Understanding drivers of species distribution change: a trait-based approach

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Declaration of Originality

This thesis is the result of my own work. Any work carried out through collaboration is acknowledged clearly within the text. I was not responsible for collecting the raw data used in this thesis, the relevant data sources are cited within text. The estimates of land use change in Britain used in chapter seven were provided by Tommaso Jucker.

Copyright Declaration

Abstract

The impacts of anthropogenic environmental change on biodiversity are well documented, with threats such as habitat loss and climate change identified as causes of change in species distributions. The high degree of variation in responses of species to environmental change can be partly explained through comparative analyses of species traits. I carried out a phylogenetically informed trait-based analysis of plant range change in Britain, discovering that traits associated with competitive ability and habitat specialism both explained variation in range changes. Competitive, habitat generalists out-performed species specialised to nutrient-poor conditions; a result which can be attributed to the impact of agricultural intensification in Britain. A limitation of the comparative approach is that the models do not directly test the impact of environmental change on species distribution patterns, but instead infer potential impacts. I tested the potential of comparative analyses from a spatial context by conducting a spatial analysis of plant distribution change in Britain, examining the direct impact of environmental change on the spatial distribution of the trait characteristics of species that have gone locally extinct. I discovered a loss of species associated with nitrogen poor soils in regions that had an increase in arable land cover, a result that supports the results from the trait-based analysis of plant range change and demonstrates that comparative studies can accurately infer drivers of distribution change. I found that the cross-region transferability of trait-based models of range change to be related to land cover similarity, highlighting that the trait-based approach is dependent on a regional context. Additionally, I discovered that traits derived from distribution data were significant predictors of range shift across many taxonomic groups, out-performing traditional life history traits. This thesis highlights the potential of the data accumulated through the increased public participation in biological recording to address previously unanswerable ecological research questions.

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Chapter 1: Introduction

1.1 Environmental change and biodiversity

Biodiversity is essential for ecosystem function and provides many ecosystem services, including the provision of food (crops, fish, livestock, etc.), regulatory processes (soil, air and water quality) and cultural services such as recreational use (Mace *et al.*, 2005; UK National Ecosystem Assessment, 2011; May, 2011; Hooper *et al.*, 2012). Despite its importance, biodiversity is consistently undervalued by decision makers using standard economic analyses and as a result lacks the protection it needs (UK National Ecosystem Assessment, 2011). Current rates of biodiversity loss are estimated at between 100 to 1000 times the average rate over the past half billion years (May, 2011; Mace *et al.,* 2005). This accelerated rate of extinction suggests we may be on the brink of a sixth mass extinction event (Wake & Vredenburg, 2008; Barnosky *et al.*, 2011; May, 2011). A wide variety of anthropogenic pressures are believed to be driving the decline in biodiversity. Habitat destruction, introduced species, overexploitation, disease, pollution and climate change are the key drivers of global biodiversity loss (Butchart *et al.,* 2010; Magurran & Dornelas, 2010; UK National Ecosystem Assessment, 2011). In Britain, three key drivers of change have been identified: land use change as a result of agricultural intensification, overexploitation of natural resources and pollution (UK National Ecosystem Assessment, 2011). Climate change and introduced species have also been cited as important drivers of change in ecosystems. Studies aimed at forecasting future drivers of change have suggested that land use change is likely to persist as the major driver of change in biodiversity, followed by climate change which will show increased importance (Sala *et al.,* 2000; UK National Ecosystem Assessment, 2011). A horizon scan of possible future global conservation issues suggests that issues relating to the impact of climate change will be a dominant concern for conservation biology (Sutherland *et al.*, 2010). Invasive species and nitrogen deposition are also predicted to have large future roles in driving biodiversity change (Sala *et al.*, 2000; Thomas *et al.*, 2004a).

1.2 Why examine species distribution change?

Species respond to environmental pressures in a range of ways (Pimm & Raven, 2000; Warren *et al.*, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Jetz *et al.*, 2007; Chown, 2010; Polce *et al.*, 2010). An area of much research has been the impact of environmental change on species' distribution patterns, with many species from many regions showing distribution changes in response to recent environmental perturbation (Thomas & Lennon, 1999; Wilson *et al.,* 2005; Franco *et al.,* 2006; Hickling *et al.*, 2006; Menéndez *et al.,* 2006; Walker *et al.,* 2009; Chen *et al.,* 2011). Distribution change can be measured in a variety of ways - in this thesis I mainly investigate change in species range size and shifts in species range position. The importance of change in range size is linked to extinction risk (IUCN, 2001). Shift in range position, commonly measured as the temporal change in a species range margin (Thomas & Lennon, 1999; Hickling *et al.,* 2006; Shoo *et al.*, 2006 Hitch & Leberg, 2007; La Sorte & Thompson III, 2007; Hassall & Thompson, 2010), has been suggested as a threat to community structure which may lead to the breakdown and collapse of ecosystem function (Lenoir *et al.,* 2008; Walther, 2010), and cross species interactions may be lost and result in trophic mismatch (Edwards & Richardson, 2004).

The rich history of biological recording in Britain has resulted in some of the best distribution datasets spanning a range of taxa for any region worldwide. These data can be used to examine species distribution change and are the main focus of this thesis. With the increase in public participation in biological recording, the size and taxonomic breadth of species distribution datasets are expected to rise (Silvertown, 2009; Dickinson *et al.*, 2012; Miller-Rushing *et al.*, 2012). This growth in data collection highlights the importance of recording schemes, their organisers and systems such as the National Biodiversity Network (NBN - http://www.nbn.org.uk/) and the Global Biodiversity Information Facility (GBIF - http://www.gbif.org/), that increase accessibility to the large-scale distribution datasets. With the growth in size and accessibility of large-scale distribution datasets, there will be new opportunities to address ecological research on poorly studied taxonomic groups that were previously unanswerable.

1.3 Trait-based approaches and species distribution change

Responses to environmental change are not uniform across all species (Parmesan *et al.,* 1999; Polce *et al.,* 2010; Angert *et al.,* 2011). There is widespread evidence that species have responded to climatic warming through poleward shifts in their distributions (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Chen *et al.*, 2011), however the intensity, and in some cases direction, of these range shifts vary within, and between taxonomic groups (Warren *et al.,* 2001; Thomas *et al.,* 2004b; Lenoir *et al.,* 2008). Hickling *et al.,* (2005) showed variation in range shift among the Odonata species in Britain between 1960 to 1995, while in a follow up study, Hickling *et al*., (2006) found a widespread variation in the mean rates of range shift between 16 taxonomic groups in Britain. In addition, evidence has shown that change in range size in response to environmental pressures can be highly variable between species (Mattila *et al.*, 2011; Botts *et al.*, 2012; Newbold *et al.*, 2012). In Britain, change in species range size was found to be highly variable in plants between 1987 to 2004 (Braithwaite *et al.*, 2006). Understanding how the drivers of biodiversity loss differ across species and over time is of great importance to biodiversity conservation (Mace *et al.,* 2010).

This variation in species response to environmental change can be partly explained by variation in species trait characteristics (Purvis *et al.*, 2000; Reynolds *et al.*, 2005; Walker & Preston, 2006; Angert *et al.*, 2011; Chessman, 2011; Grewe *et al.*, 2012; Newbold *et al.*, 2012). Comparative trait-based studies that examine whether certain character traits predispose species to distributional change during times of environmental peturbation can help shed light on the main drivers of change (Fisher & Owens, 2004, Koh *et al.,* 2004; Cardillo *et al.,* 2005). Common examples of trait –

distribution trend relationships include: habitat generalists out-performing specialists due to a greater ability to persist during times of environmental change (Fisher & Owens, 2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012), and larger range shifts associated with species with greater dispersal ability that can track a shift in their climatic niche (Thomas *et al.*, 2001; Pöyry *et al.*, 2009; Grewe *et al.*, 2012).

Trait-based comparative analysis forms a central theme of this thesis, I begin with a trait-based analysis of plant distribution change in Britain. Previous comparative studies of plant distribution change in Britain have been geographically limited and/or have not accounted for phylogeny (Preston, 2000; Preston *et al.*, 2002a; Braithwaite *et al.*, 2006; Walker & Preston, 2006; Walker *et al.*, 2009), and therefore run the risk of increased type I error rates due to phylogenetic autocorrelation (Felsenstein, 1985; Harvey & Pagel, 1991; Freckleton *et al.,* 2002; Purvis, 2008). I carried out a phylogenetically informed trait-based analysis of range change using some of the best plant distribution and trait data available in Europe and use a recently published, dated, species level plant phylogeny.

A common goal of trait-based studies is to directly assist conservation practice, but they rarely meet this target and instead act as 'calls to action' highlighting biodiversity decline (Cardillo & Meijaard, 2011). One reason for this is that, although such studies explain biodiversity responses within their own datasets, they seldom test the predictive ability of their models by, for instance, assessing transferability of the results to new regions (Fisher & Owens, 2004; Pocock, 2010; Cardillo & Meijaard, 2011). I tested the ability of trait-based models to predict plant distribution change across seven geographic regions (Flanders and six regions in Britain) that varied in terms of land-cover and species composition.

As discussed above, evidence has shown species have responded to climatic warming through poleward shifts in their distributions, but the direction and intensity of these shifts is highly variable between species. Certain character traits, such as good dispersal ability, allow species to track their climatic niche, and species that lack this ability may be of conservation concern if we assume they are lost from the now climatically unsuitable warmer range edge (Thomas *et al.*, 2004a; Perry *et al.*, 2005; Wilson *et al.*, 2005). Previous comparative studies of species range shift have primarily been restricted to birds and butterflies due to a lack of data for many other taxonomic groups. I tested the ability of traits that were derived from distribution data alongside widely available climate and land use datasets to explain variation in range shift across ten taxonomic groups in Britain. Additionally, I examined the difference in explanatory power of traits derived from distribution data to life history traits for explaining variation in butterfly and plant range shift.

A limitation of the comparative trait-based approach is that the models do not directly test the impact of environmental change on species distribution patterns, and instead are used to infer the potential impacts (Fisher & Owens, 2004; Cardillo & Meijaard, 2011). For my final data chapter I conduct a spatial analysis of plant distribution change in Britain, examining the direct impact of land use and climate change on the spatial distribution of the trait characteristics of species that have gone locally extinct. This study tests the potential of comparative trait-based models for accurately detecting environmental drivers of species distribution change.

Chapter 2: Determining change in species’ ranges: pitfalls and paths forward

2.1 Abstract

The ability to accurately measure change in species’ distributions is vital for many aspects of conservation and ecological research. Distribution change is often estimated from data taken from consecutive atlases, however, the accuracy of such range change estimates can be inhibited by many problems and constraints associated with the data. Common problems encountered include variation in recorder effort, recorder behaviour and species detectability, all of which can cause temporal variation in the probability of false absences which, if unaccounted for, can lead to bias in range change estimates. In this review, we outline the key problems encountered when using distribution data to estimate species distribution change, and discuss the various suggested remedies. We use three typical dataset examples, each having different limitations, to highlight the relative merits of different techniques. Methods to account for data constraints can be categorised into three main approaches: limiting the data, benchmarking and relative change measures. The techniques vary in their level of complexity with the most appropriate remedy relying on the quality of input data. Range change estimation is often possible despite data limitations provided that an appropriate method of analysis is chosen. Datasets with few limitations can be analysed using simple methods (such as a percentage change in occupied grid cells between time periods) which often return absolute measures of change, while data with greater limitations require more complex treatment. Limiting the data is often used alongside more complex methods to account for species-specific problems that may occur. Metadata play a crucial role in the understanding of data limitations and ultimately help determine the most appropriate method for estimating change.

2.2 Introduction

Many aspects of ecology and conservation biology rely on the ability to accurately estimate change in species' distributions. Monitoring and predicting the spread of biological invasions, investigating species' responses to environmental change and conservation prioritisation all benefit from accurate measures of distribution change. Techniques for assessing extinction risk also often rely on an effective measure of species distribution change, e.g., criteria A & B in the IUCN Red List (IUCN, 2001). For well-known taxa in well-studied parts of the world, distribution change is often estimated from species presence in a spatial grid taken from successive atlases (Telfer *et al.,* 2002; Tamis *et al.,* 2005; Mattila *et al.,* 2008; Szabo *et al.,* 2009; Robertson *et al.*, 2010). However, the use of such atlas data to determine change can be inhibited by many problems and limitations, including spatial and temporal variation in recorder behaviour, uneven recording effort and changes in species' detectability (Dennis & Thomas, 2000; Telfer *et al.,* 2002; Lips *et al.,* 2004; Rich, 2006; Tingley & Beissinger, 2009). In this review, we discuss the main problems and constraints encountered when using distribution data to estimate species distribution change, and then discuss and categorise the main approaches used to account for such constraints. We present three typical datasets which vary in data quality and highlight potential solutions to account for the data limitations while accurately estimating distribution change.

2.3 Problems and limitations

The main problems encountered when using atlas data to examine species distribution change often arise from temporal differences in aspects of data collection (Rich & Woodruff, 1992; Warren *et al.,* 2001; Telfer *et al.,* 2002; Tingley & Beissinger, 2009; Hassall & Thompson, 2010; Hill, 2012). This temporal variation can lead to a difference in the level of false absences (non-detections treated wrongly as accurate non-presences) across time periods, which can in turn lead to bias if change is estimated simply as the difference in grid cell occupancy across multiple time periods. For example, an apparent increase in species range size may be due to a greater level of false absences in the early time period. Change in species occupancy may be quantified using simple methods if the level of false absence is consistent across the time periods. In the following section we describe three main problems that can lead to variation in the levels of false absences, and therefore inhibit accurate estimates of distribution change.

2.3.1 Change in recorder effort

Variation in recorder effort is probably the most common issue encountered when examining species range dynamics using atlas data (Dennis & Thomas, 2000; Hill *et al.,* 2002; Thomas *et al.,* 2004a; Hickling *et al.,* 2006; Hortal *et al.,* 2007; Myers *et al.,* 2009). Survey effort and the number of species recorded can be highly correlated (Rich, 2006; Hortal *et al.,* 2007), and therefore richness and distribution maps can reflect not only the distribution of species, but also the recording effort (Dennis *et al.* 1999). Temporal variation in recorder effort is a common issue encountered when estimating range change from successive atlases, with a general increase of recording effort over time in Britain frequently reported (Rich & Woodruff, 1992; Dennis *et al.,* 1999; Warren *et al.,* 2001; Telfer *et al.,* 2002; Hassall & Thompson, 2010; Hill, 2011). This temporal variation in recording effort renders simple comparisons (e.g. difference in grid square occupancy) across time periods inappropriate. Declines may be missed due to higher levels of false absences in the earlier time period as a result of lower survey effort. Additionally, recorder effort can be spatially heterogeneous, for example, the number of butterfly recording visits to sites have been shown to significantly correlate with distance to a recorder’s home, species diversity and butterfly resources (Dennis & Thomas, 2000). Variation in the spatial focus of recording effort over time can reduce the accuracy of range change estimation (Maes & van Swaay, 1997; Myers *et al.,* 2009). Recorder effort can also vary by species identity. Species-specific surveys may confound the results of range change analyses as there will be disparity in the level of false absences before and after the species-specific survey (Maes & van Swaay, 1997; Hill *et al.,* 2002).

2.3.2 Variation in recorder behaviour

Recorder behaviour can vary through time, leading to disparity in the probability of false absences which reduces the ability to accurately estimate distribution change when comparing species distributions from two or more distinct time periods (Gibbons *et al.,* 1993; Tingley & Beissinger, 2009). An example of such variation in recorder behaviour was highlighted by Rich & Woodruff (1992) who discovered that the increase in records of non-native plant species in Britain was not only due to the spread of non-natives, but also due to a change in the behaviour of botanists who only recently tended to record all sightings of non-natives. Therefore, the variation in recorder behaviour was likely to have increased the probability of false absences in non-native species records in the earlier time period. Recorder behaviour can also vary in terms of the popularity of certain habitat types to the recording community (Telfer *et al.*, 2002).

2.3.3 Temporal variation in species detectability

The ease of locating and identifying a species or group of species can vary through time (Pellet, 2007; Szabo *et al.*, 2010). Such variation in detectability can be caused by the invention of new sampling techniques (e.g. bat detector, moth trap, pheromone trap), the publication of new identification keys or an increase in taxonomic awareness (Telfer *et al.,* 2002; Moritz *et al.,* 2008; Myers *et al.*, 2009). Variation in detectability can also be caused by ecological changes resulting from environmental change. For example, climate change has been associated with changes in species phenology, this variation in the timing of events such as flowing time or flight period can cause increased or decreased detectability at certain times of the year. Temporal variation in detectability will cause temporal variation in the probability of false absences, which will inhibit accurate estimation of distribution change. Tingley & Beissinger (2009) reviewed 37 studies concerned with species range shift and discovered that most of the studies recognised disparities in the methodologies that could cause differences in the detectability of species between time periods, but far fewer accounted for the resulting variation in false absences.

2.4 Addressing the problems

Many techniques have used distribution data from consecutive atlases to estimate species range change while accounting for various data limitations. We classify these methods into three broad categories: 1) Limiting the data, 2) Benchmarking and 3) Relative change measures. We use case studies, mainly focusing on change in European and North American avian and lepidopteran faunas, to highlight differences between the categories and discuss the strengths and weakness of each approach.

2.4.1 Limiting the data

Limiting the data is the most common solution used to account for data problems when estimating distribution change, and is often used alongside other techniques (Fuller *et al.,* 1995; Konvicka *et al.*, 2003; Telfer *et al.*, 2002; Hickling *et al.*, 2006; Mattila *et al.*, 2006; Sekercioglu *et al.*, 2008). Data can be limited spatially, temporally and by species identity, and the methods used to determine the exclusion criteria vary in complexity. Pöyry *et al.* (2009) used a simple exclusion criterion based on species identity when examining distribution change in Finnish butterflies. Migratory species were excluded from an analysis that found the butterflies of Finland had shifted 59.9 km polewards between 1992 – 1996 and 2000 – 2004. Rich & Karran (2006) limited the data temporally when examining floristic change in Britain. Data from the 1990s were excluded as it was a period of intensive surveying of rare plants which would potentially cause bias in the analysis of species distribution change. An example of a simple spatial exclusion criteria comes from Fuller *et al.* (1995), who examined range change of birds in Britain using successive breeding bird atlases, 1968 - 1972 (Sharrock 1976) and 1988 – 1991 (Gibbons *et al.* 1993). Recording effort was deemed comparable between the two time periods in Britain but not in Ireland. Therefore, the data were spatially limited by excluding Ireland from the analysis. Range change was then calculated as the percentage change in the number of 10 km grid cells occupied between the atlas periods, discovering that 24 of the 28 farmland birds analysed had declined in range size in Britain (Fuller *et al.*, 1995). More complex methods for identifying comparable regions have been used, with rarefaction techniques frequently used to test if certain regions have been sufficiently well surveyed (Gotelli & Colwell, 2001; Biesmeijer *et al.*, 2006; Boakes *et al.,* 2010). Wilson *et al.* (2007) examined butterfly community change across elevation gradients of the Spanish Sierra de Guadarrama Mountains, and used rarefaction to quantify sampling effort, excluding sites from the analysis that had less than 70% of expected species recorded. The study found that in 90% of the study region there had been a net decline in butterfly species richness. In an analysis of species range change across many taxonomic groups, Hickling *et al.* (2006) excluded cells from the analysis if, in either time period, they contained less than 10% of the total species list of the taxonomic group in question (Figure 2.1). Cells below this threshold number of species may have been under-recorded. Finally, Warren *et al.* (2001) examined distribution change in British butterflies and accounted for temporal variation in recorder effort by randomly sub-sampling the more heavily surveyed second time period using the number of records in the first time period. The samples were carried out separately for each 100 km grid cell to retain the overall geographic pattern of the records. Range change was then estimated as the difference in the number of grid cells occupied in each time period. Thomas *et al.* (2004b) applied the same method, finding that butterflies have experienced greater losses (71% over approximately 20 years) than birds (54% over 20 years) and plants (28% over 40 years) in Britain. A limitation of this sub-sampling technique is that as it requires multiple records for species within each grid cell (multiple record cards), much of the widely available presence only atlas data would not be sufficient for this method.

Despite its frequent use, limiting the data does not make full use of the available dataset, excluding potentially useful data, and the recorder effort with which it was collected. Limiting the data is frequently used in conjunction with other techniques to maximise reliability of range change estimated while still retaining much of the available data. A key area for future research would be to identify a technique that minimises the need to limit the data when analysing change using atlas data.

Figure 2.1 The geographic distribution of cells included in an analysis of butterfly range change based on data from two consecutive British butterfly atlases: 1970 – 1982 (Heath *et al.,* 1984), 1995 – 1999 (Asher *et al.*, 2001). The method recommended by Hickling *et al.* (2006) was used to subset the data, light grey cells are those that were surveyed (had at least one record) in both time periods, while dark grey cells are those cells that have at least 10% of the butterfly fauna of Britain present in both time periods, and can be referred to as well-recorded cells.

2.4.2 Benchmarking

Benchmarking techniques quantify recorder effort based on the frequency of a group of ubiquitous, stable, 'benchmark' species that is then used to adjust the frequency of non-benchmark species. Maes & van Swaay (1997) examined distribution change in the butterfly fauna of Northern Belgium and the Netherlands, and noted a large difference in the recording effort between the two datasets used to determine change. To account for this, a correction factor for each time period was calculated as the average number of grid cells that a set of reference species ('benchmark species') occupied. To determine the corrected range size, species occupancy in each time period was divided by the correction factor for the time period in question. Range change was estimated as the percentage change in the corrected range size between the two time periods. The range change measures identified by Maes and Van Swaay (1997) were then used to identify the threat status of butterflies in Northern Belgium and the Netherlands. A limitation of the benchmarking approach is that it does not account for variation in species detectability or recorder behaviour. A further limitation of this approach is that as the geographic size of the study area increases, finding ideal ubiquitous benchmark species becomes more difficult.

Studies have shown that species occupancy can be quantitatively estimated despite variation in species detectability or recording effort (Mackenzie et al., 2002). Such estimates can be based on species occupancy models that involve various aspects of the grid cell (Mackenzie et al., 2002; Kéry et al., 2012) or can be based on the presence of other species within a local neighbourhood (Hill, 2012). Hill (2012) extended the benchmarking technique with a measure that accounts for both temporal and spatial variation in recording effort. For each focal cell a set of neighbourhood cells were identified on the basis of geographic distance and vegetation similarity. A set of local benchmark species were identified as a fixed proportion of the most common species within the neighbourhood. The proportion of benchmark species found within the focal cell was used as a local measure of recording effort (Figure 2.2). Species frequencies were adjusted by the local recording effort multiplier and then used as probabilities to estimate trends in frequency of occurrence (Hill 2012). The novel aspect of this FRESCALO (FREquency SCAling Local) approach is that it uses species lists from neighbourhoods to account for regional variation in recorder effort. This enables the use of inadequately sampled regions to estimate trends, such regions that would likely be excluded from the analysis using other methods. A limitation of this method is that the identification of the neighbourhoods requires a second dataset consisting of a well sampled taxonomic group within the region of interest which may not always be available. However, this limitation may potentially be solved by using climate or habitat data as an alternative to the species composition training dataset used to determine cell neighbourhoods.

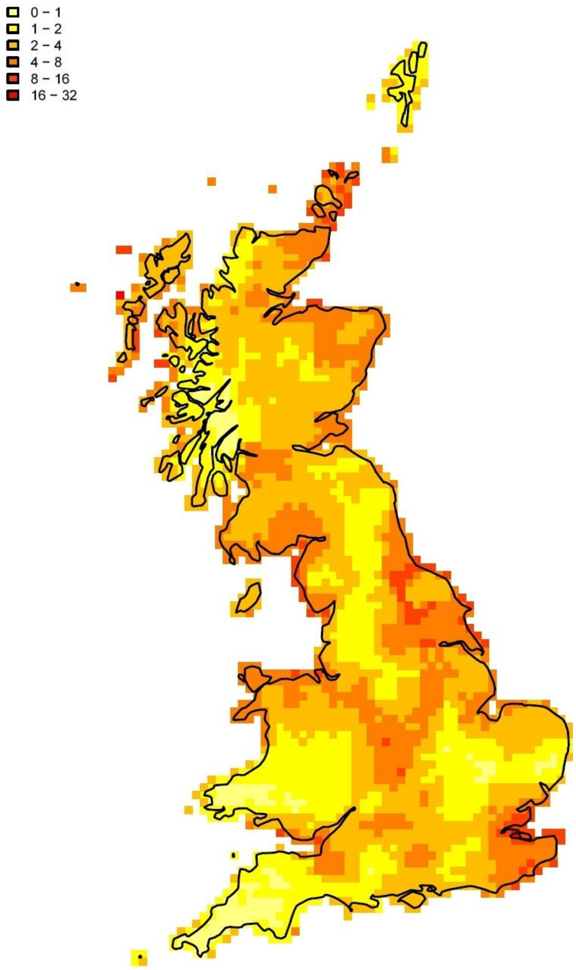


Figure 2.2 A map of the sampling effort multiplier calculated using FRESCALO on British Bryophyte distribution data between 1970-2009 with data on the flora of Britain used as a training dataset. It is essentially a map of sampling effort, the greater (redder) the sampling effort multiplier the less well-surveyed the cell is. By mapping the sampling effort multiplier we can see hotspots of under-recording such as the eastern half of Kent and North East Scotland in the county of Caithness, while southern Wales and Cornwall appear to be well surveyed with low sampling effort multipliers.

