 174-186.

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

Visser ME, van Noordwijk AJ, Tinbergen ME, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, **265**, 1867-1870.

Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B,* **268**, 289-294.

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

Waring P, Townsend M (2003) *Field Guide to the Moths of Great Britain and Ireland.* British Wildlife Publishing, Dorset.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature,* **414**, 65-68.

Weiss SB, Murphy DD, White RR (1988) Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha. Ecology*, **69**, 1486-1496.

Williamson M (1996) *Biological Invasions*. Chapman & Hall, London.

Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393-396.

Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138-1146.

Woodward FI, Lomas MR, Betts RA (1998) Vegetation-climate feedback in a greenhouse world. *Philosophical Transactions of the Royal Society of London B,* **353**, 29-39.