2.4.3 Relative change measures

Relative change measures do not identify absolute values of species distribution change, but instead estimate species change in relation to the overall trend for the group in question. Telfer *et al.* (2002) examined changes in distribution size of carabid beetles and vascular plants in Britain, presenting a technique for estimating change while accounting for temporal variation in recorder effort. The change index was calculated as the standardized residuals from a linear regression of the relationship between logit-transformed counts of grid cells in the earlier and later time periods, in which fitting of the regression line is weighted by the reciprocal of the variance in the logit proportion to account for heteroscedasticity (Figure 2.3). Species with a positive change index have been recorded in more grid cells in the later time period than expected based on the regression model, while those with a negative change index have been recorded in relatively fewer (Telfer *et al.,* 2002). This technique does not give actual values of range change between time periods, but assuming all species have received the same level of recorder effort within each time period, it gives a measure of change relative to the overall change of all species combined. A potential limitation of this method is that spatial variation in recording effort can lead to inaccurate range change estimates. For example, if recording effort was focussed in Scotland during the first time period but shifted onto England in the second, the change index is likely to show positive trends for southern species and negative trends for northern species, an artefact of spatial variation in recording effort. Additionally, latitudinal diversity gradients may lead to bias in the relative change estimates, as the overall trend that the change index residuals are derived from will be biased towards the trends in regions of high species richness.

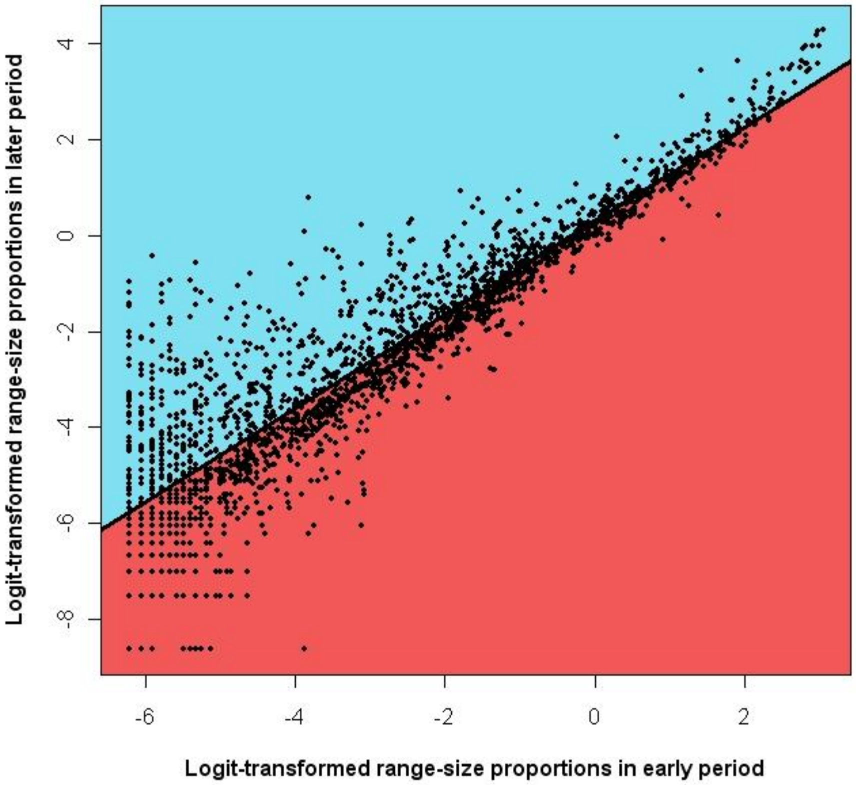


Figure 2.3 A visual representation of the change index method of Telfer *et al*. (2002). Vascular plant range size in the earlier (1930-1960) and later time periods (1987-1988) are plotted as logit-transformed proportions of total number of grid cells surveyed in Britain. The standardised residuals from the linear regression fitted to this relationship provide the index of relative change. Species with a negative change index (in the red section of the graph) have been found in relatively fewer grid cells in the later period than expected given the range size in the early period, whereas species with a positive change index (in the blue section of the graph) have been found in relatively more than expected.

Another example of a relative change measure can be found in Szabo *et al.* (2010), who examined species range dynamics based on species lists. Species lists are a common method of recording biodiversity but are widely under-analysed due to the heterogeneous nature by which they are compiled, and information regarding the time and effort used to obtain a species list is usually unknown. Szabo *et al.* (2010) modelled the relationship between the probability of recording a species on a list, given the length of the list, and the rarity of the species. Common species tend to appear frequently on short lists and, therefore, show an early increase in probability of observation as list length increases. In contrast, the probability of observing a rare species remains low until the list length approaches the total number of species found across all lists within the study region. The change in the relationship between probability of observation and list length was examined temporally for each species and used to infer range change, with an increase in species distribution reflected in an increased probability of detection given the length of the list. This technique avoids the problems associated with variation in recorder effort by including it into the modelling process in the form of the list length. The list length method is a relative technique as a change in the frequency of one species on a list influences all other species in that species pool, i.e. as one species becomes rarer the remaining species will shift to be more common (Szabo *et al.*, 2010). As with the change index method of Telfer *et al.* (2002), spatial variation in recording effort can inhibit accurate range change estimates when using the list length method. If survey effort is focussed on a certain habitat type in the earlier time periods and this focus changes with time, then specialists of the focal habitat in the earlier time period may appear to be in decline, an artefact of spatial variation in recording effort. Relative change measures are further limited by a vulnerability to species level variation in detectability and recorder behaviour.

2.5 Data quality and technique selection

As outlined above, many techniques have been presented to examine range dynamics while accounting for several data limitations. The quality and type of input data determines which technique should be used to examine range change. An in-depth understanding of the data will aid with method selection, and this level of understanding often relies on comprehensive metadata (the detailed information that describes various aspects of the data). In the following section we outline three different typical datasets with varying levels of data quality. For each dataset we suggest an appropriate technique to examine range change based upon the limitations of the data.

The first dataset can be described as ideal with very few limitations. The data are from two 5 year time periods separated by a 15 year gap. The same sites were resurveyed in the later time period by the same recorders using the same survey methods. The time of the year and effort spent recording were similar between the two time periods, and there is no temporal variation in recorder behaviour or species detectability. In this case the ideal method to measure range change would be simply the difference in the number of grid cells each species occupies in each time period. As there are very few limitations or problems with the data this simple method used by Asher *et al.* (2001) is appropriate.

The second hypothetical dataset is based on two successive atlases and suffers from two main limitations. The first is that there was greater survey effort in the later time period in comparison to the earlier, and the second is that there was a change in the behaviour of surveyors towards the recording of alien species. In the earlier time period alien species were ignored by recorders, whereas in the latter time period surveyors had begun recording non-natives. Despite these two differences there were very few other limitations of the dataset, with no difference in the spatial pattern of recording effort or species detectability across the time periods. To analyse this dataset we recommend the change index technique as proposed by Telfer *et al.* (2002). This technique is suitable as it is designed to deal with temporal variation in recorder effort which is the key limitation of the dataset in question. Species level variation in recorder behaviour can inhibit the ability of the change index method to accurately determine change, therefore alien species that have been subject to a large change in recording behaviour need to be excluded from this analysis.

Our third and final hypothetical dataset is based on two successive atlases, is limited by both spatial and temporal variation in recorder effort, and a certain group of species are known to have had an increase in records as a result of a change in detectability due to the publication of a new identification guide between the successive atlases. For the remaining species not covered in the new identification key, detectability remains stable between the time periods. Any change in the recorder behaviour between time periods is similar across all species included in the dataset. In this case the Hill (2012) method is the ideal option for analysing change: many of the other techniques account for temporal differences in recorder effort but the Hill (2012) method accounts for both spatial and temporal variation in recording effort (see above). The variation in species detectability as a result of the publication of the new identification key, however, remains a problem for this technique; to account for this species with temporal variation in detectability should be excluded from the analysis.

2.6 Conclusion

To summarize, distribution data are vital for quantifying range change but their use can be restricted by many problems and constraints. Key problems include variation in recorder effort, changes in recorder behaviour and species detectability over time. Many solutions have been suggested to address these problems, and metadata can help determine which of these limitations may be present in the data, and in turn help ensure that the correct method is used to estimate range change. Solutions can be grouped into three main categories: limiting the data, benchmarking and relative change measures. Limiting the data is perhaps the most common solution and is often used alongside more complex techniques (such as relative change estimates or benchmarking) to estimate change. A key aim of future range change techniques should be to reduce the need to limit the data while accurately estimating change from atlas data. In this review, typical dataset examples are used to help guide future studies to use the appropriate method for estimating change when faced with common problems associated with atlas data.

Chapter 3: A phylogenetically-informed trait-based analysis of range change in the vascular plant flora of Britain.

3.1 Abstract

Species distributions are changing, and knowing whether certain character traits predispose species to decline or increase during times of environmental change can shed light on the main drivers of distribution change. In addition, these trait-based analyses may enable the forecasting of how ranges will respond to future environmental scenarios. Here we conduct a trait-based analysis of range change in the flora of Britain since the 1930s using some of the best plant distribution and trait data available in Europe. We use phylogenetically-informed models based on a recently published, dated, species level plant phylogeny. Traits associated with habitat specialism and competitive ability were related to range change, with more competitive habitat generalists faring better than habitat specialists. We attribute this result to the greater ability of generalists to adapt to environmental perturbation, but also to the negative impacts of agricultural intensification on the flora of Britain, in particular the loss of open, dry habitats characterised by soils with extreme pH values. Our models suffered from low explanatory power, but despite this find support for previous evidence that agricultural intensification has been a major driver of distribution change in the flora of Britain over the past 70 years, particularly in southern England.

3.2 Introduction

The impacts of anthropogenic climate and land use change on biodiversity are well documented (e.g., Sala, 2000; Walther *et al.,* 2002; Root *et al.,* 2003; Parmesan & Yohe, 2003; Mace *et al.,* 2005; Montoya & Raffaelli, 2010; Thomas, 2010; UK National Ecosystem Assessment, 2011). An area of much interest in conservation biology has been the impact of climate and land use change on species' distributions. The distributions of many species from many regions have changed in response to recent environmental perturbation; however, not all species have responded in the same way (Thomas & Lennon, 1999; Wilson *et al.,* 2005; Franco *et al.,* 2006; Menéndez *et al.,* 2006; Walker *et al.,* 2009; Chen *et al.,* 2011). Understanding how the drivers of biodiversity loss differ across species and over time is of great importance to biodiversity conservation (Mace *et al.,* 2010). Studies that examine whether certain character traits predispose species to distributional change may help shed light on the main drivers of change (Fisher & Owens, 2004, Koh *et al.,* 2004; Cardillo *et al.,* 2005). In this study we use a comparative approach to examine the main drivers of distribution change in the flora of Britain, and to investigate which character traits have predisposed plant species to decline under recent environmental change.

There are many advantages of using vascular plants as the study organisms for this investigation: as well as being a key component of almost all terrestrial ecosystems, they have been proposed as good indicators of the impacts of environmental change on biodiversity in general (Godefroid, 2001; Landsberg & Crowley, 2004), and they have some of the best trait and distribution data available of any taxonomic group in Europe. In an attempt to identify drivers of extinction risk in the flora of lowland England, Preston (2000) and Walker & Preston (2006) examined the relationship between life history traits and extinction rates in vascular plants using data from three counties in England. Geographic range size and attributes linked with competitive ability and habitat specialism were the best predictors of extinction risk, with widespread, competitive generalist species at lowest risk of extinction. In a follow up study, Walker *et al.* (2009) investigated trends in plant diversity in Bedfordshire between 1949 and 2004, finding that a greater number of species showed negative rather than positive trends. The variation in species' trends were interpreted using a trait-based approach, which indicated that plant biodiversity was becoming homogenized, dominated by a few taller species which out-compete the smaller habitat specialists adapted to low nutrient levels. At a larger spatial scale, Braithwaite *et al.* (2006) quantified changes in the flora across Britain and related this change to species traits. They found that low-fertility habitat specialists were suffering the greatest declines and attributed this to the negative impacts of habitat fragmentation and eutrophication, a result mirrored in a comparative analysis of plant range change in Flanders, Belgium (Van Landuyt *et al.*, 2008).

None of these analyses of range change in plants have used phylogenetically-informed comparative methods. The phylogenetic relationships that inherently connect species mean that closely related species may share many similarities due to shared evolutionary history. It is for this reason that species cannot automatically be treated as independent data points in comparative analyses (Harvey & Pagel, 1991; Fisher & Owens, 2004). Comparative studies that treat species as independent data points can have elevated type I error rates due to phylogenetic pseudoreplication, and therefore may incorrectly reject null hypotheses (Felsenstein, 1985; Harvey & Pagel, 1991; Purvis, 2008). In this study, we examine the importance of both phylogeny and life history traits in explaining variation in plant distribution change in Britain, using authoritative compilations of trait and distribution data alongside a recently-published, dated, species-level phylogeny to account for phylogenetic relationships between species.

3.3 Methods

3.3.1 Distribution and trait data

Presence-only, 10 km square (hectad) distribution data for vascular plants in Britain were taken from the Vascular Plant Database (VPDB), managed by the Biological Records Centre and the Botanical Society of the British Isles. The data used here were from two distinct time periods, 1930 - 1969 and 1987 - 1999. The 1930 - 1969 data comprise records mainly collected for the *Atlas of the British*

Flora (Perring & Walters, 1962) with subsequent additions up to 1969, while the 1987 to 1999 data comprise records collected for the *New Atlas of the British and Irish Flora* (Preston *et al.,* 2002b). There were national surveys in both time periods, with the data verified by experts prior to publication. More than 1600 recorders carried out plant surveys to collect data for the VPDB, with special effort being made to achieve an even coverage of records across Britain (further detail of the methodology can be found in Preston *et al.* (2002b)). Twelve plant traits hypothesised to affect species' responses to environmental change were taken from PLANTATT (Hill *et al.,* 2004) and after checking for collinearity were reduced to a set of nine that were included in the final analyses. These are detailed in Table 3.1 alongside associated hypotheses.

Table 3.1 A list of the traits taken from PLANTATT that were included as explanatory variables in the analysis of distribution change.

Attribute name	Measure	Hypothesis
Plant height	Plant height (cm) – used as a surrogate for competitive ability	Competitive ability will be positively related to distribution change (Preston, 2000; Grime, 2001; Pilgrim *et al.,* 2004; Stevens *et al.,* 2004; Suding *et al.,* 2005; Walker & Preston, 2006).
Ellenberg L	Ellenberg value for light preference (1 = deep shade, 9 = full light)	Change index will be negatively correlated with Ellenberg L. The open habitats associated with high L specialists have undergone large-scale degradation (Godefroid, 2001; Walker & Preston, 2006).
Ellenberg S	Ellenberg values for salt tolerance (0 = absent from saline soils, 9 = extremely saline conditions)	We predict salt tolerant species will be increasing. The increased gritting of roads may be creating ideal novel habitats to complement the usual coastal habitats the salt tolerant species would occupy (Liem *et al.,* 1985).
Ellenberg N	Ellenberg values for nitrogen preference (soil fertility) (1 = extremely infertile, 9 = extremely rich in nitrogen)	Specialists of low N environments will have lower change index values due to the long-term decline in infertile habitats as a result of agricultural intensification (McCollin *et al.,* 2000; Godefroid, 2001; Stevens *et al.,* 2004; Walker & Preston, 2006).
Ellenberg R	Ellenberg values for pH (1 = extreme acid soils, 9 = high pH soils)	Change index will be positively related to Ellenberg R, due to the loss of low pH habitats to agricultural land in Britain. (Haines-Young *et al.,* 2003; Walker & Preston, 2006).
Ellenberg F	Ellenberg values for moisture preference (1 = dry, 9 = wet-site indicator)	Species specialised to dry habitats will have lower change index values due the conversion of open, dry areas to agricultural land (Walker & Preston, 2006).
Habitat Breadth	A count of the number of habitat categories the species occupies (based on the 23 categories in PLANTATT)	Habitat generalists will have greater change index scores as they are less vulnerable to environmental change in comparison to habitat specialists. (Walker & Preston, 2006).
Temperature index (^{o}C)	Mean July temperature of all UK 10 km squares occupied, 1961 – 1990	Climate change has increased the climatic suitability of the landscape to species that prefer warm conditions, we therefore predict a positive correlation between range change and species temperature index (Hulme, 2009).
Life cycle type	Species categorised as either annual, biennial or perennial	Annuals will have higher change index values in comparison to biennials and perennials as they will have benefitted from increased environmental disturbance in Britain (Hodgdon, 1989; Braithwaite *et al.,* 2006).

3.3.2 Range change measure

Studies that estimate change from atlas data often need to account for the temporal increase in survey effort that can bias range change estimates, an issue termed the 'recorder effort problem' (Prendergast *et al.,* 1993, Hill, 2012). To account for this, we estimated change using a relative change index (CI) that was designed to be relatively insensitive to increased survey effort in the second time period (Telfer *et al.,* 2002). This technique has been used in many studies to estimate range change trends while accounting for a temporal increase in survey effort (e.g., Pocock *et al.,* 2006; Van Calster *et al.,* 2008; Van Landuyt *et al.,* 2008; Mace *et al.,* 2010). The CI measures change in each species' range size between the two distinct time periods, relative to the average range change across all species. The CI is therefore calculated as the standardized residuals from a linear regression of the relationship between logit-transformed counts of grid cells in the earlier and later time periods, in which fitting of the regression line is weighted by the reciprocal of the variance in the logit proportion to account for heteroscedasticity. The intercept and slope of the regression includes the effects of change in both range size and recorder effort across all species. Species with a positive CI have been recorded in more grid cells in the later time period than expected based on the regression model, while those with a negative CI (henceforth referred to as declining species, though the decline may be relative rather than absolute) have been recorded in relatively fewer.

We applied the method to derive CI values based on the time periods 1930-1969 and 1970-1999 (for regression plot, see Appendix 3.1). To reduce bias, five categories of species or grid cells were excluded before the CI was calculated. First, we excluded species occurring in five or fewer grid cells in the first time period, as the weighted regression used in Telfer *et al.* (2002) assumes a linear relationship between the logit-transformed proportions in each time period, and at low numbers there was a tendency for this relationship to become curved as species that occur in very few grid cells have greater potential for expansion than decline. Second, only grid cells surveyed in both time periods were included in the analysis in order to reduce the influence of differences in the spatial pattern of recording or the number of grid cells visited in the two time periods (Telfer *et al.,* 2002). Third, we excluded species if changes in their taxonomic concepts or taxonomic understanding differed substantially between the two periods. Fourth, species with an Ellenberg Moisture value greater than 9 (i.e., water plants) were excluded, as survey effort of water plants in Britain was very much higher in the second time period due to targeted surveys of Scottish lochs (Preston & Croft, 1997; Preston *et al.,* 2002b). Finally, only species that were classified as native or archaeophyte by Hill *et al.* (2004) were included in the analysis to reduce the potential bias in range change estimation that could arise from the inclusion of recent introductions that have not had chance to reach population equilibrium. The final dataset used in the analysis contained 1075 species.

3.3.3 Analysis

In an attempt to identify hotspots of plant decline, we used the 1987 – 1999 distribution data to plot hectad maps of species richness of all species and for only those species with a negative CI score. We mapped the proportion of species within a cell that had a negative CI, and also mapped the mean CI score for each cell based on all species and only species with a negative CI score. Mapping species with a negative CI ensured we highlighted regional hotspots based on species that performed relatively poorly, rather than those that performed relatively well in terms of change in range size.

To help determine the drivers of plant range change we initially ran single-predictor models of CI against each trait in turn, testing the significance of the quadratic term to identify curved relationships. We ran a multi-predictor regression model starting with the maximum model containing all traits (again including quadratic terms if significant) then simplified the model based on the stepwise deletion of least significant terms until the minimum adequate model (MAM) was reached. Akaike's information criterion (AIC) was calculated for each iteration of the model to ensure the new model had a lower AIC score (Burnham & Anderson, 2002).

To account for phylogenetic non-independence we used phylogenetic generalised linear models (PGLM) as implemented in the '*caper*' package in R (*pgls* function, Orme *et al.*, 2012). For all analyses we compared the results of three types of model: simple non-phylogenetic linear regression, PGLMs with estimated Pagel's (1999) λ and PGLMs with λ set to 1. Pagel's λ is a measure of phylogenetic signal shown by a variable – here, the residuals from the regression model – and is bounded between 0 and 1, with a λ value of 0 indicative of phylogenetic independence and a λ of 1 suggesting complete phylogenetic dependence (Pagel, 1999; Freckleton *et al.,* 2002). A benefit of estimating λ by maximum likelihood is that the problems associated with under-correcting (λ = 0) and over-correcting (λ = 1) for phylogenetic autocorrelation are reduced (Freckleton *et al.,* 2002, Purvis, 2008). We used the newly published species level, dated phylogeny '*Daphne*' (Durka & Michalski, 2012) in all phylogenetic analyses. All statistical analyses in this study were carried out using R version 2.14.2 (R Development Core Team, 2012).

3.4 Results

3.4.1 Patterns of richness and decline

The geographic pattern in species richness was highly similar between the map of all species and the map of only species with a negative CI, with the highest values of species richness occurring at low latitude (Figure 3.1a & b). The proportion of species with negative CI scores within each cell appears to increase with latitude (Figure 3.1c). Mean CI within each cell for all species appears to decline with increasing latitude, while the equivalent map using only those species with a negative CI seems to show a trend of decreasing CI from western to eastern Britain (Figure 3.1d & e).

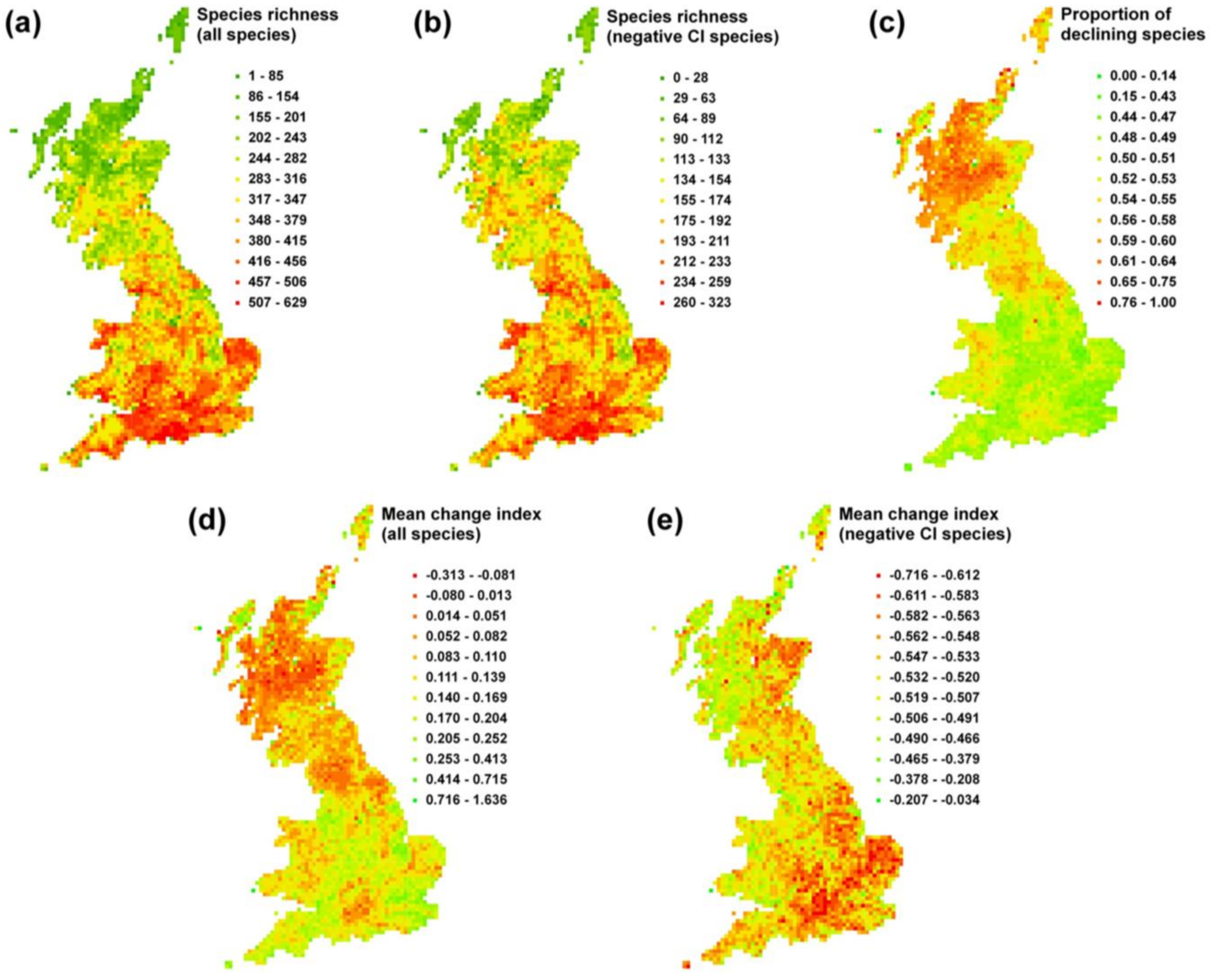


Figure 3.1 Hectad maps for the later time period (1987 – 1999) showing (a) richness of all plants included in the analysis, (b) richness of species that had a negative CI, (c) the proportion of species within a cell that had a negative CI, (d) mean CI score for all species and (e) mean CI of only those species that had a negative CI score. CI was measured between 1930 – 1969 and 1987 – 1999.

3.4.2 Trait-based analysis of change

Using AIC we found that PGLMs with estimated λ had a better fit to the data than non-phylogenetic regression or PGLMs with λ set to 1 for all single predictor and multi-predictor models. The direction and significance of the trait-based relationships remained broadly similar regardless of the level of phylogenetic correction applied (Appendix 3.2). Henceforth, we therefore only present the results from PGLMs with estimated λ. A significant moderate level of phylogenetic signal was found across the single-predictor and multi-predictor models with λ estimates varying between 0.162 and 0.211. The results of the single-predictor models are shown in Table 3.2, with the individual factor coefficients for life cycle type shown in Table 3.3. Moisture preference (Ellenberg F), soil fertility preference (Ellenberg N), habitat breadth and log height were all significantly positively correlated with CI (Table 3.2). Life cycle type was also significantly related to CI, with annual plants showing lower CI values compared to biennial and perennial plants (Table 3.3). A significant humped relationship between Ellenberg R and CI was found. The variance explained by each model was low with a maximum r^2 value of 0.014. The multi-predictor MAM for explaining variation in CI included four predictors (Ellenberg F, Ellenberg R, habitat breadth and log height) and explained 3.4% of the variation (Table 3.4). Ellenberg F, log height and habitat breadth were positively correlated with CI, while the relationship between Ellenberg R and CI was humped (Figure 3.2).

Table 3.2 Coefficients from single-predictor trait-based PGLMs of CI (n = 1075 species). For all analyses, PGLMs with estimated λ out-performed the other modelling approaches based on AIC (see Appendix 3.2). Estimated λ was significantly different (p < 0.001) from 0 and 1 for all models. The only significant curved relationship was that of Ellenberg R, the coefficients of the quadratic term are shown in brackets.

Trait	**slope**	**std. error**	**F**	**r^2**	**p**	**AIC**	**λ**
Life cycle type	NA	NA	2.836	0.003	0.037	3004.2	0.211
Temp. index (°C)	0.030	0.025	1.414	3.85x10-4	0.244	3006.4	0.203
Ellenberg L	-0.037	0.024	2.398	0.001	0.091	3005.4	0.201
Ellenberg F	0.052	0.018	8.696	0.007	<0.001	2999.2	0.210
Ellenberg R	0.326 (-0.030)	0.101 (0.009)	5.230	0.008	0.001	2999.4	0.187
Ellenberg N	0.060	0.016	13.5	0.012	<0.001	2994.4	0.183
Ellenberg S	0.033	0.029	1.307	2.86x10-4	0.271	3006.5	0.198
Habitat Breadth	0.135	0.041	10.55	0.009	<0.001	2997.3	0.190
log Height (cm)	0.119	0.029	16.2	0.014	<0.001	2991.8	0.175

Table 3.3 Factor level coefficients from the single predictor model of CI with life cycle type.

Life cycle type	**b**	**std. error**	**t**	**p**
Annual	-0.026	0.244	-0.106	0.915
Biennial	0.236	0.145	1.809	0.071
Perennial	0.135	0.076	2.101	0.036

Table 3.4 Coefficients of each of the predictors in the PGLM MAM with λ estimated for the model. Overall model coefficients are as follows: *λ* = 0.162, *n* = 1075, *F* = 8.487, r^2 = 0.034, *p* < 0.001, *AIC* = 2974.27.

Predictor	**slope**	**std. error**	**t**	**p**
(Intercept)	-1.381	0.344	-4.018	<0.001
Ellenberg F	0.045	0.018	2.535	0.011
Ellenberg R	0.272	0.100	2.724	0.007
Ellenberg R^2	-0.025	0.009	-2.689	0.007
Habitat Breadth	0.134	0.041	3.253	0.001
Log Height (cm)	0.106	0.030	3.571	<0.001

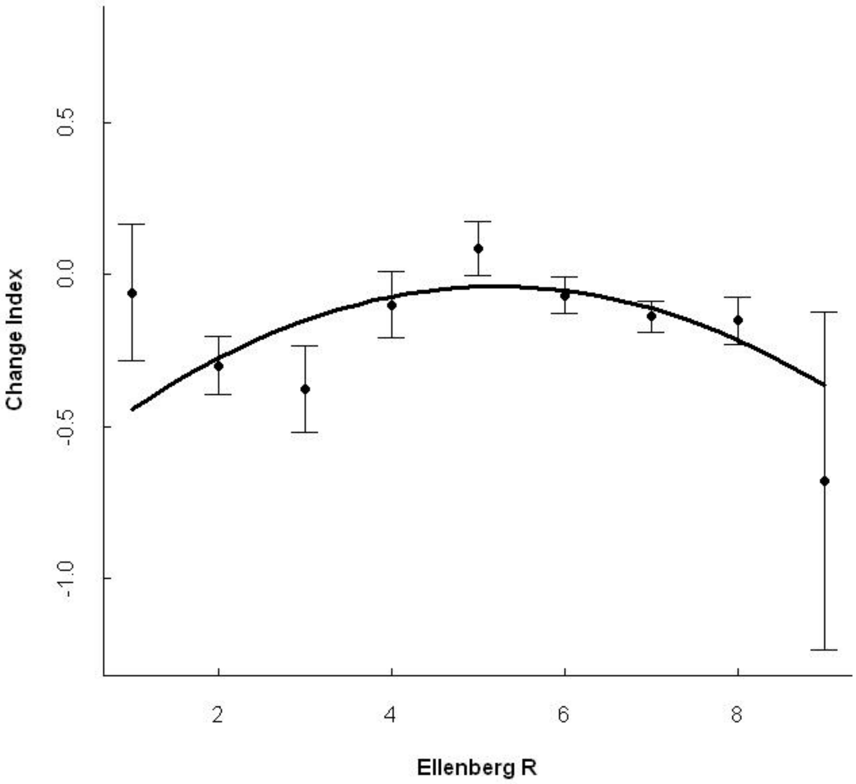


Figure 3.2 The relationship between Ellenberg R and CI in the MAM. Each point represents mean value of the change index across all species within each Ellenberg R interval, with bars representing standard error of the means.

3.5 Discussion

3.5.1 Patterns of richness and decline

Northwest Scotland is relatively species-poor (Figure 3.1a), and its most frequent species are plants of acidic, nutrient-poor habitats. These species have remained relatively stable in the northwest but have low CI scores due to severe declines in southern Britain (highlighted by the five most frequent species with CI scores less than -0.5 in northwest Scotland: *Potentilla erecta, Eriophorum angustifolium, Carex echinata, Erica cinerea* and *Erica tetralix*). Figure 3.1c shows the proportion of species with negative CI scores is greatest in northwest Scotland and therefore, as expected, the mean CI across all species within a cell is lowest in the northwest (Figure 3.1d). However, if only species with a negative CI are considered, mean CI is lower in southeast Britain (Figure 3.1e). Some of the species contributing to this low CI value in southeast Britain are the mirror image of the northwest species, i.e. they remain present in the southeast but have been declining at the northern end of their range. Additionally, other species, in particular many arable weeds, are declining throughout their predominantly south-eastern range.

The species richness maps in this study highlight central southern England and Norfolk as hotspots of plant biodiversity (Figure 3.1a & b). These regions, particularly Norfolk, were also highlighted as hotspots of decline in the mean CI map based on species with a negative CI (Figure 3.1e). These regions could be considered as priority areas for targeted conservation effort as they may be reflect refugia for declining plant species. Preservation of the natural habitat in northwest Scotland is important as it is the last remaining stronghold for many acidic, nutrient-poor habitat specialist species that have suffered widespread declines southern Britain and elsewhere in Europe (Tamis *et al.,* 2005; Van Landuyt *et al.,* 2008). The scale of these maps (10 x 10 km) is not ideal for planning conservation effort as declining species may only be utilizing a small patch of habitat within a cell. In addition, our maps are based on relative range change and do not include any aspect of range size itself which is an important criterion of extinction risk (IUCN, 2001).

3.5.2 Trait-based analysis of change

We demonstrate that traits associated with specialism and competitive ability were most strongly correlated with CI, and hypothesise that these trait-trend relationships are likely driven by change in land-use. After accounting for phylogeny, we find the results of our trait-based analyses were congruent with those of trait-based studies of extinction risk and range change in European plants

(Preston, 2000; Preston *et al.,* 2002a; Tamis *et al.,* 2005; Braithwaite *et al.,* 2006; Walker & Preston, 2006; Van Landuyt *et al.,* 2008; Walker *et al.,* 2009).

Taller species had more positive CI in both the single-predictor model and in the MAM. We believe this result provides evidence that agricultural intensification and the associated increased nitrogen availability has enabled taller, more competitive species to out-compete smaller, competitively weaker species in regions that were originally nutrient-poor (Pilgrim *et al.,* 2004; Walker & Preston, 2006; Walther, 2010). This theory is further supported by the significant positive relationship between soil fertility preference (Ellenberg N) and CI in the single predictor analysis.

We found that habitat generalists are out-performing habitat specialists, emphasised by the significant positive relationship between habitat breadth and CI. Habitat generalists can persist in multiple habitats, and therefore have an increased ability to adapt to different environmental conditions, meaning they are less vulnerable to environmental change than specialists (Travis, 2003; Bennie *et al.,* 2006; Walker *et al.,* 2009). The humped relationship between soil pH preference (Ellenberg R) and CI suggests that species specialised to habitats characterised by high or low soil pH values are in decline. These declines again point to the likely impact of land-use change, in particular the conversion of strongly acidic and strongly basic soil habitats to agricultural land (Haines-Young *et al.,* 2003; Walker & Preston, 2006). The significant positive correlation between soil moisture preference (Ellenberg F) and CI is also probably due to the land-use change with conversion of open, dry habitats (such as dwarf-shrub heath) to agricultural land (Stevens *et al.,* 2004; Smart *et al.,* 2005; Walker & Preston, 2006).

A moderate level of phylogenetic signal was detected in the single and multi-predictor models with λ estimates varying between 0.162 and 0.211. All λ values were significantly greater than 0 and models with estimated λ consistently out-performed non-phylogenetic models and models that assume complete phylogenetic dependence (i.e. those with λ = 1). This finding supports the view that there is a need to correct for phylogenetic relationships when conducting multispecies comparative studies, even when the traits of interest were not evolved along branches of a phylogeny (Purvis, 2008; Revell, 2010).

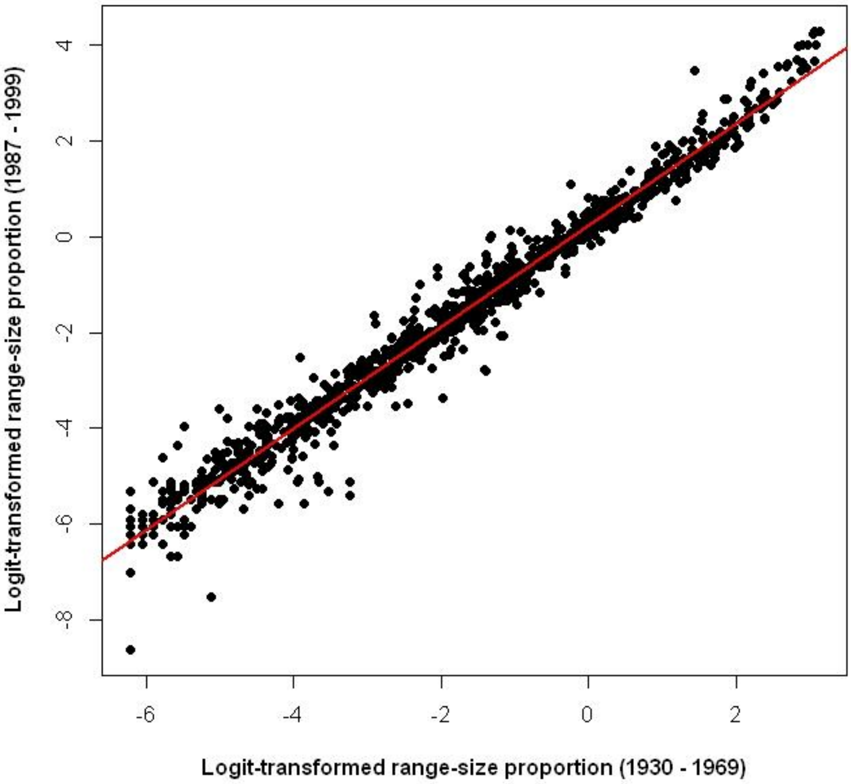
Despite finding that both phylogeny and traits were important in determining change in range size, the amount of variation explained by the best model was very low (3.4%). Land-use change has been shown to be an important determinant of extinction risk in many taxonomic groups (Sala *et al.,* 2000; Pereira *et al.,* 2004; Jetz *et al.,* 2007). We believe that including a direct measure of land-use change endured by each species may improve the amount of variation explained in the models and would be an ideal area for future study. However, it should be noted that trait-based analyses of a large numbers of species often explain only a small amount of variation in the response (Pöyry *et al.,* 2009; Angert *et al.,* 2011).

3.5.3 Conclusion

To summarize, we found that traits associated with habitat specialism and competitive ability were strongly-correlated with CI in the flora of Britain, with more competitive generalist species out-performing the smaller specialist species. We attribute these trait-based results to the negative impacts of agricultural intensification on the flora of Britain, in particular the conversion of open, dry habitats that are characterised by soils with extreme pH values, to arable land. Additionally, the impact of agricultural intensification was detected in the maps of Figure 3.1, with northwest

Scotland being a refugium for many acidic, nutrient-poor habitat specialist species that have suffered widespread declines in southern Britain due to agricultural intensification. We found that trait-based analyses can be useful in determining the drivers of distribution change, but ignoring local-scale landscape factors can lead to a loss of explanatory power.

3.6 Supplementary material



Appendix 3.1 The relationship between the logit-transformed proportional counts in 1930 – 1969 and 1987 – 1999. The residuals from this relationship are the change index values that are used as our relative measure of range change.

Appendix 3.2 The coefficients from the single predictor trait-based models for each of the three modelling approaches. Estimated λ was significantly different ($p < 0.001$) from 0 and 1 for all models. If the quadratic term of the trait was significant the coefficients of the quadratic term are shown in brackets.

Model	slope	std. error	d.f.	F	r^2	p	AIC	λ
Life cycle type								
LM	NA	NA	1072	2.84	0.003	0.059	3042.3	NA
PGLM esti. λ	**NA**	**NA**	**1072**	**2.836**	**0.003**	**0.037**	**3004.2**	**0.211**
PGLM λ = 1	NA	NA	1072	7.161	0.011	<0.001	3808.9	1
Temp. index (^{o}C)								
LM	0.005	0.024	1073	0.049	-0.001	0.824	3046.0	NA
PGLM esti. λ	**0.030**	**0.025**	**1073**	**1.414**	**$3.85\mathrm{x}10^{-4}$**	**0.244**	**3006.4**	**0.203**
PGLM λ = 1	0.027	0.025	1073	1.178	$1.66\mathrm{x}10^{-4}$	0.308	3820.0	1
Ellenberg L								
LM	-0.042	0.023	1073	3.281	0.002	0.070	3042.7	NA
PGLM esti. λ	**-0.037**	**0.024**	**1073**	**2.398**	**0.001**	**0.091**	**3005.4**	**0.201**
PGLM λ = 1	-0.082	0.030	1073	7.721	0.006	<0.001	3813.4	1
Ellenberg F								
LM	0.055	0.017	1073	10.39	0.009	0.001	3035.7	NA
PGLM esti. λ	**0.052**	**0.018**	**1073**	**8.696**	**0.007**	**<0.001**	**2999.2**	**0.210**
PGLM λ = 1	0.041	0.022	1073	3.41	0.002	0.033	3817.7	1
Ellenberg R								
LM	0.295 (0.028)	0.099 (0.009)	1072	4.677	0.007	0.009	3038.7	NA
PGLM esti. λ	**0.326 (-0.030)**	**0.101 (0.009)**	**1072**	**5.230**	**0.008**	**0.001**	**2999.4**	**0.187**
PGLM λ = 1	0.524 (-0.045)	0.120 (0.011)	1072	9.586	0.016	<0.001	3804.1	1
Ellenberg N								
LM	0.051	0.016	1073	10.17	0.008	0.001	3035.9	NA
PGLM esti. λ	**0.060**	**0.016**	**1073**	**13.5**	**0.012**	**<0.001**	**2994.4**	**0.183**
PGLM λ = 1	0.065	0.021	1073	10.08	0.008	<0.001	3811.1	1
Ellenberg S								
LM	0.041	0.029	1073	2.054	0.001	0.152	3044.0	NA
PGLM esti. λ	**0.033**	**0.029**	**1073**	**1.307**	**$2.86\mathrm{x}10^{-4}$**	**0.271**	**3006.5**	**0.198**
PGLM λ = 1	0.013	0.038	1073	0.121	-0.001	0.886	3821.0	1
Habitat Breadth								
LM	0.134	0.042	1073	10.17	0.008	0.001	3035.9	NA
PGLM esti. λ	**0.135**	**0.041**	**1073**	**10.55**	**0.009**	**<0.001**	**2997.3**	**0.19**
PGLM λ = 1	0.163	0.040	1073	16.9	0.015	<0.001	3804.3	1
Log Height (cm)								
LM	0.122	0.028	1073	18.73	0.016	<0.001	3027.4	NA
PGLM esti. λ	**0.119**	**0.029**	**1073**	**16.2**	**0.014**	**<0.001**	**2991.8**	**0.175**
PGLM λ = 1	-0.423 (0.077)	0.188 (0.024)	1073	11.12	0.018	<0.001	3801.1	1

Chapter 4: Can trait-based analyses of species distribution change be transferred to new geographic areas?

4.1 Abstract

Anthropogenic environmental change is having a major impact on biodiversity. By identifying traits that correlate with species range change, comparative studies can shed light on the driving mechanisms of this change; but such studies will be more useful for conservation if they have true predictive power – i.e., if their trait-based models can be transferred to new regions. We tested the ability of trait-based models to predict plant distribution change across seven geographic regions (Flanders and six regions in Britain) that varied in terms of land-cover and species composition. The regional trait-based models gave insights into the regional variation in the main drivers of range change but suffered from low r^2 values (ranging from 0.21 to 0.06). A key cross-region difference was the variation in the relationship between soil nutrient preference (Ellenberg N) and distribution change, which was strongly positive in Flanders and southern England, but significantly negative in northern Scotland. We found transferability between regions was significantly correlated to the level of similarity in land cover, and therefore conclude, that trait-based models have potential for predicting broad scale changes in species distributions in regions that share similar land-cover composition.

4.2 Introduction

The impacts of anthropogenic environmental change on biodiversity are well documented, with threats such as habitat loss, climate change and invasive species all frequently related to changes in species distributions (Parmesan & Yohe, 2003; Blackburn *et al.*, 2004; Mace *et al.*, 2005; Butchart *et al.*, 2010). However, not all species respond in the same way to these environmental pressures

(Chen *et al.*, 2011), with species' life history traits explaining some of the variation (Purvis *et al.*, 2000; Koh *et al.*, 2004; Reynolds *et al.*, 2005; Walker *et al.*, 2009; Murray *et al.*, 2010; Angert *et al.*, 2011; also see chapter 3). An advantage of such trait-based approaches is that they can allow generalisations to be extended to other species and can help determine the potential drivers of change (Fisher & Owens, 2004). Many comparative studies have found relationships between change in species distribution size and life history traits (e.g. Verheyen *et al.*, 2003; Walker & Preston, 2006; Mattila *et al.*, 2008; Van Landuyt *et al.*, 2008; Ozinga *et al.*, 2009). However, there is little evidence of such studies directly affecting conservation practice – rather, they have acted as 'calls to action' highlighting biodiversity decline (Cardillo & Meijaard, 2011). One reason for this is that, although such studies explain biodiversity responses within their own datasets, they seldom test the *predictive* ability of their models by, for instance, assessing transferability of the results to new regions (Fisher & Owens, 2004; Pocock, 2010).

The transferability of trait-based comparative models has been examined using population abundance trends in European and North American farmland birds (Pocock, 2010). The study found that the relationships from one region poorly predicted population trends in other regions, and that there was no significant improvement in model predictions when comparing environmentally similar regions (Pocock, 2010). These findings support the view that inconsistencies in the results of comparative studies are a key barrier to their applied use within conservation (Cardillo & Meijaard, 2011). In this study we extend the predictive work of Pocock (2010) by using a larger, high-quality dataset of the spatiotemporal distribution of plants from Flanders (Belgium) and six environmental regions of Britain, to examine if the results from trait-based approaches can be used to predict change in new regions. We aim to test whether transferability is related to land cover similarity and/or similarity of species composition between regions in an attempt to understand if, and when, it is possible to predict change from trait-based models.

Vascular plants are an ideal taxon for this investigation: they are the primary producers of most terrestrial ecosystems, are good indicators of the state of the environment (Godefroid, 2001; Landsberg & Crowley, 2004), and have some of the best trait and distribution data of any taxonomic group in Great Britain. Previous analyses have shown that similar drivers of range change can have similar effects across different regions. For example, the flora of Flanders has shown marked declines of species specialised for nutrient-poor habitats, probably because of increased nitrogen deposition, while analogous relationships were found in a trait-based study of trends in plant species prevalence in Bedfordshire, England (Walker *et al.*, 2009; Van Landuyt *et al.*, 2008). However, trait-trend relationships are not always congruent across regions; for example Fritz *et al.*, (2009) showed marked geographic variation in trait-based relationships of extinction risk in mammals. In this study, our trait-based models for each of the seven regions will test a range of proposed drivers of distribution change, and in turn will aid our understanding of the mechanisms that cause variation in predictive ability. We test the hypothesis that there will be significant variation between the regional trait-based model results and that this variation will be reflected in the predictive ability of the pair-wise regional comparisons.

4.3 Materials and Methods

4.3.1 Overview

In this study, Britain was split into six environmental regions as identified by the Centre for Ecology & Hydrology Countryside Survey (Haines-Young *et al.*, 2000). The division is based mainly on the geographic distribution of the major land classes but is also split by the English-Scottish border (Figure 4.1). An overview of the study areas can be found in Appendix 4.1. We ran trait-based analyses of plant distribution change independently for Flanders and each region in Britain. Sample size varied between regions with 685, 908, 919, 735, 663, 638 & 593 species included in the models for Flanders and regions 1 to 6, respectively. Each regional model was then used to predict change in all other regions and the resulting measure of transferability was related to land cover and species compositional similarity.

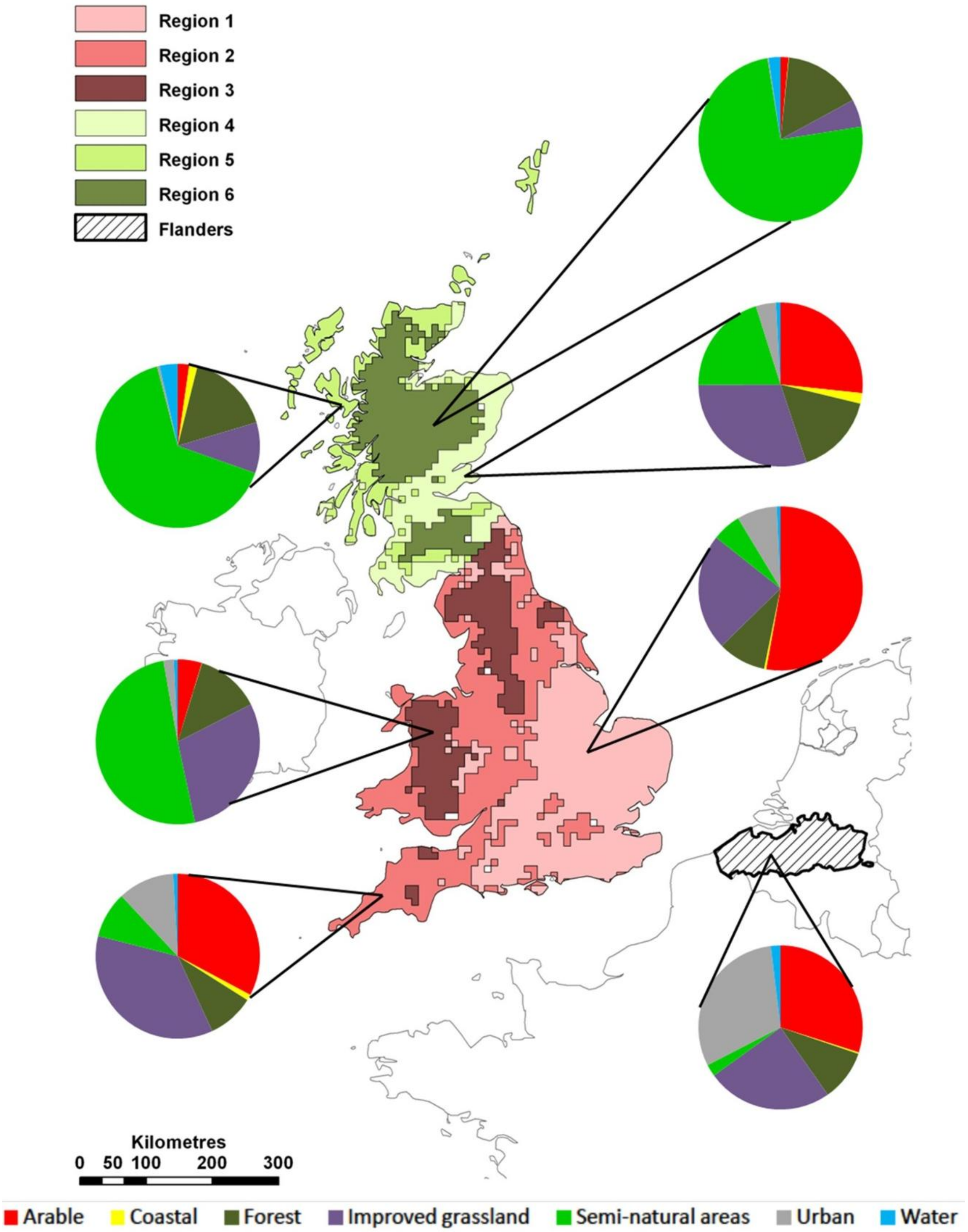


Figure 4.1 A map showing Flanders and the six environmental regions of Britain. The pie charts represent the proportional land cover for each region.

Distribution and trait data

Presence-only gridded distribution data for vascular plant species in Britain (10x10 km grid) and Flanders (4x4 km grid) were taken from two plant atlases (Preston *et al.*, 2002b and Van Landuyt *et al.*, 2006, respectively). The time periods used for each dataset were comparable: Britain 1930-1969 and 1987-1999, Flanders 1939-1971 and 1972-2004. Recently established alien species may have distributions that have not reached equilibrium range dynamics since their introduction, and therefore we only included native and archaeophyte species in the analyses. Plant life history trait data were taken from PLANTATT (Hill *et al.*, 2004). Eleven traits were included in the analyses, all of which have been associated with plant distribution change, and are listed and briefly described in Appendix 4.2 (Liem *et al.,* 1985; Preston, 2000; Godefroid, 2001; Haines-Young *et al.,* 2003; Braithwaite *et al.,* 2006; Walker & Preston, 2006; Van Landuyt *et al.,* 2008; Hulme, 2009). Species with an Ellenberg Moisture value greater than 9 (aquatic plants) were excluded from the analysis, as there was increased survey effort of water plants in Britain in the second time period due to targeted surveys of Scottish lochs (Preston *et al.*, 2002b; Preston & Croft, 1997), which would give water plants artificially high distribution change estimates.

4.3.2 Regional analysis

A Change Index (CI) was used to measure change in species range size relative to the expected range change across all species, over the two time periods (Telfer *et al.*, 2002). The CI was calculated as the residuals from a weighted linear regression of the relationship between counts of grid cells in the earlier and later time periods, and was calculated separately for each region used in the analysis. The intercept and slope of the regression include the effects of change in range size and variation in recorder effort across all species. Small ranged species have a greater capacity for expansion than decline which can cause curvature in the relationship between grid cell counts in the earlier and later time periods. To account for this, species that occupy fewer than five grid cells in the first time period were excluded from the analysis (for full details see Telfer *et al.*, 2002). This widely used CI measure reduces problems associated with temporal variation in recorder effort, which were likely to be present in the data (Telfer *et al.*, 2002; Pocock *et al.*, 2006; Van Calster *et al.*, 2008; Van Landuyt *et al.*, 2008; Mace *et al.*, 2010).

For each region we carried out a multi-predictor trait-based model of CI that included all traits listed in Appendix 4.2. Trends from these multi-predictor trait-based models were examined to detect variation in the main drivers of distribution change across regions. In all analyses we tested for curved relationships by including the quadratic term for each continuous explanatory variable, significant quadratic terms were retained in the full model. We checked for colinearity in the explanatory variables in all analyses. Treating species as independent data points in statistical analyses runs the risk of increasing type I error rates (incorrectly rejecting the null hypothesis) as closely related species share more evolutionary history than distant relatives (Harvey, 1996). To account for this non-independence we used phylogenetic generalised linear models (PGLMs) with estimated Pagel's λ in all trait-based models (Pagel, 1999; Freckleton *et al.*, 2002). Pagel's λ is a measure of phylogenetic signal within a variable. It is bounded between 0 and 1, with a λ value of 0 indicative of phylogenetic independence, while a λ of 1 is complete phylogenetic dependence. A benefit of estimating Pagel's λ, as part of model-fitting, is that problems associated with under correcting ($\lambda = 0$) and over correcting ($\lambda = 1$) for phylogenetic autocorrelation are reduced. We used the online tool Phylomatic (Webb & Donoghue, 2005) to generate the phylogenetic framework of all species included in our analyses. The Phylomatic phylogeny is based on a tree developed by the Angiosperm Phylogeny Group (Chase *et al.*, 2009), and in this study all branch lengths were set to one. All analyses were carried out using R version 2.14.2 (R Development Core Team, 2012), with the *pgls* function from the *caper* package used for the PGLMs (Orme *et al.*, 2012).

4.3.3 Transferability

Using the regional trait-based models we carried out cross-region predictive analyses. For each region, CI was predicted for all species present using the trait-trend relationships transferred from the multi-predictor models from the other regions, resulting in six sets of species' CI predictions for each region. Observed CI was then regressed against each set of predicted CI values to identify the transferability (Pearson's product moment correlation coefficient) of trait-based models from the other regions. Observed CI for each species was calculated separately for each region using only the grid cells that were present in that region. For all pair-wise regional comparisons transferability was correlated with the level of similarity in species composition and percentage similarity in land cover to help identify if, and when, trait-based models can be transferred to new regions. Due to the non-independence of the pair-wise regional comparisons, the significance was estimated using Mantel tests with 1000 iterations (Manly, 2007). Land cover similarity was estimated from the proportional cover of each broad land-use class for each region from data derived from satellite imagery: Britain (Morton *et al.*, 2011) and Flanders (Wils *et al.*, 2004) (Figure 4.1). We used an index of percentage similarity (Renkonen, 1938; Jost *et al.*, 2011) to calculate land cover similarity, while Conditional Sorensen's similarity index (Lennon *et al.*, 2001) was used to calculate similarity of species composition.

4.4 Results

4.4.1 Comparison of regions

The percentage cover of each broad land-use type is shown in Figure 4.1. In terms of land cover, Flanders is most similar to regions 1 and 2 in southern Britain (Table 4.1); these regions are characterised by intensive agriculture and a moderate to high proportion of artificial surfaces. In contrast, regions 5 and 6 are predominantly forest and semi-natural areas with only a small amount of agricultural and artificial land. In terms of species composition, regions 1, 2 and 4 are most similar to Flanders and in general geographically closer regions tended to have similar species compositions (Table 4.1).

Table 4.1 Similarity scores for all pair-wise region comparisons. Conditional Sorensen's index of the similarity of species composition between regions is above the diagonal (shades of blue), while Renkonen's percentage similarity index of land cover between regions is below the diagonal (shades of red). Colour shade relates to the level of similarity, the darker shade of the colour the greater the similarity.

	Flanders	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6
Flanders	-	0.90	0.88	0.79	0.79	0.76	0.76
Region 1	0.74	-	0.94	0.92	0.96	0.91	0.89
Region 2	0.78	0.80	-	0.94	0.97	0.93	0.90
Region 3	0.45	0.46	0.55	-	0.91	0.90	0.92
Region 4	0.69	0.70	0.81	0.70	-	0.92	0.89
Region 5	0.27	0.29	0.33	0.77	0.52	-	0.93
Region 6	0.22	0.23	0.26	0.71	0.45	0.91	-

4.4.2 *Transferability*

The variation explained by the regional models varied between 21% and 6% with the most variance explained in the Flanders model (Table 4.2). When using these models to predict change in the other regions, we found transferability varied across regions in terms of significance and variance explained (Table 4.3). Flanders was best predicted by region 1 and with decreasing predictive power by regions 2, 3 and 4, all with a positive correlation between observed and predicted CI score (Figure 4.2). A significant negative relationship was found between observed CI in Flanders and predicted CI from the region 5 model. This suggests that species with a positive CI in region 5 were likely to have a negative CI in Flanders and vice versa. Land cover similarity (Renkonen's percentage similarity index of land cover) was significantly positively correlated with transferability (*correlation coefficient* = 0.789, *Mantel p* < 0.01, Figure 4.3), whereas no significant relationship was found between similarity of species composition (Conditional Sorensen's species similarity index) and transferability (*correlation coefficient* = 0.275, *Mantel p* = 0.403). The amount of variance explained in the predictive models varied between 8.05 x 10^{-5} and 0.14, with the higher r^2 values generally associated with comparisons of regions with similar land cover composition (Table 4.3).

Table 4.2 Model coefficients from the PGLS trait-based models for each region. Models with estimated λ were significantly different from models with *λ* set to 0 or 1 for all British regions. However, in the Flanders model, no significant difference was found between estimated *λ* and *λ* set to 0.

Region	DF	F	r^2	λ (95% conf. int.)	Model p
Flanders	666	9.962	0.212	0.045 (0, 0.188)	<0.001
Region 1	892	5.235	0.081	0.565 (0.333, 0.737)	<0.001
Region 2	902	5.458	0.088	0.273 (0.117, 0.481)	<0.001
Region 3	720	3.287	0.060	0.345 (0.113, 0.612)	<0.001
Region 4	646	3.843	0.087	0.201 (0.054, 0.468)	<0.001
Region 5	623	4.632	0.094	0.247 (0.077, 0.519)	<0.001
Region 6	577	5.608	0.127	0.081 (0.024, 0.238)	<0.001

Table 4.3 Coefficients from the cross region predictive models (regression models). The table is split by the observed region to be predicted.

Region	Slope	std. error	F	r	r^2	p
(a) Predicts observed Flanders CI (df = 683)						
Region 1	1.219	0.116	109.600	0.372	0.138	<0.001
Region 2	1.160	0.127	82.880	0.329	0.108	<0.001
Region 3	0.915	0.171	28.540	0.200	0.040	<0.001
Region 4	0.738	0.130	32.110	0.212	0.045	<0.001
Region 5	-0.482	0.128	14.210	-0.143	0.020	<0.001
Region 6	-0.005	0.100	0.002	-0.002	<0.001	0.961
(b) Predicts observed Region 1 CI (df = 906)						
Flanders	0.528	0.068	60.670	0.251	0.063	<0.001
Region 2	0.884	0.109	66.200	0.261	0.068	<0.001
Region 3	0.799	0.141	32.180	0.185	0.034	<0.001
Region 4	0.455	0.103	19.370	0.145	0.021	<0.001
Region 5	-0.152	0.113	1.820	-0.045	0.002	0.178
Region 6	0.022	0.083	0.073	0.009	<0.001	0.787

Region	Slope	std. error	F	r	r^2	p
(c) Predicts observed Region 2 CI (df = 917)						
Flanders	0.388	0.067	33.930	0.189	0.036	<0.001
Region 1	0.888	0.110	65.460	0.258	0.067	<0.001
Region 3	0.604	0.139	18.820	0.142	0.020	<0.001
Region 4	0.368	0.107	11.850	0.113	0.013	<0.001
Region 5	-0.185	0.111	2.794	-0.055	0.003	0.095
Region 6	-0.078	0.071	1.206	-0.036	0.001	0.272
(d) Predicts observed Region 3 CI (df = 733)						
Flanders	0.181	0.069	6.861	0.096	0.009	0.009
Region 1	0.422	0.125	11.400	0.124	0.015	<0.001
Region 2	0.322	0.131	6.099	0.091	0.008	0.014
Region 4	0.667	0.113	34.770	0.213	0.045	<0.001
Region 5	0.431	0.129	11.170	0.123	0.015	<0.001
Region 6	0.343	0.104	10.870	0.121	0.015	0.001
(e) Predicts observed Region 4 CI (df = 661)						
Flanders	0.196	0.079	6.109	0.096	0.009	0.014
Region 1	0.267	0.129	4.280	0.080	0.006	0.039
Region 2	0.273	0.127	4.649	0.084	0.007	0.031
Region 3	0.963	0.170	32.040	0.215	0.046	<0.001
Region 5	0.461	0.133	11.970	0.133	0.018	<0.001
Region 6	0.348	0.103	11.430	0.130	0.017	<0.001
(f) Predicts observed Region 5 CI (df = 636)						
Flanders	-0.141	0.067	4.362	-0.083	0.007	0.037
Region 1	-0.206	0.134	2.364	-0.061	0.004	0.125
Region 2	-0.258	0.132	3.808	-0.077	0.006	0.052
Region 3	0.493	0.161	9.371	0.120	0.015	0.002
Region 4	0.359	0.116	9.658	0.122	0.015	0.002
Region 6	0.516	0.103	25.330	0.196	0.038	<0.001
(g) Predicts observed Region 6 CI (df = 591)						
Flanders	-0.079	0.064	1.513	-0.051	0.003	0.219
Region 1	-0.132	0.135	0.958	-0.040	0.002	0.328
Region 2	-0.311	0.135	5.285	-0.094	0.009	0.022
Region 3	0.347	0.131	7.008	0.108	0.012	0.008
Region 4	0.341	0.102	11.210	0.136	0.019	<0.001
Region 5	0.727	0.137	28.260	0.214	0.046	<0.001

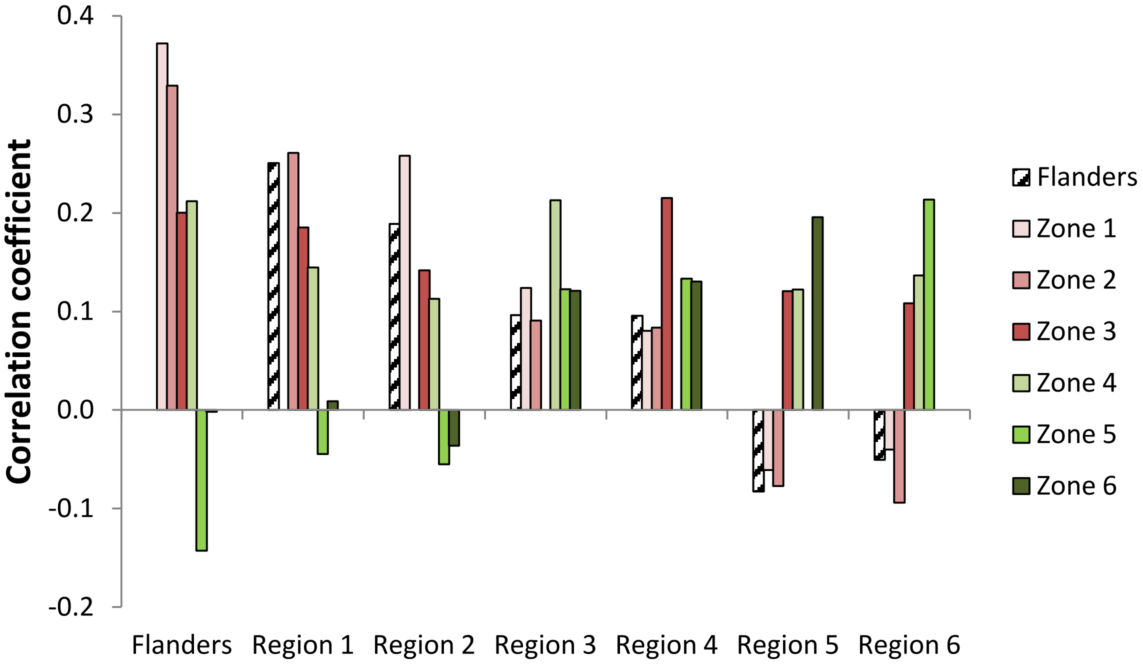


Figure 4.2 The Pearson's product-moment correlation coefficients between observed CI and predicted CI for each pair-wise regional comparison.

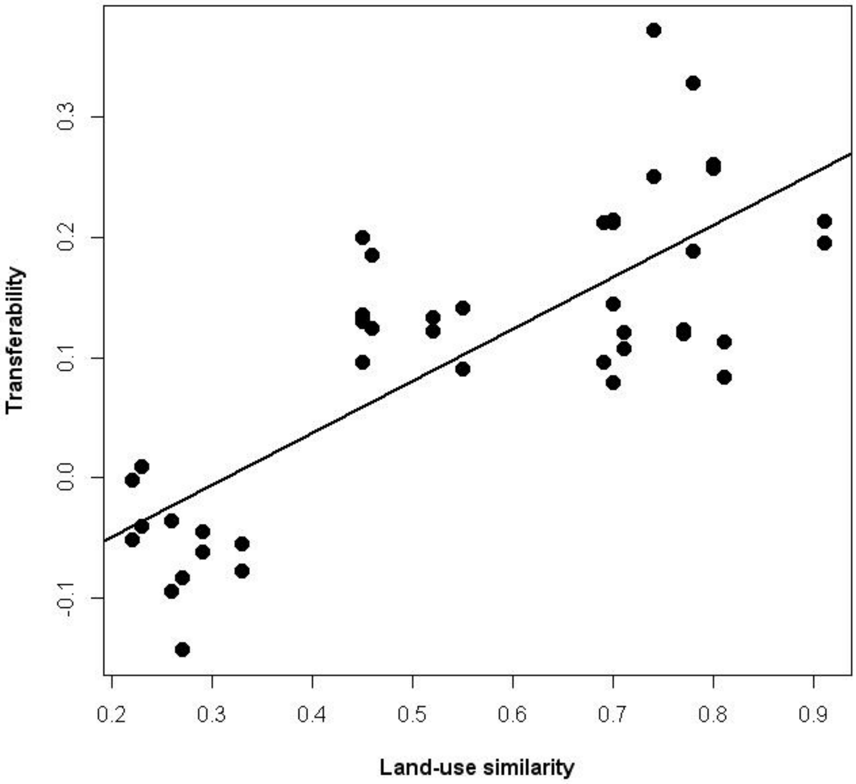


Figure 4.3 The significant positive relationship between transferability (pair-wise Pearson's product-moment correlations) and land cover similarity for all pair-wise regional comparisons (*slope* = 0.433*, s.e.* = 0.053*, t* = 8.108*, Mantel p* < 0.01).

4.4.3 Trait-based relationships

All regions had significant trait-based models with the number of significant traits in each model varying from three in region 3 to nine in region 2. The direction and strength of trait relationships varied considerably across regions (Appendix 4.3). A key cross-region difference was the variation in the relationship between Ellenberg N and CI: strongly positive in Flanders and region 1 (and to a lesser extent region 2), but significantly negative in region 6 (Figure 4.4). Life cycle type was only a significant predictor of change in region 5, where annual plants showed significantly lower CI scores compared to biennial and perennial plants. We found that it was important to account for phylogeny in our analysis, as all models, except Flanders, showed a significantly moderate level of phylogenetic dependence (λ values in Table 4.2).

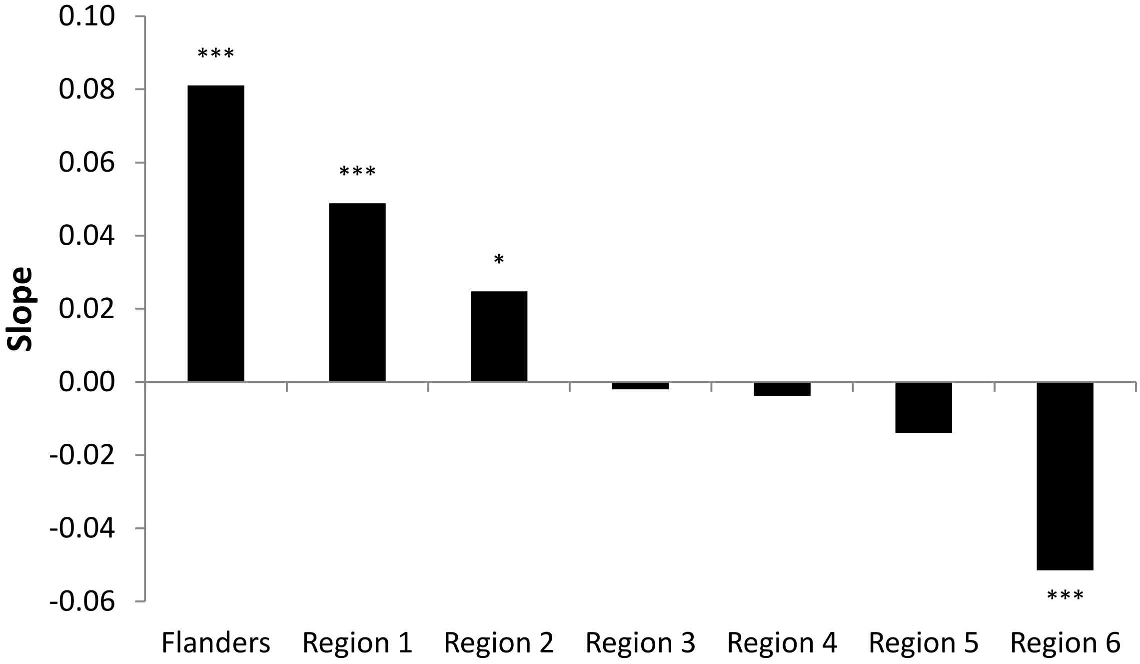


Figure 4.4 The slope of the relationship between Ellenberg N and residual CI for each region. The residuals were taken from the regional models with Ellenberg N excluded. (* = P < 0.05, ** = p < 0.01, *** = p < 0.001).

4.5 Discussion

In this study we examined the ability of trait-based models to predict distribution change in new geographic regions. We found that transferability varied across the pair-wise regional comparisons, and was explained by the level of similarity in land cover. These results contrast with those of a previous study on bird abundance, which found that transferability was not improved when comparing regions that share similar landscape characteristics (Pocock, 2010). This difference may be due to the greater variation in the intensity and direction of the trait-trend relationships in our study. The models in Pocock (2010) were broadly consistent across regions (declining population size tended to share such traits as medium body size, small brain size, undertaking long distance migration and specialising on farmland habitat), whereas we found that the sign of one significant relationship – that between Ellenberg N and CI – changed from positive in southern regions to negative in northern regions (Figure 4.4). It should also be noted that the plant models in this study are based on approximately 25 times more species than the bird abundance models (Pocock, 2010). In addition to having fewer species, farmland birds are likely to be a more uniform group than the plants of Flanders and Britain, meaning there will be less opportunity for variation to occur in the trait-trend relationships between regions and this may explain the reduced variation in transferability.

Range change dynamics in Flanders (the most isolated region in this study) were best predicted by the models from regions 1 and 2 in Britain. These regions of southern Britain were most similar to Flanders in terms of current land cover but also past changes in land-use. Over the time period of this study the landscapes of Flanders and southern Britain (regions 1 & 2) have undergone extensive agricultural intensification (Haines-Young *et al.,* 2000; Stoate *et al.,* 2001; Robinson & Sutherland 2002; Van Landuyt *et al.*, 2008), which was detected in the trait-based models: Ellenberg N significantly positively related to CI. Agricultural intensification and the widespread use of fertilizers results in high levels of nitrogen deposition and in turn the decline of less competitive species that are dependent upon nutrient poor habitats (Preston 2000; Braithwaite *et al.,* 2006; Walker & Preston 2006; Van Landuyt *et al.,* 2008; Walker *et al.,* 2009; McClean *et al.,* 2011). This result suggests that shared environmental drivers may be having similar effects on biodiversity across multiple regions, which can be detected separately by the regional trait-based models. The region 5 model predicted the reverse CI trends in the flora of Flanders, i.e. a species with a positive CI value in Flanders was likely to have a negative CI value in region 5, and vice versa. This supports our finding that transferability is low between regions with dissimilar landscapes, as region 5 has a landscape dominated by semi-natural habitats – dramatically different from that of Flanders. The trait signal in region 5 was different from Flanders; life cycle type was significant with annual plants undergoing strong declines. This again reflects the history of land-use change: the trends are probably due to the decline in arable weeds as a result of a reduction in small-scale arable cultivation, as mixed farming gave way to purely pastoral agriculture in northern Scotland and the Scottish islands (Pearman & Preston 2000; Evans *et al.,* 2002; Pearman *et al.,* 2008). This is emphasised by the top three declining annual plants (excluding *Euphrasia spp.* which may have artificially low CI scores due to taxonomic uncertainty) in region 5 which are all arable weeds (*Chrysanthemum segetum* CI = -4.79, *Anthemis cotula* CI = -3.96, *Stachys arvensis* CI = -2.51). The variation in the direction and significance of predictors across our regional trait-based models provides support to the work by Fritz *et al.*, (2009), who found widespread geographic variation in the predictors of mammalian extinction risk that was linked to spatial variation in anthropogenic pressures on biodiversity.

We found low r^2 values associated with our regional trait-based models and also with the transferability of our models (also seen in Pocock, 2010). We may not expect high r^2 values as local, fine-scale drivers, including species interactions, may influence plant distribution change but will not be detected in the regional trait-based models. Also, despite using a CI method to account for recorder effort bias, there may have been a small amount of residual error in range change estimation that could have contributed to noise in the data. To reduce noise in our range change estimates a possible solution would be to only include grid cells that have been heavily recorded (see section 5.3.1 of chapter 5.). However, this would likely reduce the number of species and habitat diversity in this study, which in turn would reduce variation between predicted regions. The traits included in this study were chosen as evidence has suggested they can influence a species response to environmental change (Liem *et al.,* 1985; Preston, 2000; Godefroid, 2001; Haines-Young *et al.,* 2003; Braithwaite *et al.,* 2006; Walker & Preston, 2006; Van Landuyt *et al.,* 2008; Hulme, 2009).

Including a measure of the direct impact that land use change has had on each species may improve model r^2. Despite the low r^2 values of the regional trait models we were still able to detect a relationship between transferability and land-use. We believe that by reducing the noise in the estimates of distribution change, the predictive model r^2 would improve, and consequently would provide compelling evidence that trait-based models may be used to predict change in new regions given similar land-use characteristics. Currently, however, due to the low r^2 values of the predictions we cannot confirm that trait-based models may be used to predict change in new regions. We instead find evidence of inconsistencies in the results of comparative studies that are a key barrier to their applied use within conservation (Cardillo & Meijaard, 2011).

In conclusion, we found trait-based models were sensitive to geographic variation in the main drivers of change, showing that they can detect the impact of agricultural intensification in southern England and Flanders, but also the loss of annual plants due to a shift in the agricultural practices in northern Scotland. The regional trait-based models suffered from low r^2 values but despite this we were still able to detect that the transferability of these models was positively related to land-cover similarity. The low r^2 values of the model predictions means we were unable to confirm that trait-based models can be used to predict distribution change in new regions. However, this study highlights the potential value that well specified trait-based models may have in making further progress in this area of predictive modelling for the benefit of conservation.

4.6 Supplementary material

Appendix 4.1 An overview of each region included in the analysis. The final two columns contain information on the proportion of unique and ubiquitous species in each region. Ubiquitous species were classified as those species that were present in all regions included in the analyses, while unique species were only present in one region.

Region	Land Area (km^2)	Total species	Ubiquitous species	Unique species
Flanders	13848	685	0.53	0.11
Region 1	65027	908	0.40	0.04
Region 2	58620	919	0.40	0.04
Region 3	26973	735	0.50	0.02
Region 4	22518	663	0.55	0.01
Region 5	23506	638	0.57	0.01
Region 6	32505	593	0.62	0.06

Appendix 4.2 A list and description of the species' traits included in the analyses.

Trait	Description
Plant height (cm)	Plant height
Mean January Temperature (^{o}C)	Mean January temperature of all UK 10 km squares occupied, 1961 – 1990
Mean annual precipitation (mm)	Mean annual precipitation of all UK 10 km squares occupied, 1961 – 1990
Ellenberg L	Ellenberg value for light preference (1 = deep shade, 9 = full light)
Ellenberg S	Ellenberg values for salt tolerance (0 = absent from saline soils, 9 = extremely saline conditions)
Ellenberg N	Ellenberg values for nitrogen preference, soil fertility (1 = extremely infertile, 9 = extremely rich in nitrogen)
Ellenberg R	Ellenberg values for pH (1 = extreme acid soils, 9 = high pH soils)
Ellenberg F	Ellenberg values for moisture preference (1 = dry, 9 = wet-site indicator)
Habitat breadth	A count of the number of habitat categories the species occupies (based on the 23 categories in PLANTATT)
Biome	Major biome of the species European range. Northern (1-5 in PLANTATT), Widespread (6 in PLANTATT), Temperate (7 in PLANTATT), Southern (8-9 in PLANTATT)
Life cycle type	Species categorised as either annual, biennial or perennial

Appendix 4.3 Parameter estimates taken from the trait-based models for each region. Bold font has been used to highlight significant relationships.

(a) Flanders

Trait	Coefficient	SE	t	p
Intercept	-2.277	0.997	-2.283	0.023
Mean January temperature (°C)	**-0.246**	**0.113**	**-2.183**	**0.029**
Mean Precipitation (mm)	**0.004**	**0.002**	**2.868**	**0.004**
Mean Precipitation (mm)^2	**-1.893x10^{-6}**	**<0.001**	**-2.530**	**0.012**
Ellenberg L	0.006	0.035	0.170	0.865
Ellenberg F	**-0.353**	**0.147**	**-2.406**	**0.016**
Ellenberg F^2	**0.029**	**0.012**	**2.430**	**0.015**
Ellenberg R	**0.431**	**0.149**	**2.898**	**0.004**
Ellenberg R^2	**-0.035**	**0.013**	**-2.609**	**0.009**
Ellenberg N	**0.182**	**0.030**	**6.079**	**<0.001**
Ellenberg S	0.046	0.045	1.017	0.310
Log Height	**-0.357**	**0.145**	**-2.456**	**0.014**
Log Height^2	**0.047**	**0.015**	**3.083**	**0.002**
Habitat Breadth	**0.128**	**0.047**	**2.722**	**0.007**
Life cycle - biennial	0.105	0.176	0.597	0.551
Life cycle - perennial	-0.167	0.103	-1.629	0.104
Biome – southern	**0.245**	**0.117**	**2.094**	**0.037**
Biome – temperate	**0.209**	**0.094**	**2.225**	**0.026**
Biome – widespread	0.291	0.252	1.155	0.248

(b) Region 1

Trait	Coefficient	SE	t	p
Intercept	-1.423	0.660	-2.156	0.031
Mean January temperature (°C)	0.118	0.082	1.431	0.153
Mean Precipitation (mm)	**4.496x10^{-4}**	**<0.001**	**2.010**	**0.045**
Ellenberg L	-0.014	0.030	-0.457	0.648
Ellenberg F	-0.018	0.022	-0.833	0.405
Ellenberg R	0.035	0.027	1.264	0.207
Ellenberg N	**0.068**	**0.025**	**2.733**	**0.006**
Ellenberg S	-0.005	0.033	-0.165	0.869
Log Height	**-0.218**	**0.145**	**-1.499**	**0.134**
Log Height^2	**0.039**	**0.016**	**2.425**	**0.016**
Habitat Breadth	**0.134**	**0.043**	**3.094**	**0.002**
Life cycle – biennial	0.168	0.160	1.050	0.294
Life cycle – perennial	0.014	0.092	0.155	0.877
Biome – southern	0.062	0.106	0.585	0.558
Biome – temperate	-0.095	0.088	-1.085	0.278
Biome – widespread	**0.486**	**0.234**	**2.080**	**0.038**

(c) Region 2

Trait	Coefficient	SE	t	p
Intercept	-1.498	0.717	-2.090	0.037
Mean January temperature (^{o}C)	**0.164**	**0.064**	**2.570**	**0.010**
Mean Precipitation (mm)	**0.001**	**<0.001**	**3.019**	**0.003**
Ellenberg L	**-0.369**	**0.171**	**-2.158**	**0.031**
Ellenberg L^2	**0.031**	**0.014**	**2.264**	**0.024**
Ellenberg F	-0.008	0.021	-0.393	0.694
Ellenberg R	**0.070**	**0.026**	**2.661**	**0.008**
Ellenberg N	**0.052**	**0.024**	**2.135**	**0.033**
Ellenberg S	**-0.188**	**0.068**	**-2.754**	**0.006**
Ellenberg S^2	**0.027**	**0.011**	**2.526**	**0.012**
Log Height	**0.064**	**0.037**	**1.748**	**0.081**
Habitat Breadth	**0.234**	**0.043**	**5.469**	**<0.001**
Life cycle – biennial	-0.010	0.160	-0.065	0.948
Life cycle – perennial	-0.048	0.089	-0.540	0.590
Biome – southern	0.111	0.102	1.082	0.280
Biome – temperate	-0.047	0.086	-0.555	0.579
Biome – widespread	**0.472**	**0.233**	**2.023**	**0.043**

(d) Region 3

Trait	Coefficient	SE	t	p
Intercept	-1.609	0.728	-2.210	0.027
Mean January temperature (^{o}C)	**0.237**	**0.093**	**2.543**	**0.011**
Mean Precipitation (mm)	1.365×10^{-4}	<0.001	0.558	0.577
Ellenberg L	-0.034	0.034	-1.007	0.314
Ellenberg F	**0.086**	**0.025**	**3.436**	**0.001**
Ellenberg R	-0.013	0.029	-0.433	0.665
Ellenberg N	0.018	0.029	0.624	0.533
Ellenberg S	-0.004	0.075	-0.060	0.953
Log Height	0.050	0.042	1.174	0.241
Habitat Breadth	**0.135**	**0.047**	**2.880**	**0.004**
Life cycle – biennial	0.057	0.189	0.299	0.765
Life cycle – perennial	-0.070	0.113	-0.621	0.535
Biome – southern	-0.024	0.122	-0.195	0.846
Biome – temperate	0.006	0.097	0.063	0.950
Biome – widespread	0.116	0.268	0.435	0.664

(e) Region 4

Trait	Coefficient	SE	t	p
Intercept	-3.826	0.975	-3.925	<0.001
Mean January temperature (°C)	-0.063	0.103	-0.616	0.538
Mean Precipitation (mm)	**0.003**	**0.001**	**2.144**	**0.032**
Mean Precipitation (mm)^2	**-1.330×10^{-6}**	**<0.001**	**-2.182**	**0.029**
Ellenberg L	0.028	0.036	0.789	0.430
Ellenberg F	**0.111**	**0.024**	**4.559**	**<0.001**
Ellenberg R	**0.366**	**0.135**	**2.713**	**0.007**
Ellenberg R^2	**-0.034**	**0.013**	**-2.635**	**0.009**
Ellenberg N	0.021	0.030	0.707	0.480
Ellenberg S	-0.014	0.039	-0.357	0.721
Log Height	0.049	0.044	1.122	0.263
Habitat Breadth	**0.099**	**0.047**	**2.082**	**0.038**
Life cycle – biennial	-0.088	0.188	-0.467	0.641
Life cycle – perennial	-0.063	0.107	-0.588	0.557
Biome – southern	0.042	0.119	0.352	0.725
Biome – temperate	0.142	0.096	1.485	0.138
Biome – widespread	**0.520**	**0.236**	**2.201**	**0.028**

(f) Region 5

Trait	Coefficient	SE	t	p
Intercept	0.327	0.671	0.488	0.626
Mean January temperature (°C)	0.027	0.084	0.325	0.745
Mean Precipitation (mm)	**-0.001**	**<0.001**	**-2.382**	**0.018**
Ellenberg L	-0.014	0.035	-0.416	0.678
Ellenberg F	**0.108**	**0.024**	**4.494**	**<0.001**
Ellenberg R	-0.043	0.028	-1.512	0.131
Ellenberg N	-0.011	0.030	-0.387	0.699
Ellenberg S	-0.057	0.041	-1.372	0.171
Log Height	**-0.096**	**0.041**	**-2.319**	**0.021**
Habitat Breadth	**0.107**	**0.046**	**2.298**	**0.022**
Life cycle – biennial	**0.527**	**0.204**	**2.585**	**0.010**
Life cycle – perennial	**0.424**	**0.109**	**3.891**	**<0.001**
Biome – southern	0.003	0.114	0.029	0.977
Biome – temperate	-0.060	0.092	-0.654	0.513
Biome – widespread	0.252	0.230	1.097	0.273

(g) Region 6

Trait	Coefficient	SE	t	p
(Intercept)	0.802	0.630	1.273	0.203
Mean January temperature (^{o}C)	0.132	0.128	1.029	0.304
Mean January temperature (^{o}C)^{2}	**-0.080**	**0.033**	**-2.468**	**0.014**
Mean Precipitation (mm)	**-0.001**	**<0.001**	**-3.096**	**0.002**
Ellenberg L	-0.046	0.037	-1.222	0.222
Ellenberg F	**0.121**	**0.025**	**4.793**	**<0.001**
Ellenberg R	-0.026	0.028	-0.951	0.342
Ellenberg N	**-0.085**	**0.032**	**-2.667**	**0.008**
Ellenberg S	**0.116**	**0.059**	**1.972**	**0.049**
Log Height	**0.186**	**0.041**	**4.517**	**<0.001**
Habitat Breadth	0.095	0.051	1.871	0.062
Life cycle – biennial	0.145	0.218	0.666	0.506
Life cycle – perennial	-0.003	0.126	-0.022	0.982
Biome – southern	-0.133	0.138	-0.964	0.336
Biome – temperate	-0.042	0.104	-0.408	0.684
Biome – widespread	-0.141	0.268	-0.525	0.600

Chapter 5: Can traits derived from distribution data explain variation in species range shifts across multiple taxonomic groups?

5.1 Abstract

Poleward shifts in species distributions have been widely reported and are likely due to the poleward shift in species' climatic niches as a result of climate change. The direction and strength of range shift is not consistent within, or between taxonomic groups and may party be explained by examining differences in species ecology. Such trait-based studies of range shifts have primarily been restricted to birds and butterflies due to a lack of data for many less well studied taxonomic groups. Here we use traits derived from distribution data, collected principally by volunteers, alongside widely available climate and land use datasets to examine correlates of range shift across ten taxonomic groups in Britain. These distribution based traits included: species temperature index, species moisture index, fractal dimension, habitat marginality, range size and change in range size. A key trait-trend relationship was a negative relationship between range shift and the habitat marginality, a measure of how marginal the species' habitat requirement is compared to the available habitat in Britain. This result can be linked to the importance of habitat availability for range shift, with species' ability to track their climatic niche reliant on successful dispersal into the newly climatically available habitat patches. We highlight the value of the citizen science, particularly the increase in public participation in biological recording, showing that data collected primarily by volunteers can be used to explain changes in species distributions for many taxonomic groups that were previously poorly studied.

5.2 Introduction

Species from a variety of taxonomic groups in many regions across the globe have shown shifts in their distributions as a result of environmental change (e.g. Crozier, 2004; Hickling *et al.,* 2006; Shoo *et al.,* 2006; La Sorte & Thompson, 2007; Lima *et al.,* 2007; Colwell *et al.,* 2008; Sorte *et al.,* 2010; Walther, 2010). Range shifts towards higher latitudes have been widely reported and are likely due to the poleward shift in species' climatic niches as a result of climate change (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Chen *et al.*, 2011). The intensity, and in some cases direction, of these range shifts is not uniform within, or between taxonomic groups (Warren *et al.,* 2001; Thomas *et al.,* 2004a; Hickling *et al.,* 2005; Lenoir *et al.,* 2008). The potential impact of this variation on community structure and in turn the functioning and resilience of ecosystems is a cause for concern (Lenoir *et al.,* 2008; Walther, 2010), with evidence showing that change in community structure can result in mismatch between trophic and functional groups that could ultimately lead to ecosystem collapse (Edwards & Richardson, 2004; Lauzeral *et al.*, 2010; Thackeray *et al.*, 2010; Schweiger *et al.*, 2012).

The variation in species response to environmental change can be partly explained through comparative analyses of species traits (Angert *et al.*, 2011; Chessman, 2011; Mattila *et al.*, 2011; Grewe *et al.*, 2012). By identifying traits that enable species to shift to track climate warming it is possible to highlight those species that lack this ability to shift, and that therefore may be of conservation concern (Thomas *et al.*, 2004a; Perry *et al.*, 2005; Angert *et al.*, 2011; Mattila *et al.*, 2011). In addition, examining variation in the results of these comparative analyses across multiple taxonomic groups may support efforts to determine possible ecological mismatches (such as trophic relationships, Schweiger *et al.*, 2012). Previous comparative studies of range shift have predominantly been restricted to bird and butterfly species (Devictor *et al.*, 2008; La Sorte & Thompson III, 2007; Pöyry *et al.*, 2009; Mattila *et al.*, 2011), and therefore the consistency of the trait-trend relationships across less well studied taxonomic groups is not known. The main cause of the limited taxonomic scope of previous comparative studies is that comparative analyses tend to be data hungry, requiring detailed distribution, trait and ideally phylogenetic data that are lacking for many groups.

The rapid growth in citizen science, in particular the public participation in biological recording, has resulted in the collation of many large-scale distribution datasets covering a wide variety of taxonomic groups (Silvertown, 2009; Sullivan *et al.*, 2009; Boakes *et al.*, 2010; Dickinson *et al.*, 2012; Miller-Rushing *et al.*, 2012; Tweddle *et al.*, 2012). This growth in data collation and the increased accessibility to large-scale distribution datasets through systems and organisations such as the Biological Records Centre (BRC - http://www.brc.ac.uk/), National Biodiversity Network (NBN - http://www.nbn.org.uk/) and Global Biodiversity Information Facility (GBIF - http://www.gbif.org/), allows new opportunities to examine distribution change in previously poorly studied taxonomic groups. Despite the increase in distribution data, comparative studies of range shift across multiple taxonomic groups remain limited due to the lack of species life-history trait data. However, it is possible to derive species trait data that are based on the newly available distribution data alongside some widely available climatic and land-use datasets. A couple of example traits include: the species climatic niche and the marginality of the species habitat requirements (Hirzel *et al.*, 2002; Hill *et al.*, 2004; Thuiller *et al.*, 2004; Devictor *et al.*, 2008). Currently however, the explanatory power of distribution-based traits for explaining variation in range shift is untested. In this study, we examine range shift across ten broad taxonomic groups in Britain, and test whether traits derived from distribution data can explain variation in range shift. We predict traits which affect the ability of species to disperse into newly climatically available habitat patches will be important predictors of species range shift, with the likelihood of successful dispersal positively correlated with range shift (Warren *et al.*, 2001; Pöyry *et al.*, 2009; Mattila *et al.*, 2011; Grewe *et al.*, 2012). We examine the consistency of the trait-trend relationships across taxonomic groups, and discuss the relevance of the results to conservation efforts aimed at mitigating the negative impacts of environmental change on the biodiversity of Britain.

5.3 Methods

5.3.1 Distribution data and range shift calculation

We extracted species level, presence only, 10 km grid square distribution data in Britain from the Biological Records Centre (BRC) for each of the ten taxonomic groups included in the study (listed in Table 1). Distribution data were obtained from two distinct time periods, each separated by a minimum of 10 years (see Table 1 for exact dates) that ensured a considerable gap between the two time periods while maintaining a large number of records for the analysis (Hickling *et al.* 2006). For each species the northern range margin was estimated in both time periods as the mean latitude of the ten most northerly occupied grid cells. Range shift was subsequently calculated as the difference between the northern range margin in the early and later time period (Thomas & Lennon, 1999; Hickling *et al.*, 2005; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Grewe *et al.*, 2012).

There was an increase in biological recording in Britain during the time periods of this study (Telfer *et al.*, 2002; Hickling *et al.*, 2006; Tweddle *et al.*, 2012), this increased in survey effort must be accounted for when examining temporal change in species' distributions between two time periods (Prendergast *et al.*, 1993; Telfer *et al.*, 2002; Tingley & Beissinger, 2009; Boakes *et al.*, 2010; Hill, 2012). To account for variation in recorder effort, we focussed on excluding cells that were under-recorded in the early time period (Hickling *et al.*, 2006; Grewe *et al.*, 2012). Following Hickling *et al.* (2006), range shift was calculated for three subsets of the data, first, we included only those cells that had a minimum of one species recorded as present in both time periods for the taxonomic group in question (moderately recorded cells). Second, cells were included if they had at least 10%

of the total species count for the group in question in both time periods (well recorded cells), with the final subset including the equivalent cells using 25% rather than 10% (heavily recorded cells) .

In addition to limiting data based on grid cell attributes, data were limited based on four attributes of the species. First, only native species were included in the analysis to ensure range margin shifts were not an artefact of overall range expansion of recent arrivals. Second, species with unreliable distribution data due to taxonomic uncertainty during the time periods used in this study were excluded. Thirdly, species that occupied fewer than 20 cells across the time periods were excluded to reduce unreliable shift estimates based on rare or poorly recorded species (Hickling *et al.,* 2006). Finally, only species with a northern range margin in Britain were included in the analysis to ensure that shift was not geographically limited by proximity to the coast. Species were classified as having a range margin in Britain if their range margin in the early time period was 100 km below the northern edge of mainland Scotland. This distance is likely to allow sufficient area for species to shift based on the result of Hickling *et al.,* (2006) who found mean range shift was 56 km north with a maximum shift of 105 km. Additionally, we limited the plant dataset by excluding plant species with an Ellenberg Moisture value greater than 9 (water plants), as targeted plant surveys of Scottish lochs in the second time period, was likely to result in artificially increased northerly range shifts of aquatic plants (Preston & Croft, 1997; Preston *et al.,* 2002b).

5.3.2 Species traits

We used species distribution data in conjunction with habitat and climate data to derive six species traits: temperature index, moisture index, fractal dimension, marginality, range size and change in range size. The two climate indices were included as there is some evidence that suggests species responses to climate change is partly based on their climatic niches (Devictor et al., 2008, Devictor et al., 2012). Fractal D measures the level of fragmentation of a species distribution, aggregated distribution patterns are thought to reflect range expansion, while a fragmented distribution is thought to reflect the process of range decline (Wilson et al., 2004). Habitat marginality measures how different a species habitat requirement is from the available habitat of the study region. Species with marginal habitat requirements will have fewer opportunities to disperse into newly climatically available habitat patches. The majority of species within this study have a distribution range that extends beyond Britain, and so there may be reason to use the entire distribution range for trait estimation. Despite this, we use the distribution data in Britain alone to derive trait estimates, as many of the distribution based traits relate specifically to the study region. For example, the marginality trait measures a species' habitat requirement relative to that available in the entire study region (Britain). Additionally, Britain has high-quality distribution data across multiple taxonomic groups, but it is unlikely that consistently high-quality distribution data will be available across the entire distribution range of many species in this study.

Two climate indices were calculated for each species, the temperature index and the moisture index. Climate data were taken from CRU ts2.1 (Mitchell & Jones, 2005) and CRU 61-90 climate (New *et al.,* 1999) datasets interpolated to the 10 km UK grid. The mean temperature of the warmest month (MTWA, ^{o}C) and the mean ratio of actual to potential evapotranspiration (APET, used as the moisture index) were extracted for each grid cell in Britain between 1969 and 1999. The climate indices were calculated as the mean value of the climate variable across all grid cells that the species occupied in the first time period. The fractal dimension (fractal D) of the species distribution was calculated as the slope of the relationship between the log of the area of occupancy at the 10 km and 100 km scale plotted against the log of the length grid cell at each scale (Wilson *et al.,* 2004). The measure is bound between 0 and 2, with a value of 2 indicating that occupied cells at the smaller scale completely fill all cells at the larger scale, while 0 is indicative of one small scale cell presence in each larger cell. Species with higher values of fractal D have more aggregated distribution patterns which are thought to reflect recent range expansion, whereas those with smaller fractal D values have fragmented distribution patterns that are characteristic of declining species (Wilson *et al.,* 2004). Fractal D was calculated using the species distribution data from the second time period as it is a method which estimates past distribution changes from current distribution patterns. We used ecological niche factor analysis (ENFA) to estimate the level of marginality in the habitat requirement of each species compared to the overall habitat composition of Britain (Hirzel *et al.*, 2002). ENFA compares the species niche breadth in multivariate space to the niche breadth of the overall study region, with the difference between the two forming the marginality score (the higher the marginality score the more marginal the niche breadth of the species relative to the study region). Habitat data were taken from the CEH land cover map 2007 (Morton *et al.*, 2011). We collapsed the original land-use data into 13 broad habitat land-use classes (for details see Appendix 5.1) and identified proportional coverage of each class within each 10 km grid cell. Marginality was calculated using the distribution data from the later time period to ensure the estimate reflected the current marginality score of the species given recent land use changes. Finally, for each species we identified total range size – a count of occupied grid cells in the early time period, and change in range size – the difference in number of grid cells occupied between the two time periods. Total range size may be considered as a surrogate of rarity, with rare species tending to have smaller total range size (Gaston, 2003), while change in range size was included to account for overall range expansion.

5.3.3 Statistical analysis

Prior to the trait-based analyses we examined levels of colinearity between our explanatory variables using Pearson's product-moment correlation tests. Mean MTWA and mean APET were highly correlated (r = -0.90) and therefore APET was excluded from the analysis. We ran trait-based multi-predictor regression models of range shift for each taxonomic group separately. Initially we fitted the maximum model containing all traits as explanatory variables and simplified by the stepwise deletion of non-significant terms to identify the minimum adequate model (MAM) for each group. At each model iteration we used AIC to ensure the new model was a better fit to the data.

The quadratic term of each explanatory variable was included in the full model to test for non-linearity. Range size and marginality were logged to ensure both were normally distributed prior to analysis. All statistical analyses were carried using R 2.14.2 (R Development Core Team, 2012).

5.3.4 Phylogenetic comparative analysis

Treating species as independent data points can inflate type 1 error rates as closely related species share more evolutionary history than distant relatives (Harvey, 1996). We therefore ran a second analysis that accounted for phylogenetic non-independence by using phylogenetic generalised least squares (PGLS) with estimated Pagel's λ (Pagel, 1999; Freckleton *et al.*, 2002). Pagel's λ, as estimated through maximum likelihood ratio tests, is a measure of phylogenetic signal in the model and is used to alter the variance covariance matrix of the least squares regression model. PGLS using estimated Pagel's λ is an improvement on techniques that under-correct for phylogenetic associations by assuming no phylogenetic dependence ($\lambda = 0$) or those that over-correct by assuming complete phylogenetic dependence ($\lambda = 1$) (Freckleton *et al.*, 2002; Purvis, 2008). We initially attempted to build a phylogeny based on genetic data for all species included in the analysis. However, due to the lack of genetic data for a large number of species included in the study, we built a phylogeny that was based on species taxonomy. We used the *as.phylo* function from the R package *ape* (Paradis *et al.*, 2005) to convert the taxonomy (Kingdom, Phylum, Class, Order, Family, Genus, Species) into a tree with polytomies at each node and branch lengths set to 1. Phylogenetic analyses were carried out using the *pgls* function from the R package *caper* (Orme *et al.*, 2012). The phylogenetic modelling protocol matched that of the non-phylogenetic analysis, first fitting the maximum model and the sequential deletion of non-significant terms to identify the MAM for each taxonomic group.

5.4 Results

Range shift estimates were very similar across the three data subsets based on the levels of recording intensity (moderately recorded – well recorded $r = 0.68$, well recorded – heavily recorded $r = 0.72$, moderately recorded – heavily recorded $r = 0.61$), and we therefore only present results from models based on the intermediate measure of well recorded grid cells. The use of the well recorded grid cells ensured a good balance between maintaining a large number of records for the analysis while excluding the most poorly surveyed grid cells.

We found that 7 of the 10 taxonomic groups were significantly shifting north, while fish, terrestrial vertebrates and bryophytes showed no significant directional shift (Table 5.1, Figure 5.1). Across all groups there was a significant mean northwards shift of 13.2 km ($t = 6.13$, $df = 1359$, $p < 0.001$ 95% confidence intervals = 8.96 – 17.40).

Table 5.1 An overview of the time periods, number of species and mean shift (error and significance) of the taxonomic groups included in the analysis.

Taxonomic group	**Time 1**	**Time 2**	**Species number**	**Mean shift (km)**	**Standard error**	***p***
Bryophytes	1965-1975	1990-2000	89	-16.93	36.26	0.356
Butterflies	1970-1982	1995-1999	35	23.74	17.50	0.009
Chilopoda & Diplopoda	1965-1975	1990-2000	20	70.10	40.79	0.002
Fish	1965-1975	1990-2000	22	33.68	36.24	0.067
Moths	1970-1980	1990-2000	558	10.96	4.89	<0.001
Odonata	1960-1970	1985-1995	23	90.74	24.85	<0.001
Orthoptera*	1960-1970	1985-1995	22	19.32	18.20	0.039
Plants	1930-1969	1987-1999	423	8.40	6.77	0.015
Spiders**	1965-1975	1990-2000***	140	21.45	7.03	<0.001
Terrestrial vertebrates****	1960-1970	1985-1995	28	45.54	67.55	0.178

* Orthoptera group contains Orthoptera, Dermaptera and Dictyoptera species that met the minimum data requirements.

** Spiders group contains Araneae and Opiliones species that met the minimum data requirements.

*** Opiliones (16 species) time period 2 was 1985-1995.

**** Terrestrial vertebrate group contains all mammals, amphibians and reptiles that met the minimum data requirements.

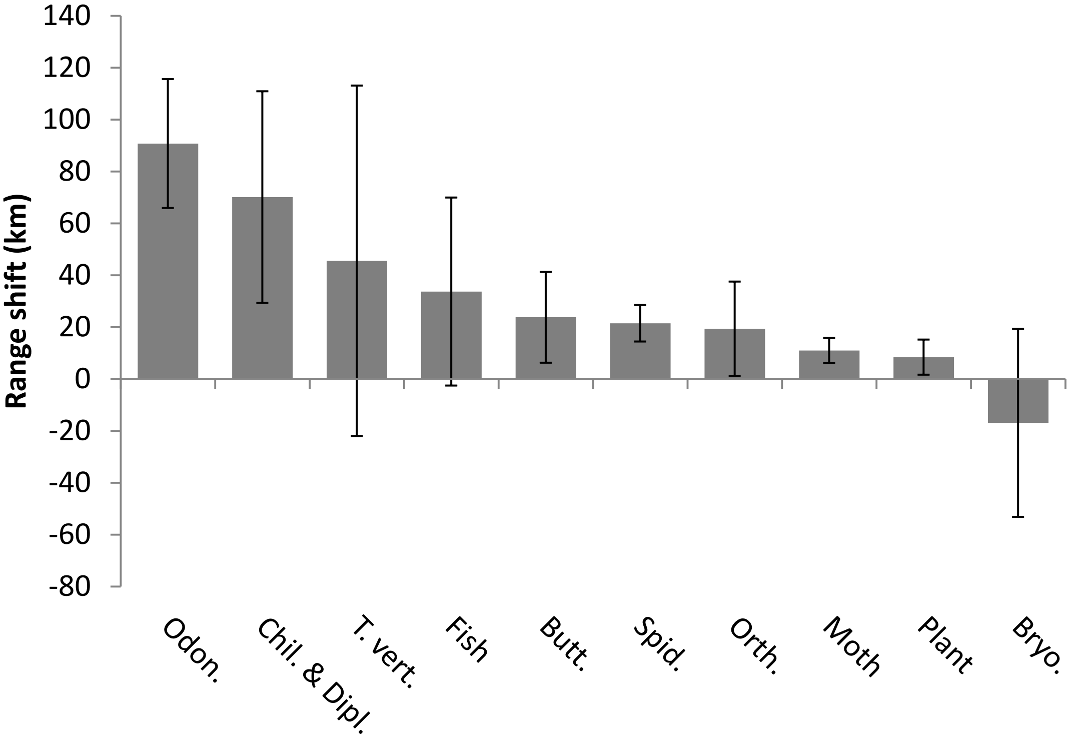


Figure 5.1 Mean shift (with 95% confidence intervals) in the northern range margin of each of the taxonomic groups included in our study.

Pagel's λ was estimated to be 0 for all PGLMs. In this study, PGLM with $\lambda = 0$ was not identical to standard linear modelling as the phylogenetic trees used were not ultrametric. However, the direction and significance of the parameter coefficients were highly similar between the MAMs derived from the PGLMs and the non-phylogenetic regression models, and we therefore only present results from the PGLMs (non-phylogenetic regression results are shown in Appendix 5.2).

Range shift was significantly positively correlated with MTWA in four taxonomic groups: chilopoda & diplopoda, fish, moths and spiders (Table 5.2), suggesting that species that occupy warmer regions were likely to have undergone greater positive range shift. The relationship between fractal D and range shift was not consistent across groups, significantly positive in the spider and terrestrial vertebrate MAMs, but significantly negative in the odonata MAM. Marginality was consistently negatively correlated with range shift, significantly so in four MAMs: fish, moths, plants & terrestrial vertebrates. This result suggests that species with less marginal habitat usage show greater positive range shifts. As expected, range shift was significantly positively correlated with change in range size, significantly so in the MAMs of seven taxonomic groups. The relationship between range size and range shift was not consistent across the taxonomic groups, with significant negative correlations found in the MAM for bryophytes, plants, spiders and terrestrial vertebrates, while a significant positive correlation was found in the moth MAM.

Variance in range shift explained by the MAMs varied considerably across taxonomic groups, from 16% by the plant MAM to 65% by the terrestrial vertebrate MAM (Table 4.2). The mean amount of variation in range shift explained by the MAMs was 40%.

Table 5.2 The coefficients and parameter estimates taken from the phylogenetic minimum adequate model for each taxonomic group. For each significant trait-based relationship the regression slope is shown, standard error of the slope is shown in brackets and significance level indicated by the number of asterisk (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). For all models λ was estimated to be 0, indicating no phylogenetic signal.

Group	MTWA ($^{\circ}$C)	Fractal D	Log Marginality	Size Change (km^2)	Log Range Size (km^2)	n	F	Std. error	r^2	p
Bryo.	ns	ns	ns	4.71 (0.55) ***	-62.86 (17.00) ***	89	48.48	48.05	0.52	<0.001
Butt.	ns	ns	ns	0.18 (0.04) ***	ns	35	22.44	16.17	0.39	<0.001
Chil. & Dipl.	114.71 (36.72) **	ns	ns	5.18 (1.99) *	ns	20	15.64	23.43	0.61	<0.001
Fish	135.90 (53.15) *	ns	-71.84 (32.77) *	ns	ns	22	3.715	31.6	0.21	0.029
Moth	12.70 (6.35) *	ns	-16.81 (6.02) **	0.57 (0.05) ***	11.59 (2.46) ***	558	43.03	19.99	0.23	<0.001
Odon.	ns	-216.95 (63.88) **	ns	3.55 (1.14) **	ns	23	6.284	18.76	0.32	0.004
Orth.	ns	ns	ns	2.12 (0.41) *** †	ns	22	17.66	10.94	0.61	<0.001
Plant	ns	ns	-24.79 (5.48) ***	0.28 (0.04) ***	-21.36 (2.73) ***	423	28.73	27.89	0.16	<0.001
Spider	16.54 (7.15) *	108.79 (17.28)***	ns	ns	-56.69 (9.69) ***	140	25.07	13.25	0.34	<0.001
T. Vert.	ns	310.53 (61.87) ***	-107.98 (33.57) **	ns	-153.46 (24.35) ***	28	17.79	42.62	0.65	<0.001

† The relationship between Orthoptera range shift and change in range size was significantly curved (*quadratic term b* = 0.08, *std. error* = 0.02, $p < 0.01$).

5.5 Discussion

We found an overall positive trend in range margin shifts of species from a variety of taxonomic groups in Britain. On average, species' northern range margins have shifted north by 13.2 km over an approximately 15 year period, a poleward shift rate that is of a similar magnitude to those presented in other range shift studies (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011, although considerably larger shifts have been reported in Pöyry *et al.*, 2009; Grewe *et al.*, 2012). While we do not directly link range shift with climate change, our findings support the growing evidence base that suggests species distributions are shifting polewards to track the shift in their climatic niche (Thomas & Lennon, 1999; Crozier, 2004; Walther *et al.*, 2002; Walther *et al.*, 2007; Chen *et al.*, 2011).

In this study, we demonstrated that it was possible to use traits that are derived from distribution data to explain variation in species range shift. The use of these traits enabled us to conduct comparative analyses across a variety of taxonomic groups, many of which lack the life-history trait datasets that are essential for traditional comparative analyses. The absence of life-history trait data did not result in low explanatory power of the models, conversely the models explained a good amount of variation (range: 16 – 65%, mean: 40%) that exceeded or was similar to that of other trait-based models, many of which use life-history trait data (Pöyry *et al.*, 2009 Angert *et al.*, 2011; Grewe *et al.*, 2012). We found it is possible to use large-scale citizen science datasets in combination with widely available land-cover and climate data to identify and explain biodiversity change. This finding highlights the potential benefits of the rapid growth in public participation in biological recording, and the resulting increased availability of large-scale distribution datasets, to ecological research.

A key trait-trend relationship found in this study was the significant negative correlation between range shift and marginality, which suggests species with more marginal habitat requirements have a reduced capacity to shift than species whose habitat requirement matches that of the study region. We believe this result highlights the importance of habitat availability to shifting populations, with species ability to track a shift in their climatic niche reliant on their ability to disperse into newly climatically available habitat patches. Previous comparative studies of range shift have arrived at a similar conclusion using results that were based on different species traits. For example, habitat generalists have a greater capacity to shift than specialists due to increased habitat availability for generalists (Warren *et al.*, 2001; Hill *et al.*, 2002; Pöyry *et al.*, 2009) and species with greater dispersal ability can shift to colonise to new climatically available habitat patches that are too isolated for poor disperses (Devictor *et al.*, 2012; Grewe *et al.*, 2012).

Range shift was significantly positively related to species temperature index, suggesting that species with warmer climatic niches are showing greater positive range shifts than those with the cooler climatic niches. In addition to latitudinal range shifts, species can adapt to environmental change through altitudinal range shifts (Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006; Wilson *et al.*, 2007; Devictor *et al.*, 2008; Lenoir *et al.*, 2008). We believe the positive relationship between species temperature index and range shift reflects the greater potential for northerly distributed species (cool temperature index) to adapt to climate warming through elevation range shifts than southern species, due to the increased within cell elevational range in the north compared to the south (Appendix 5.3). Additionally, there may be widespread range expansions of species that prefer warmer climates due to the increased climatic suitability of the British landscape associated with climatic warming (Devictor *et al.*, 2008; Devictor *et al.*, 2012). Fractal D measures the level of fragmentation in a species distribution, with the theory that fragmented distribution patterns (lower fractal D scores) reflect decline while aggregated patterns (higher fractal D score) reflect expansion (Wilson *et al.*, 2004). This theory is supported by the positive correlation between fractal D and range shift in the spider and terrestrial vertebrate MAMs, but fractal D and range shift were negatively correlated in the odonata MAM. Lentic species of odonata rely on semi-permanent standing water bodies and therefore are thought to have adapted greater dispersal ability than lotic species (Grewe *et al.*, 2012). The reliance on semi-permanent habitats may result in a more fragmented distribution pattern (lower fractal D), but the increased dispersal ability will increase the capacity of lentic species to shift, which may explain the negative relationship between fractal D shift in the odonata MAM. We found no consistent relationship between range shift and range size across taxonomic groups. Similar inconsistencies in the shift – size relationship have been previously shown in odonata, birds, mammals and plants (Angert *et al.*, 2011). As expected, change in range size was positively correlated with range shift across most taxonomic groups, reflecting the shift in the northern range margin of species that are undergoing overall range expansion

The widespread variation in species range shift within, and across, taxonomic groups may result in ecological and trophic mismatches which could ultimately result in species extinction and ecosystem collapse (Walther, 2010; Schweiger *et al.*, 2012). However, further study into the impact of range shift on the vital interactions between species (for example, predators and prey, herbivores and their host plants, etc) is needed to fully understand the conservation implication of species range shift. Species that are unable to track their climatic niche may be at risk of extinction (Perry *et al.*, 2005; Thomas *et al.*, 2004a), based on the results of this study, these species of conservation concern would include species with marginal habitat requirements. Landscape management aimed at increasing habitat connectivity, particularly of those habitat types favoured by specialists, species with poor dispersal ability and species with marginal habitat requirements, may help mitigate the negative impacts of climate change (La Sorte & Jetz, 2012). However, it should be noted that species can adapt to environmental change through altitudinal shifts, changes in phenology, behavioural changes and phenotypic plasticity, all of which would be undetectable by the analyses in this study (Roy & Sparks, 2000; Hickling *et al.*, 2006; Phillimore *et al.*, 2010; Bellard *et al.*, 2012). Dispersal ability is likely to be a key factor in determining variation in species range shift, an interesting area for future work would be to extract an estimate of species dispersal ability based on distribution patterns and include this in the modelling process.

5.5.1 Conclusions

To summarise, we demonstrated that it is possible to use traits that were derived from distribution data to explain variation in species range shift. We found substantial variation in the correlates of range shift across a wide selection of taxonomic groups in Britain, with a key relationship being the negative correlation between range shift and the marginality of species habitat requirement. This can be linked to the importance of habitat availability to species range shift, with a species' ability to track a shift in its climatic niche reliant on successful dispersal into newly climatically available habitat patches. We highlight the value of citizen science, showing that data collected primarily by volunteers can be used alongside climate and land use datasets to identify and explain change in species distributions. The models in this study explain a decent amount of variation in range shift; however, it would be interesting to examine the additional explanatory power that life-history traits may contribute.

5.6 Supplementary material

Appendix 5.1 A list showing the LCM 2007 broad land-use categories and the aggregate classes they were collapsed into for use in this study.

LCM 2007 Broad land-use class	Aggregate land-use class
Broadleaf woodland	Forest
Coniferous woodland	Forest
Arable	Arable
Improved Grassland	Improved Grassland
Rough grassland	Semi-natural areas
Neutral grassland	Semi-natural areas
Calcareous grassland	Calcareous grassland
Acid grassland	Semi-natural areas
Fen, marsh, swamp	Fen
Dwarf heathland	Heathland *
Bog	Montane habitat
Montane habitat	Montane habitat
Saltwater	Water
Freshwater	Water
Supra littoral rock	Coastal
Supra littoral sediment	Coastal
Littoral rock	Coastal
Littoral sediment	Coastal
Urban	Urban

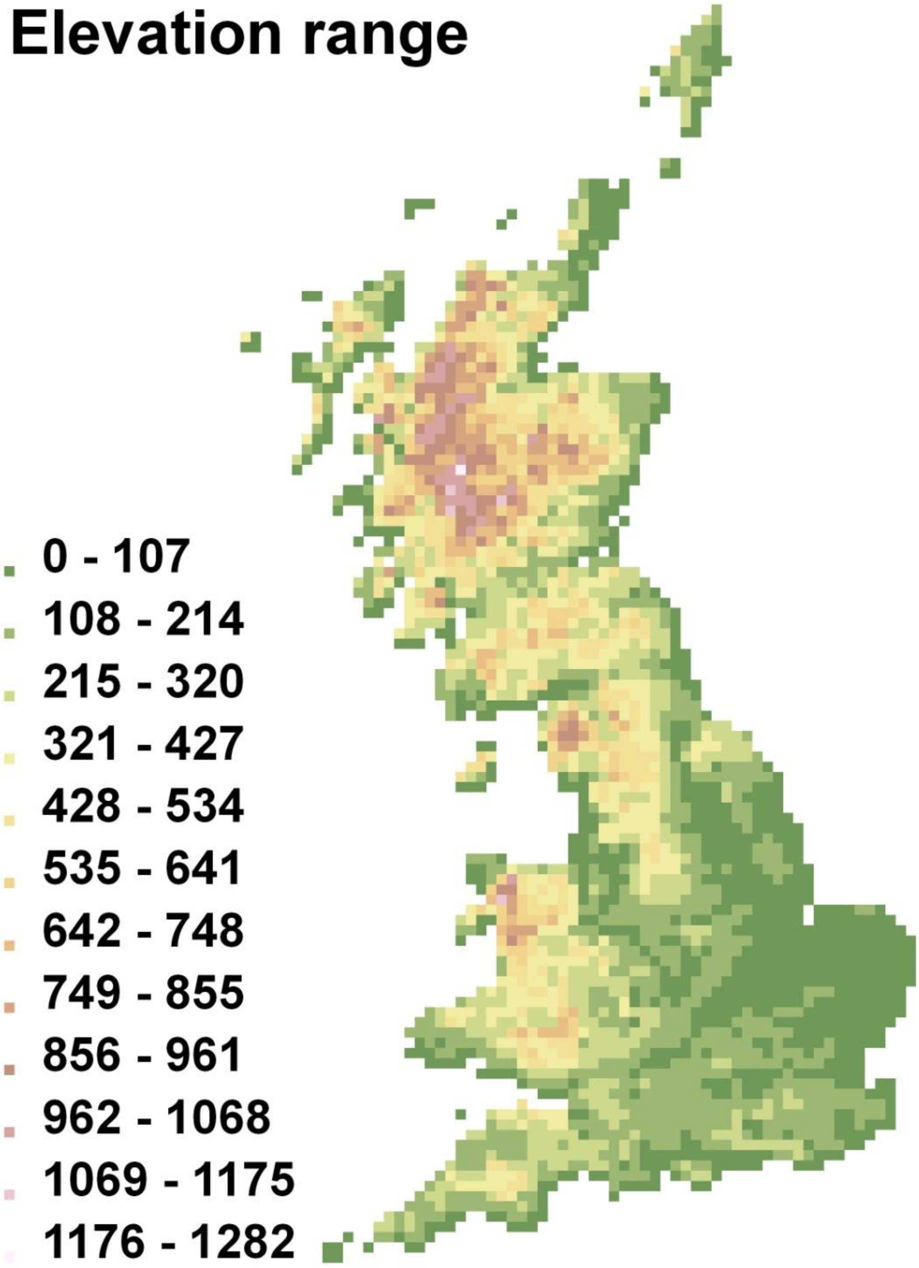
* Heathland was split into two categories, upland heath and lowland heath, with the divide set at 300 m using a digital elevation model (above 300 m = upland heath, below 300 m = lowland heath).

Appendix 5.2 The coefficients and parameter estimates taken from the non-phylogenetic minimum adequate model for each taxonomic group. For each significant trait-based relationship the regression slope is shown, standard error of the slope is shown in brackets and significance level indicated by the number of asterisk (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Group	**MTWA (^{o}C)**	**Fractal D**	**Log Marginality**	**Size Change (km^2)**	**Log Range Size (km^2)**	**n**	**F**	**Std. error**	**r^2**	**p**
Bryo.	ns	ns	ns	4.56 (0.55) ***	-70.03 (16.96) ***	89	48.75	119.20	0.52	<0.001
Butt.	ns	ns	ns	0.18 (0.04) ***	ns	35	22.44	39.90	0.39	<0.001
Chil. & Dipl.	112.06 (36.09) **	ns	ns	5.40 (1.92) *	ns	20	15.95	54.33	0.61	<0.001
Fish	135.77 (51.4) *	ns	-75.3 (32.81) *	ns	ns	22	4.01	72.07	0.22	0.04
Moth	18.79 (6.54) **	-32.55 (9.62) ***	-16.29 (6.32) *	0.61 (0.05) ***	ns	558	40.42	51.87	0.22	<0.001
Odon.	ns	-219.35 (63.67) **	ns	3.58 (1.12) **	ns	23	6.55	46.85	0.34	0.01
Orth.	ns	ns	ns	2.02 (0.43) *** †	ns	22	13.61	27.67	0.55	<0.001
Plant	ns	ns	-24.38 (5.49) ***	0.28 (0.04) ***	-21.56 (2.76) ***	423	28.71	64.77	0.16	<0.001
Spider	34.28 (11.30) **	112.54 (17.21)***	-14.00 (7.09)	ns	-60.20 (9.89) ***	140	20.32	33.74	0.36	<0.001
T. Vert.	ns	299.36 (63.84) ***	-105.71 (34.93) **	ns	-151.47 (24.44) ***	28	17.04	104.40	0.64	<0.001

† The relationship between Orthoptera range shift and change in range size was significantly curved (*quadratic term b* = 0.07, *std. error* = 0.02, *p* = 0.01).

Appendix 5.3 Elevation range (m) in 10 km grid squares Britain (derived this from the NextMap UK 5m DTM data: http://www2.getmapping.com/Products/NEXTMap).



Chapter 6: Distribution-based traits outperform life history traits in explaining variation in rates of range shift.

6.1 Abstract

There is widespread evidence that species have responded to climatic warming through poleward shifts in their distributions. However, not all species respond the same way to these climatic pressures, and this variation may lead to a breakdown in community structure through trophic and functional mismatch. Comparative trait-based studies can be used to determine traits that may predispose species to shift during times of environmental perturbation, and can therefore highlight species that lack the ability to track climatic niche shifts. Such comparative studies require detailed distribution, trait and phylogenetic information and therefore have mainly been limited to butterflies and birds. Here, we compare the explanatory power of traits that can be derived from species distribution patterns to traditional life history traits for explaining variation in plant and butterfly range shift. We find models based on traits derived from distribution data can out-perform traditional comparative models based on readily available life history traits. We believe this highlights the value of distribution-based traits for comparative studies, and in turn draws attention to the value of citizen science, particularly the data accumulated through public participation in biological recording, for addressing ecological research questions that were previously unanswerable.

6.2 Introduction

Poleward shifts in species distributions have been widely reported and are probably a response to climatic warming (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Chen *et al.*, 2011). These range shifts are predicted to continue based on future climate scenarios (Warren *et al.*, 2001; Thuiller *et al.*, 2005; Alsos *et al.*, 2012). The direction and intensity of species range shift is highly variable within, and between, taxonomic groups (Hill *et al.*, 2002; Thomas *et al.* 2004a; Hickling *et al.* 2005; Hickling *et al.*, 2006; Lenoir *et al.* 2008). This variation is a cause for conservation concern as it may result in a breakdown in ecological communities, through trophic and functional mismatch, and in turn may lead to ecosystem collapse (Edwards & Richardson 2004; Lenoir *et al.* 2008; Schweiger *et al.*, 2008; Lauzeral *et al.*, 2010; Thackeray *et al.*, 2010; Walther 2010; Schweiger *et al.*, 2012).

Comparative studies have shown that certain character traits can predispose species to shift during times of environmental change (Pöyry *et al.*, 2009; Angert *et al.*, 2011; Chessman, 2011; Mattila *et al.*, 2011; Grewe *et al.*, 2012). Determining traits that correlate with range shift enables the identification of species that lack the ability to track shifts in their climatic niche. Such species are likely to become threatened with extinction, if we assume they are lost from the now climatically unsuitable warmer edge of their range (Thomas *et al.*, 2004a; Perry *et al.*, 2005; Wilson *et al.*, 2005). Traits that affect the ability of species to disperse into newly climatically available habitat patches are important predictors of species range shift (Warren *et al.*, 2001; Pöyry *et al.*, 2009; Mattila *et al.*, 2011; Grewe *et al.*, 2012). For example, dispersal ability was used to explain variation in range shift in butterfly and bird species, with stronger dispersers showing greater range expansion (Pöyry *et al.*, 2009; Devictor *et al.*, 2012), while habitat breadth was an important predictor of butterfly range shift, with habitat generalists showing a greater capacity to shift than specialists (Warren *et al.*, 2001; Hill *et al.*, 2002; Pöyry *et al.*, 2009). Such trait-based comparative studies require detailed distribution, trait and phylogenetic data and consequently have mainly been restricted to birds and butterflies.

Increased public participation in biological recording has led to a vast increase in the collection of distribution data (Silvertown, 2009; Boakes *et al.*, 2010; Dickinson *et al.*, 2012; Miller-Rushing *et al.*, 2012), much of which can be accessed through national organisations such as the National Biodiversity Network (NBN - http://www.nbn.org.uk/) and international systems such as the Global Biodiversity Information Facility (GBIF - http://www.gbif.org/). This increased availability of distribution data has opened up new opportunities to examine distribution change in many previously poorly studied taxonomic groups; however, comparative studies are still limited by a lack of life history trait data. Distribution data can be used alongside widely available land use and climate data to derive species traits, such as climate indices and habitat breadth (Hirzel *et al.*, 2002; Hill *et al.*, 2004; Thuiller *et al.*, 2004; Devictor *et al.*, 2008). Using such traits enables comparative analyses to be carried out on many poorly studied taxonomic groups (see chapter 5). Here, we examine range shift in butterfly and plant species in Britain, and compare the explanatory power of traditional life history traits to traits that were derived from distribution data. We hypothesise that both life history and distribution-based traits will explain significant variation in species range shift, highlighting the value of distribution-based traits, and in turn the increased public participation in biological recording, for addressing ecological research questions that were previously unattainable. We predict that habitat generalists and species with good dispersal ability will show the greatest range shifts as they have an increased ability to successfully colonise newly climatically available habitat patches.

6.3 Methods

6.3.1 Distribution data and range shift

Gridded, 10 x 10 km scale, distribution data were extracted from the butterfly and vascular plant atlases of Britain. For each taxonomic group, data were split into two distinct time periods that utilize data collected for consecutive atlases, as follows: Butterflies early period = 1970 – 1982

(Heath *et al.*, 1984), late period = 1995 – 1999 (Asher *et al.*, 2001); plants early period = 1930 – 1969 (Perring & Walters, 1962), late period = 1987 – 1999 (Preston *et al.*, 2002b). For each species, we identified the northern range margin in each time period as the mean latitude of the ten most northerly occupied grid cells. We subsequently estimated change in range shift as the difference between the northern range margin in the early and later time period (Thomas & Lennon 1999; Hickling *et al.*, 2005; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Grewe *et al.*, 2012).

An increase in recorder effort between the two time periods was likely to be present in the data used in this study, and needed to be accounted for to ensure range shift was estimated accurately (Prendergast *et al.*, 1993; Telfer *et al.*, 2002; Hickling *et al.*, 2006; Tingley & Beissinger, 2009; Boakes *et al.*, 2010; Hill, 2012). We accounted for variation in recorder effort by excluding cells that were under recorded (Hickling *et al.*, 2006; Grewe *et al.*, 2012). Range shift was estimated from two subsets of the data. First, we excluded cells from the analysis if, in either time period, they had less than 10% of the total species list of the taxonomic group in question recorded; we term those remaining “well-recorded cells”. Second, the process was repeated but using 25% (those remaining are “heavily-recorded cells”), instead of 10% of the total species list (Hickling *et al.*, 2006). Data were additionally limited based on attributes of the species. Non-native species were excluded to ensure range margin shifts were not an artefact of overall range expansion of recent arrivals. Species with unreliable distribution data due to taxonomic uncertainty were excluded. We excluded species that occupied fewer than 20 cells across the time periods to reduce unreliable shift estimates based on very rare or poorly recorded species (Hickling *et al.,* 2006). Only species with a northern range margin well within Britain (at least 100 km below northern edge of mainland Scotland) in the first time period were included in the analysis, ensuring shift was not geographically limited by proximity to the coast. Finally, we removed plant species with an Ellenberg Moisture value greater than 9 (water plants), as targeted plant surveys of Scottish lochs in the second time period were likely to result in artificially increased northerly range shifts of aquatic plants (Preston & Croft 1997; Preston *et al.* 2002b). The final dataset included in the analysis consisted of 218 plant and 34 butterfly species.

6.3.2 Trait data

In this study, we examine both life history traits and traits that were derived from species distribution data. We ensured each trait tested a specific hypothesis that previous evidence have shown were likely to influence species response to environmental change. Using a refined set of traits also ensured there was equal opportunity for both life history and distribution based traits to explain variation in range shift. Distribution-based traits were: temperature index, moisture index, fractal dimension, marginality and range size. The two climate indices (temperature and moisture) were calculated for each species, using climate data that were taken from CRU ts2.1 (Mitchell & Jones, 2005) and CRU 61-90 climate (New *et al.,* 1999) datasets interpolated to the 10 km UK grid. The mean temperature of the warmest month (MTWA, ^{o}C) and the mean ratio of actual to potential evapotranspiration (APET, used as the moisture index) for each grid cell in Britain between 1969 and 1999 were extracted, with species climate indices calculated as the mean climate value across all grid cells that the species occupied in the early time period. We used the method of Wilson *et al.* (2004) to calculate the fractal dimension of the species distribution patterns. Fractal D was calculated as the slope of the relationship between the log of the area of occupancy at the 10 km and 100 km scale plotted against the log of the length grid cell at each scale (Wilson *et al.,* 2004). This measure is bounded between 0 and 2, with higher values of fractal D indicating a more aggregated distribution pattern which is thought to reflect range expansion, whereas small fractal D values represent fragmented distribution patterns that are characteristic of declining species (Wilson *et al.,* 2004). We use the species occupancy of the second time period to calculate fractal D as this technique estimates past distribution changes from current distribution patterns. The marginality of the species habitat requirement was estimated using ecological niche factor analysis (ENFA, Hirzel *et* *al.*, 2002). ENFA compares the species niche breadth in multivariate space to the niche breadth of the overall study region, with the difference forming the marginality score. The higher the marginality score, the more marginal the habitat requirement of the species relative to the study region. Habitat data, taken from the CEH land cover map 2007 (Morton *et al.*, 2011), were collapsed into 13 broad habitat land-use classes (for details see Appendix 6.1) and the proportional coverage of each class within each 10 km grid cell was identified. Marginality was calculated using these proportions and the distribution data from the later time period. Finally, for each species we identified total range size – a count of occupied grid cells in the early time period. Total range size may be considered as a surrogate of rarity, with rare species tending to have smaller total range size (Gaston, 2003).

Life history data for plants were primarily taken from PLANTATT (Hill *et al.*, 2004), where we extracted life cycle type (species classified as annual, biennial or perennial), plant height, and habitat breadth (scale of 1 – 4, 1 = single habitat specialists, 4 = habitat generalist, occurring in multiple habitat types). We obtained a binary measure of species dispersal ability from Ozinga *et al.*, (2009), in which species were split into those with no long distance dispersal adaptations (1) and those that have at least one long distance dispersal attribute (0). Butterfly life history traits were taken from Dapporto & Dennis (2013) and were: niche breadth, symbiosis with ants, wing span (mm), length of flight period. Niche breadth was included as a measure of habitat specialism, and was estimated by the range of ecological gradients occupied by each species' host plants, while symbiosis with ants was used as a measure of behavioural specialism, with species classified on a gradient from 1 (highly dependent on ants) to 4 (no dependence on ants).

6.3.3 Phylogenetic comparative analysis

We carry out phylogenetically informed comparative analyses to account for the evolutionary history relationships that inherently connect species. Comparative studies that treat species as independent data points run the risk of increasing type I error rates due to phylogenetic autocorrelation (Harvey, 1996). For all models, we use phylogenetic generalised least squares with estimated λ, using the *pgls* function in the R package *caper* (Orme *et al.*, 2012). Pagel's λ is a measure of phylogenetic signal shown by a variable, in this case, the residuals from the regression model, and is bounded between 0 and 1, with a λ value of 0 indicative of phylogenetic independence and a λ of 1 suggesting complete phylogenetic dependence (Pagel 1999; Freckleton *et al.* 2002). A benefit of estimating λ by maximum likelihood is that the problems associated with under-correcting ($\lambda = 0$) and over-correcting ($\lambda = 1$) for phylogenetic autocorrelation are reduced (Freckleton *et al.* 2002, Purvis 2008). We used dated, species level phylogenies in the analysis, '*Daphne*' (Durka & Michalski, 2012) for plants, and a new British butterfly phylogeny (Pearse *et al.,* unpublished), that was based on *cytochrome c oxidase subunit I* sequences and constrained using recently published lepidopteran phylogenies of Wahlberg *et al.* (2009) and Mutanen *et al.* (2010). We ran separate models for life history traits and distribution-based traits for each taxonomic group. Initially, we fitted a model containing all traits of interest, then simplified the model though the stepwise deletion of non-significant terms to determine the MAM. We tested for curved relationships by including the quadratic term of each continuous explanatory into the modelling process; curved relationships were retained if significant. All statistical analyses in this study were carried out using R version 2.14.2 (R Development Core Team, 2012).

6.4 Results

The results of models based on heavily and well recorded cell subsets were highly similar and we therefore only present results from the well recorded grid cells.

Mean shift in the northern range margin of the plant species included in this study was 1.1 km polewards over the two time periods; this shift value was not significantly different from 0 (p = 0.792, t = 0.264, df = 217, 95% CI = -7.1 to +9.3). However, a significant 26.3 km poleward shift over the two time periods was found for butterfly species (p = 0.004, t = 3.111, df = 33, 95% CI = +9.1 to +43.5).

Both life history traits and traits derived from distribution data significantly explained variation in butterfly range shift (Table 6.1). Length of flight period was positively related to range shift in the life history trait MAM, while a significant u-shaped relationship with fractal D was the sole significant variable in the distribution-based traits MAM. The MAM for explaining plant range shift using distribution-based traits consisted of a negative relationship with range size and positive relationship with fractal D. However, no significant relationship was found between life history traits and plant range shift. MAMs based on traits derived from distribution data had greater explanatory power than MAMs based on life history traits, for explaining variation in butterfly range shift (Table 6.1).

Table 6.1 The model and parameter coefficients for the MAMs of (a) distribution derived trait-based analysis of butterfly range shift, (b) life history trait-based analysis of butterfly range shift, (c) distribution derived trait-based analysis of plant range shift. For all models estimated λ was not significantly different from 0.

Variable	**slope**	**SE**	**t**	**p**
(a) *Butterfly DBT (df = 31, F = 5.2, SE = 88.1,* r^2 *= 0.20, p = 0.005)*				
Intercept	150.502	76.953	1.956	0.060
Fractal D	-308.067	143.319	-2.150	0.040
Fractal D^2	155.491	62.542	2.486	0.019
(b) *Butterfly LHT (df = 32, F =8.0 , SE = 89.7,* r^2 *= 0.18, p = 0.002)*				
Intercept	-79.923	38.382	-2.082	0.045
Flight Period	32.500	11.503	2.825	0.008
(c) *Plant DBT (df = 215, F = 3.5, SE = 5.0,* r^2 *= 0.02, p = 0.016)*				
Intercept	34.353	16.988	2.022	0.044
Range size (10 km grid cell occupancy)	-18.702	7.076	-2.643	0.009
Fractal D	60.119	25.846	2.326	0.021

6.5 Discussion

In this study, we compared the explanatory power of life history traits to that of traits based on distribution data for explaining range shift in comparative analyses, finding that traits derived from distribution data can out-perform life history traits. Life history traits explained 18% of the variation in butterfly range shift, but no significant relationships were found between life history traits and plant range shift. In contrast, traits derived from distribution data were significant predictors of butterfly and plant range shift, explaining 20% and 2% of the variation respectively. This result highlights the potential of using traits derived from distribution data as an alternative, or addition, to traditional life history traits in comparative studies of range change, and other ecological phenomena. A major benefit of using distribution-based traits is that it enables comparative studies to be carried out where life history trait data are lacking, and with the accumulation of species distribution data from citizen science projects (Silvertown, 2009; Dickinson *et al.*, 2012; Miller-Rushing *et al.*, 2012), there is ample opportunity to examine drivers of distribution change in many poorly studied taxonomic groups.

Flight period was the sole significant life history trait found in this study, and was positively correlated with butterfly range shift. Species with long flight periods have longer to disperse, and therefore are thought to have a greater capacity for dispersal (Dennis *et al.*, 2000). This positive correlation provides further evidence of the importance of good dispersal ability for species to efficiently track a shift in their climatic niche (Warren *et al.*, 2001; Pöyry *et al.*, 2009; Mattila *et al.*, 2011; Devictor *et al.*, 2012; Grewe *et al.*, 2012). Fractal D was the only significant distribution-based trait for explaining variation in butterfly range shift. The relationship was significantly curved, with species at the extremes of fractal D showing the greatest positive range shifts. Aggregated distribution patterns are thought to reflect species with expanding distributions, a trend that we find evidence for; however, the increased shift of species with the most fragmented distribution patterns contrasts this theory. This relationship appears to be driven by the loss of southern grid cells of rare species that have fragmented distribution patterns (such as, *Papilio machaon, Argynnis adippe* and *Melitaea athalia*). Dapporto & Dennis (2013) found that species at the extremes of the habitat specialism gradient were out-performing those of intermediate specialism scores, with extreme generalists utilising a wide variety of habitats, while extreme specialists monopolise the highly fragmented specialist habitats. This may potentially explain the U-shaped relationship between fractal D and range shift, as the species with the most fragmented distribution patterns are likely to be those that are specialised to a certain fragmented habitat types. Fractal D was positively related to plant range shift, providing further evidence that aggregated distribution patterns in plants are characteristic of range expansion. The plant range shift MAM also contained range size, which was negatively correlated with plant range shift. Previous research has shown inconsistent relationships between range shift and range size across a wide range of taxonomic groups (Angert *et al.*, 2011). Our result suggests that smaller ranged species have shown the greatest poleward range shifts.

Life history traits were non-significant as predictors of range shift in plants, a result that contrasts with previous research that found dispersal ability partly explained variation in range shift (Nathan *et al.*, 2011). Our binary measure of dispersal ability may have been too coarse to detect a relationship with range shift (Ozinga *et al.*, 2009). Improving the detail of our dispersal measure may increase sensitivity to the relationship between dispersal ability and range shift, and would be an ideal area for future work. In addition, it should be noted that species can adapt to environmental change through altitudinal shifts, behavioural changes and through phenotypic plasticity, all of which would be undetectable by the analyses in this study (Roy & Sparks, 2000; Hickling *et al.*, 2006; Phillimore *et al.*, 2010). Indeed, much of the previous research into the impact of climate change on plant distributions has focussed on altitudinal, rather than latitudinal range shifts (Kelly & Goulden, 2008; Lenoir *et al.*, 2008).

To summarise, we found models based on traits that were derived from distribution data can out-perform models based on life history data for explaining shift in butterflies and plants. We believe this highlights the value of distribution-based traits for comparative studies of species range change, and in turn draws attention to the value of citizen science, particularly the data accumulated through public participation in biological recording, for addressing ecological research questions that were previously unattainable.

6.6 Supplementary material

Appendix 6.1 A list showing the LCM 2007 broad land-use categories and the aggregate classes they were collapsed into for use in this study.

LCM 2007 Broad land-use class	**Aggregate land-use class**
Broadleaf woodland	Forest
Coniferous woodland	Forest
Arable	Arable
Improved Grassland	Improved Grassland
Rough grassland	Semi-natural areas
Neutral grassland	Semi-natural areas
Calcareous grassland	Calcareous grassland
Acid grassland	Semi-natural areas
Fen, marsh, swamp	Fen
Dwarf heathland	Heathland *
Bog	Montane habitat
Montane habitat	Montane habitat
Saltwater	Water
Freshwater	Water
Supra littoral rock	Coastal
Supra littoral sediment	Coastal
Littoral rock	Coastal
Littoral sediment	Coastal
Urban	Urban

* Heathland was split into two categories, upland heath and lowland heath, with the divide set at 300 m using a digital elevation model (above 300 m = upland heath, below 300 m = lowland heath).

Chapter 7: Land use change drives spatial variation in the trait characteristics of species that have gone locally extinct.

7.1 Abstract

There is widespread evidence of the impact of environmental change on biodiversity, with changes in species distributions frequently related to environmental perturbation. Species responses are highly variable, and this variation has been partly explained though comparative analysis of species traits. A limitation of the comparative approach is that the models do not directly test the impact of environmental change on species distribution patterns, and instead infer the potential drivers of change. We test the potential of comparative analyses from a spatial context, by conducting a spatial analysis of plant distribution change in Britain, examining the direct impact of environmental change on the spatial distribution of the trait characteristics of species that have gone locally extinct. Land use change appeared to be a greater driver of plant distribution change than climate change given the spatial and temporal scale of the analysis. We found agricultural intensification was key driver of plant distribution change in Britain, with declines in species specialised to nutrient poor conditions in regions that have shown marked increases in arable land cover. Our results provide direct spatial evidence that supports previous research into the drivers of plant range change, much of which has been inferred from comparative trait-based analyses.

7.2 Introduction

The impacts of environmental change on biodiversity are well documented, with threats such as habitat loss and climate change frequently related to changes in species distributions (Pimm & Raven, 2000; Warren *et al.*, 2001; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Jetz *et al.*, 2007; Polce *et al.*, 2010). Evidence suggests species turnover, range shifts, extinction and change in species richness have been driven by land use and climate change (Hill *et al.*, 1999a; Thomas & Lennon, 1999; Brooks *et al.*, 2002; Fahrig, 2003; Smart *et al.*, 2005; Thuiller *et al.*, 2005; Hickling *et al.*, 2006; Menéndez *et al.*, 2006; Menéndez *et al.*, 2007; Devictor *et al.*, 2008; José-María *et al.*, 2010). The combined impact of habitat destruction and climate change on biodiversity has been labelled a “deadly anthropogenic cocktail”, with habitat loss expected to exacerbate the negative impact of climate change (Travis, 2003; Newbold *et al.*, 2012).

The responses of species to environmental change are highly variable and this variation can be partly explained through comparative analyses of species traits (Pöyry *et al.*, 2009; Angert *et al.*, 2011; Botts *et al.*, 2012; Newbold *et al.*, 2012). Common examples of trait – distribution trend relationships include: habitat generalists out-performing specialists due to a greater ability to persist during times of environmental change (Fisher & Owens, 2004; Menéndez *et al.*, 2006; Botts *et al.*, 2012), and larger range shifts associated with species with greater dispersal ability that can track a shift in their climatic niche (Thomas *et al.*, 2001; Pöyry *et al.*, 2009; Grewe *et al.*, 2012). In Britain, comparative studies have aimed at explaining variation in plant distribution change. Such studies have highlighted agricultural intensification and nitrogen deposition as key drivers of plant distribution change, in particular driving widespread declines of species specialised to nutrient poor conditions (McCollin *et al.*, 2000; Preston *et al.*, 2002a; Robinson & Sutherland, 2002; Smart, 2003; Smart *et al.*, 2005; Braithwaite *et al.* 2006; Walker *et al.* 2009; also see chapter 3). Increased nutrient availability has enabled taller, more competitive, habitat generalist species to expand and out-compete many of the smaller habitat specialists that are adapted to low nutrient soils (Walker *et al.* 2009). This relationship has also been detected in comparative studies of plant extinction risk, with widespread competitive generalist species at lowest risk of regional extinction (Preston 2000; Walker & Preston, 2006). Additionally, increased urbanization has been linked to declines in rare plant species (Thompson & Jones, 1999). Fewer studies have examined the impact of climatic change on plant distribution change in Britain. However, species distribution models have been used to predict future distributions of plants in Britain based on future climate scenarios, finding that sensitivity to climate change is linked to current habitat associations, with species of montane heathland communities losing the highest proportion of climatically suitable habitat (Berry *et al.*, 2002).

A limitation of the comparative approach is that the models do not directly test the impact of environmental change on species distribution patterns, and instead are used to infer the potential impacts. Here we conduct a spatial analysis of plant distribution change in Britain, examining the direct impact of environmental change on the spatial distribution of the trait characteristics of species that have gone locally extinct. Additionally, we compare the relative importance of land use and climate change in driving change in plant distribution patterns. To test the potential of comparative analyses from a spatial context, we test three specific hypotheses of plant distribution change as identified though comparative trait based studies. 1) We predict that regions characterised by an increase in arable land will show marked losses of plants that are weak competitors specialised to nutrient poor conditions. 2) We predict that regions that have gained urban cover are likely to have increased in competitive generalist species that are able to adapt to the anthropogenic environments. 3) We hypothesise that areas of Britain that have become warmer and drier will be characterised by a loss of species that prefer moist conditions.

7.3 Methods

7.3.1 Distribution data

Gridded 10 x 10 km distribution data of 1229 species of plants in Britain were taken from two separate time periods, 1930 – 1969 and 1987 – 1999. These data were collected primarily for the two British and Irish plant atlases (Perring & Walters, 1962; Preston *et al.*, 2002b). We examined change in species distribution patterns between the two time periods and therefore needed to ensure the two datasets were comparable. First, only native and archaeophyte (established pre-1500) species were included in the analyses, ensuring all species have had sufficient time to reach a stable distribution equilibrium with the landscape (i.e. the rapid range expansion associated with recent invasive species was removed). We excluded species with an Ellenberg moisture preference score greater than nine (aquatic species) as Scottish lochs were targeted for water plant surveys in the second time period, and the resulting spatiotemporal variation in recorder effort would have caused bias in our distribution change estimates (Preston & Croft 1997; Preston *et al.* 2002b). We further reduced species in our study by excluding those that had unreliable distribution data in either time period due to taxonomic uncertainty. In addition to limiting the data by species, we also limited by grid cell, removing those cells that were under recorded (Hickling *et al.*, 2006; Grewe *et al.*, 2012). We ran the analysis on two subsets of the data, the first subset comprising cells that contained at least 10% of all recorded species (well recorded), while second comprised cells that contained a minimum of 25% of the recorded species (heavily recorded).

7.3.2 Trait data

Data on seven traits, including plant height (cm), habitat breadth (scale of 1 – 4, 1 = single habitat specialists, 4 = habitat generalists occurring in 4 or more habitat types), lifecycle type (perennial or annual) and Ellenberg preference scores for light (L), substrate moisture (F), substrate pH (R) and substrate nutrient preference (N), were obtained from PLANTATT (Hill *et al.* 2004). Ellenberg scores represent the species' preferred niche along ecological gradients and are derived from subjective expert opinion alongside objective calculations (see Hill *et al.* 1999b). Traits included in the study are listed in Table 7.1 alongside a brief explanation. The traits included in the analysis were chosen as evidence has shown them to be important in explaining variation in species response to environmental change (Liem *et al.,* 1985; Preston, 2000; Godefroid, 2001; Haines-Young *et al.,* 2003; Braithwaite *et al.,* 2006; Walker & Preston, 2006; Van Landuyt *et al.,* 2008; Hulme, 2009, also see chapter 3).

Table 7.1 The seven analysed traits listed alongside a brief explanation taken from PLANTATT (Hill *et al.*, 2004).

Attribute name	**Measure**
Plant height	Plant height (cm)
Ellenberg L	Ellenberg value for light preference (1 = deep shade, 9 = full light)
Ellenberg N	Ellenberg values for nitrogen preference (soil fertility) (1 = extremely infertile, 9 = extremely rich in nitrogen
Ellenberg R	Ellenberg values for pH (1 = extreme acid soils, 9 = high pH soils)
Ellenberg F	Ellenberg values for moisture preference (1 = dry, 9 = wet-site indicator)
Habitat Breadth	A count of the number of habitat categories the species occupies (based on the 23 categories in PLANTATT)
Life cycle type	Binary variable with species categorised as either annual (n = 270) or perennial (n = 852). Biennial species (n = 65) were classed as perennials for this analysis.

7.3.3 Climate and land cover data

Climate data were extracted from the Met Office UK Climate Projections gridded dataset (UKCP09). For each 10 km grid cell in Britain we calculated the mean July temperature and the mean annual precipitation for both time periods (1930 – 1969 and 1987 – 1999). The original data were available at a 5 km grid resolution, which we averaged up to the 10 km grid scale to match our species distribution data. We calculated change in temperature and precipitation for each cell as the difference in the mean climate score between the first and second time period.

The land cover within each grid cell for the early time period was identified from scanned images of the First Land Utilization Survey (FLUS) that was carried out between 1931 – 1941 (Baily, 2007). Five broad terrestrial land classes (forest and woodland; meadow and permanent grassland; arable land; heathland and moorland; urban) were mapped onto Ordnance Survey maps at the one inch to the mile scale. Each FLUS map had to be individually treated using image editing software to account for variation in colour tonality and underlying map detail prior to digitization. The maps were digitized and reassembled into a single raster map of Britain using ArcGIS 9.3. Finally, a 10 km grid in the British National Grid (BNG) projection was overlaid on top of the digitalized FLUS map and the number of pixels of each land class was summed for each cell. The proportional cover of each land class in each cell was calculated from the summed pixel counts. The CORINE land cover map 2000 (EEA, 2000) was used to measure the proportional cover of each land use class in each cell for the later time period. The 100 m ground resolution CORINE data has 45 separate land classes which were reclassified to best match the five classes of the FLUS map (Appendix 7.1). As with the FLUS map data, a 10 x 10 km grid (BNG projection) was overlaid on top of the CORINE data and the proportion of each land use class extracted for each 10 km grid square. Land use change was calculated as the difference in the proportional cover of each land use class between the CORINE and FLUS maps.

7.3.4 Analysis

For each 10 km grid square, the species recorded as present in the early time period were split into two groups, those that were absent from the later time period and those that persisted. For each trait we calculated the difference in the mean trait score of the lost species compared to those that persisted (subsequently referred to as trait difference). These trait differences indicate the type of species lost based on their trait characteristics given the original trait composition of the cell. The seven trait differences were analysed separately as response variables throughout the analyses. We carried out multiple regression for each response variable with change in land cover and climate included as explanatory variables. We checked for curvature in all relationships by including the quadratic term of each explanatory variable in the modelling process, with significant quadratic terms retained in the final models. All possible models were fitted and the best model selected using AIC. Spatial autocorrelation can lead to bias in parameter estimates in standard modelling approaches and can increase the type I error rate (the wrongful rejection of the null hypothesis) due to the non-independence of data points. Using Moran's I correlograms we found evidence of spatial autocorrelation in the residuals of all models (Dormann *et al.*, 2007). We accounted for this spatial autocorrelation using generalized least-squares (GLS) modelling with exponential spatial covariance structure fitted using the x and y cell centroids as spatial variables (Dormann *et al.*, 2007). Gaussian or spherical spatial correlation structure did not qualitatively change the results of the models (results not shown).

7.4 Results

Results from MAM for explaining spatial variation in soil pH preference of the lost species are not shown as we found a strong positive correlation (r = 0.79) between the soil nutrient preference trait difference and soil pH preference trait difference scores and therefore model results were highly similar, with the MAMs containing the same significant terms. The MAMs identified through analysis of the heavily recorded grid cells showed no difference in the direction or significance of the model parameters in comparison to the MAMS from the well recorded grid cells, we therefore only present results from models based on well recorded grid cells. Finally, we found results between the linear models and the spatial GLS model were highly similar and we therefore only present results from the linear models (spatial GLS model results are shown in Appendix 7.2).

Change in both land use and climate were important for explaining spatial variation in the trait characteristics of lost species (Table 7.2), with the key trait – trend relationships (partial r^2 > 0.02) plotted in Figure 7.1. The MAM for explaining spatial variation in the soil nutrient preference of lost species had the greatest explanatory power of all MAMs, at 36%, and consisted of four explanatory variables. Increased heathland, arable land cover and temperature resulted in a loss of species that prefer nutrient poor conditions. These relationships explained the majority of the spatial variation in the soil nutrient preference of locally extinct species. As with the soil nutrient preference model, spatial variation in the height of lost species was negatively correlated with change in heathland, arable land and temperature in the MAM which explained 14% of the variation. An increased in forest and grassland cover was associated with a loss of species that prefer dry conditions, in a model that explained approximately 11% of the spatial variation in soil moisture preference of lost species. The MAMs for the final three traits, Ellenberg L, habitat breadth and the proportion of perennials, had very low explanatory power, 4%, 0.7% and 0.1% respectively (Table 7.3). The strongest relationship (greatest partial r^2) of these remaining models was a positive correlation between the light preference of lost species and temperature change (Table 7.2), suggesting that an increase in temperature results in a loss of species that prefer open, lighter habitats.

Key trends in land cover change in Britain over the last ~70 years appear to be the conversion of grassland to arable land (r = -0.86) in south east of Britain, and the conversion of heathland to grassland (r = -0.73) in the west of Britain (Figure 7.2). Southern Britain appears to have undergone the greatest amount of climatic warming, while north western Britain has experienced the greatest increase in precipitation. The spatial distribution of the trait characteristics of the lost species highlight the level of similarity between the patterns of soil nutrient preference and soil pH preference of lost species, both showing losses of species with low Ellenberg scores in the south east region of Britain (Figure 7.3). Other notable patterns include the apparent loss of shorter species that prefer moist conditions in south east Britain.

Table 7.2 Parameter coefficients taken from the linear regression minimum adequate models explaining variation in the difference in trait score of lost species for each trait. The regression slope is shown alongside the standard error of the slope (in brackets). Significance level is indicated by the number of asterisk (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Variable	**Δ Forest**	**Δ Grassland**	**Δ Heathland**	**Δ Arable**	**Δ Urban**	**Δ Temperature**	**Δ Precipitation**
Ellenberg L	non-sig	-0.11 (0.02) ***	non-sig	non-sig	-0.47 (0.09) ***	0.22 (0.04) ***	non-sig
Ellenberg F	-0.60 (0.10) ***	-0.41 (0.03) ***	non-sig	non-sig	non-sig	non-sig	non-sig
Ellenberg N	non-sig	non-sig	-1.06 (0.06) ***	-0.69 (0.06) ***	non-sig	-0.66 (0.07) ***	0.01 (0.001) ***
Habitat breadth	non-sig	non-sig	non-sig	-0.02 (0.01)	non-sig	non-sig	non-sig
Height (cm)	non-sig	non-sig	-0.27 (0.03) ***	-0.16 (0.02) ***	non-sig	-0.20 (0.03) ***	non-sig
Prop. Perennials	non-sig	non-sig	non-sig	non-sig	0.13 (0.03) ***	non-sig	non-sig

Table 7.3 The overall model coefficients for the minimum adequate model for each trait.

Model	**DF**	**F**	**Std. error**	**r^2**	**p**
Ellenberg L	2536	38.35	0.317	0.042	<0.001
Ellenberg F	2537	160.4	0.455	0.112	<0.001
Ellenberg N	2535	356.6	0.568	0.359	<0.001
Habitat breadth	2538	3.175	0.151	0.001	0.07
Height (cm)	2536	132.8	0.247	0.135	<0.001
Prop. Perennials	2538	19.34	0.110	0.007	<0.001

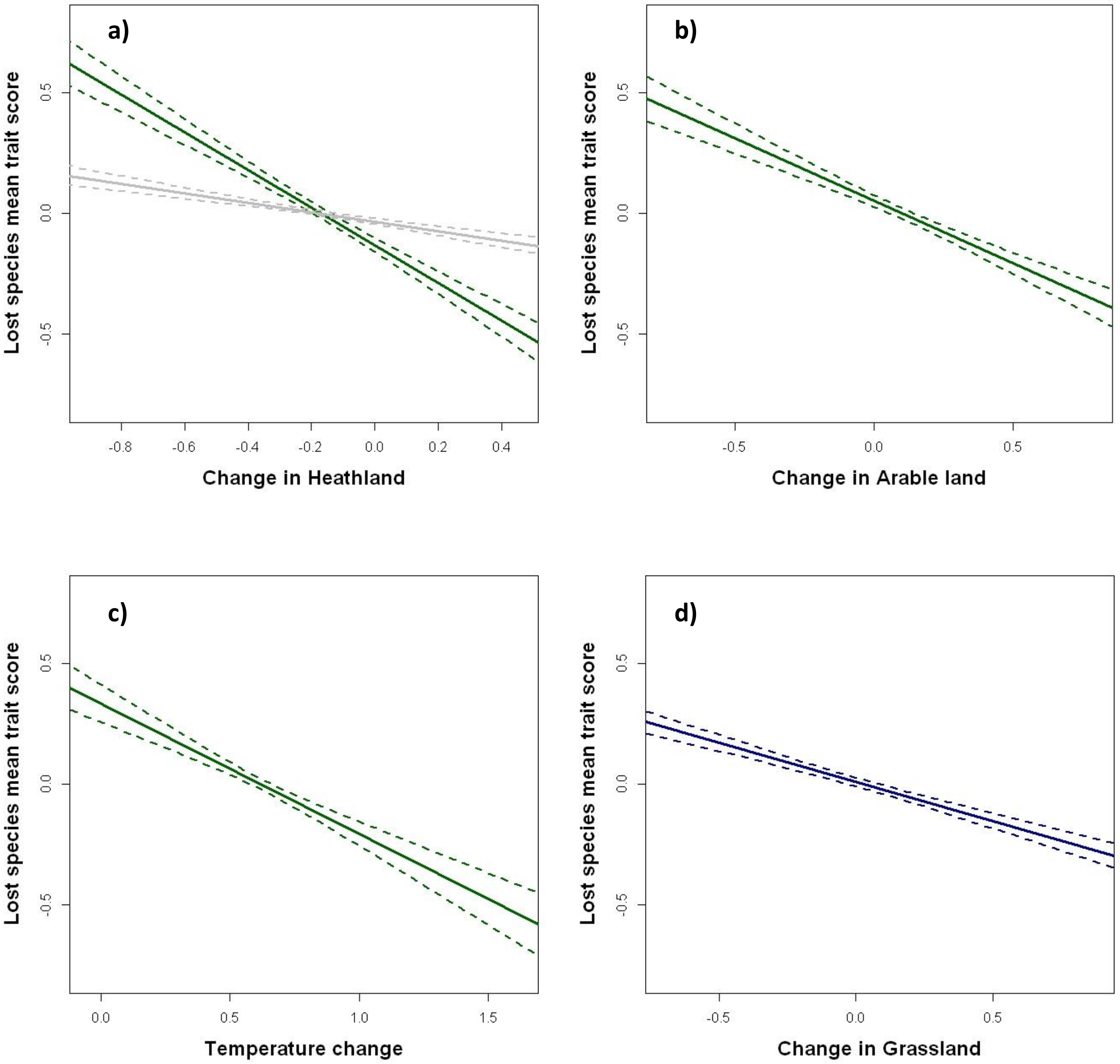


Figure 7.1 Graphs showing the relationship between change in a) heathland, b) arable land, c) mean temperature, d) grassland and the trait characteristics of species that have gone locally extinct. Green lines represent Ellenberg N (soil nutrient preference), the grey line represents log plant height and the blue line represents Ellenberg F (soil moisture preference). To ensure only the key trends are presented, we plot relationships with a partial r^2 greater than 0.2. For all plots, residuals were taken from the trait MAM (excluding the environmental variable of interest) and used as the response to isolate and illustrate the correlation between trait difference and land use / climate change.

Figure 7.2 Hectad maps of Britain showing the change in land cover classes between FLUS and CORINE and showing climatic change between 1930 – 1969 and 1987 – 1999.

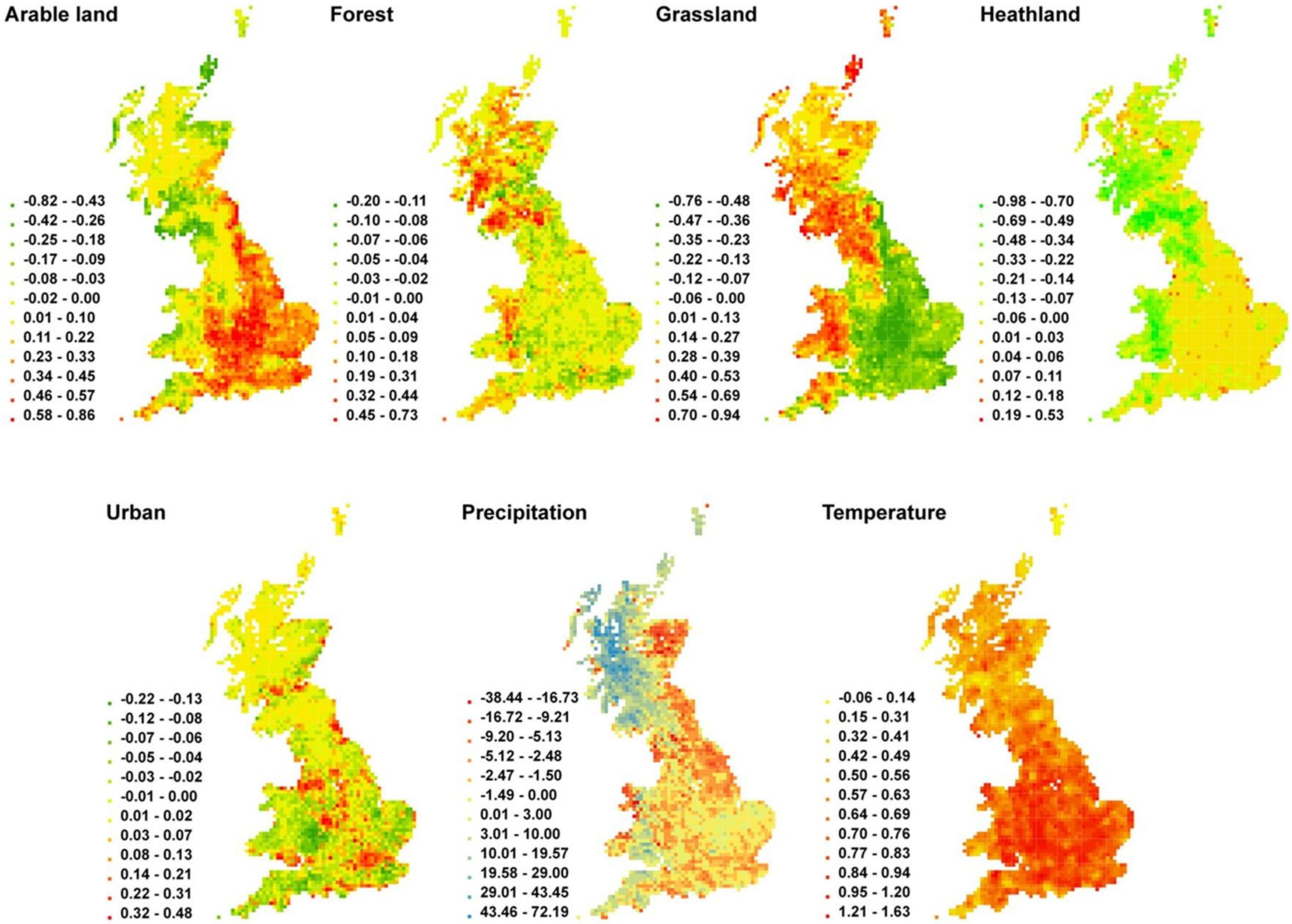
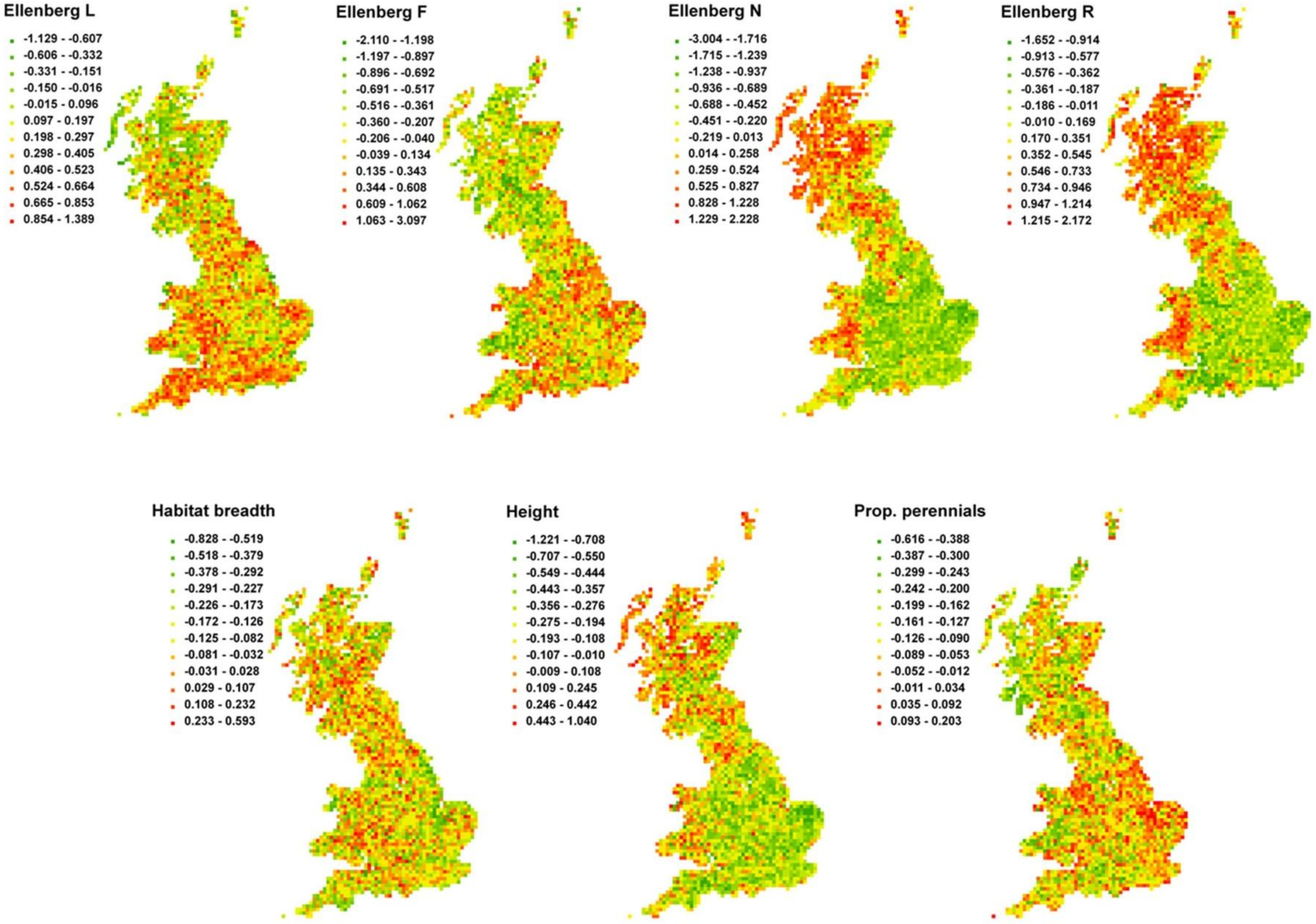


Figure 7.3 Hectad maps of Britain showing, for each trait, the difference in the mean trait value of species lost to the mean trait value of species that persist between 1930 – 1969 and 1987 – 1999.



7.5 Discussion

In this study, we conducted a spatial analysis of plant distribution change, testing the impact of both land use and climate change on a measure of plant biodiversity in Britain. We found widespread change in the landscape and climatic conditions of Britain over the past ~70 years, change which was reflected in the spatial distribution of the trait characteristics of lost species. Arable land cover expanded in south east of Britain where it appears to have replaced grassland, a trend also found by Haines-Young *et al.* (2003). Another key trend in land use appeared to be the conversion of heathland to grassland in western Britain, a relationship not found by Haines-Young *et al.*, (2003) who instead found the conversion of grassland to arable land was the main land use trend in the southwest England and Wales (Haines-Young *et al.* 2003). This difference is probably due to the different time scales of the two studies, with our study comparing land use change over a substantially longer time period than that of Haines-Young *et al.* (2003).

The MAM for explaining spatial variation in the soil nutrient preference of lost species showed the greatest explanatory power of all MAMs in this study, explaining 36% of the spatial variation. A key trend in this MAM was the negative relationship between the soil nutrient preference of lost species and change in arable land, suggesting that an increase in arable land cover resulted in a loss of species characterised by a preference for nutrient poor soils. This result provides spatial evidence of the negative impact of agricultural intensification on nutrient poor habitat specialists, a result that supports the inferences of comparative trait-based studies that suggest increased nutrient availability associated with arable land cover has driven declines in nutrient poor soil specialists (McCollin *et al.*, 2000; Preston *et al.*, 2002a; Robinson & Sutherland, 2002; Smart *et al.*, 2005; Braithwaite *et al.* 2006; Walker *et al.* 2009; also see chapter 3). Southern Britain has experienced a greater level of climatic warming than the north (Figure 7.2); we believe that the negative correlation between soil nutrient preference of lost species and temperature change is likely to be an artefact of increased land cover change in southern Britain (Haines-Young *et al.*, 2003), in particular the increase in arable land (Figure 7.2). Temporal change in the geographic coverage of heathland was characterised by declines in western Britain, while only a very few cells had increased heathland cover. Regions with little or no change in heathland appear to be the south east of Britain, which are also characterised by large increases of arable land. We believe that the loss of species specialised to nutrient poor habitats in the south east may be driving the negative relationship between heathland and soil nutrient preference of the lost species, again an artefact of agricultural intensification. Spatial variation in the soil nutrient preference of lost species was strongly positively correlated with spatial variation in soil pH preference, a result that suggests that regions losing specialists of nitrogen poor soils are also losing species that prefer acidic soils. Again, this reflects the dramatic loss and decline in quality of nutrient poor acidic habitats, particularly in southern England where it has been converted for agriculture (Walker & Preston, 2006; Hulme et al., 2009).

The impact of agricultural intensification was highlighted by the negative relationship between the mean height of lost species and change in arable land cover, with smaller species lost when the proportion of arable land within a cell is increased. Smaller species tend to be competitively weaker species that thrive in environments where larger, more competitive species cannot persist, our height – arable land cover result provides support to comparative studies that have shown competitive ability was positively related to species range change, and that the increased nutrient availability from agricultural intensification has driven declines in weaker species that excel in nutrient poor conditions (Preston, 2000; Braithwaite *et al.,* 2006; Walker & Preston, 2006; Walker *et al.,* 2009).

The negative relationship between change in grassland and change in arable land appears to be strongly influenced by the conversion of grassland to arable in the south east. We believe this relationship explains the negative correlation found between soil moisture preference of the lost species and change in grassland. Agricultural intensification has been linked with drainage of wetlands in Britain and the drainage ditches of arable land have been shown to be species poor, factors that will result in a loss of species that prefer wetter conditions (Rich & Woodruff, 1996; Mountford & Arnold, 2006). These artefacts highlight the complexity of spatial analyses that involve multiple intercorrelated environmental change variables, and draw attention the difficulty in isolating the impact of a change in a particular environmental variable on species distribution change.

On average, land cover change appeared to be a greater driver of plant distribution change than climate change, a result that we would expect given the spatial and temporal scale of this study. The impacts of climate variables on species distribution patterns tend to be best detected at coarse scales, while the ability to detect the impact of land use change improves at finer scales (Hartley & Kunin, 2003). This relationship reflects the scale at which these drivers of species distribution patterns operate (Rahbek, 2005). Additionally, over the relatively short time period of this study it appears Britain has undergone more dramatic changes in land use compared to climate (Figure 7.2).

A limitation of the FLUS map data is that grassland was measured as a single category, and therefore improved grassland and natural grassland share a category, despite being very different habitats for plant biodiversity. There has been widespread conversion of acid grassland to improved grassland in Britain, with the increase in the nutrient enriched soils of improved grassland associated with declines of species specialised to nutrient poor conditions (Haines-Young *et al.*, 2003; Walker *et al.,* 2009). Our land use change metrics are unable to detect this evidently important change in land use. A possible solution to this problem would be to overlay a geology/soil pH layer onto the FLUS map and classify grassland regions that intersect with acid soils as acid grassland, assuming these areas were unimproved in the early time period.

To summarise, we found spatial evidence of the impact of agricultural intensification on plant biodiversity in Britain, in particular the decline in species specialised to nutrient poor conditions in regions that have shown marked increases in arable land cover. Our results provide direct spatial evidence that supports previous research into the drivers of plant range change, much of which has been inferred from trait-based analyses (see chapter 3). Land use change appears to be a greater driver of species distribution change than climate change given the spatial and temporal scale of the analysis.

7.6 Supplementary material

Appendix 7.1 The reclassification of the 45 CORINE land classes into the six terrestrial classes that match the FLUS maps.

CORINE land cover class	Corresponding FLUS class
Agro-forestry areas	Forest
Broad-leaved forest	Forest
Coniferous forest	Forest
Mixed forest	Forest
Natural grasslands	Grassland
Pastures	Grassland
Non-irrigated arable land	Arable land
Permanently irrigated land	Arable land
Rice fields	Arable land
Annual crops associated with permanent crops	Arable land
Complex cultivation patterns	Arable land
Land principally occupied by agriculture	Arable land
Moors and heathland	Heathland
Sclerophyllous vegetation	Heathland
Transitional woodland-shrub	Heathland
Bare rocks	Heathland
Sparsely vegetated areas	Heathland
Burnt areas	Heathland
Inland marshes	Heathland
Peat bogs	Heathland
Salt marshes	Heathland
Continuous urban fabric	Urban
Discontinuous urban fabric	Urban
Industrial or commercial units	Urban
Road and rail networks and associated land	Urban
Port areas	Urban
Airports	Urban
Mineral extraction sites	Urban
Dump sites	Urban
Construction sites	Urban
Green urban areas	Urban
Sport and leisure facilities	Urban
Vineyards	Urban
Fruit trees and berry plantations	Urban
Olive groves	Urban
Beaches, dunes, sands	Sea and inland waters
Glaciers and perpetual snow	Sea and inland waters
Salines	Sea and inland waters
Intertidal flats	Sea and inland waters
Water courses	Sea and inland waters
Water bodies	Sea and inland waters
Coastal lagoons	Sea and inland waters
Estuaries	Sea and inland waters
Sea and ocean	Sea and inland waters

Appendix 7.2 Parameter coefficients taken from the GLS minimum adequate models explaining variation in the difference in trait score of lost species for each trait. The regression slope is shown alongside the standard error of the slope (in brackets). Significance level is indicated by the number of asterisk (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Variable	**Forest**	**Grassland**	**Heathland**	**Arable**	**Urban**	**Temperature**	**Precipitation**
Ellenberg L	non-sig	-0.14 (0.03) ***	non-sig	non-sig	-0.42 (0.10) ***	0.15 (0.05) ***	non-sig
Ellenberg F	-0.48 (0.12) ***	-0.39 (0.04) ***	non-sig	non-sig	non-sig	non-sig	non-sig
Ellenberg N	non-sig	non-sig	-0.89 (0.09) ***	-0.51 (0.08) ***	non-sig	-0.54 (0.10) ***	4.2x10-^{3} (1.5x10^{-3}) **
Habitat breadth	non-sig	non-sig	non-sig	-0.02 (0.02)	non-sig	non-sig	non-sig
Log Height (cm)	non-sig	non-sig	-0.23 (0.04) ***	-0.13 (0.03) ***	non-sig	-0.20 (0.04) ***	non-sig
Prop. Perennials	non-sig	non-sig	non-sig	non-sig	0.09 (0.03) **	non-sig	non-sig

Chapter 8: Conclusion

In this thesis, I examined the impact of environmental change across many taxonomic groups in Britain using data that was collected primarily by volunteer recorders. I found widespread variation in species response to environmental pressures and show the value of using species trait characteristics for understanding this variation.

The first chapter outlines the evidence surrounding the impacts of environmental change on species distribution patterns. I discuss numerous studies which show variation in species response to environmental perturbation, with particular reference to those that have used trait-based comparative analyses to explain such variation and shed light on the main drivers of change.

Estimating species distribution change from atlas data forms a core aspect of the research in this thesis, however, the accuracy of range change estimates can be inhibited by many problems and constraints associated with such data. In chapter two, I review the use of atlas data for trend analysis, discussing the main problems encountered and the methods used to account for these data limitations while estimating distribution change. Common problems that inhibit accurate range change estimation include variation in recorder behaviour, change in species detectability, and spatial and temporal variation in recorder effort. Suggested remedies can be classified into three broad categories: limiting the data, benchmarking and relative change measures, with the most appropriate remedy relying on the quality of input data. Metadata play a crucial role in the understanding of data limitations and can ultimately help determine the most appropriate method for estimating change.

As a result of this review, in chapter three I use a relative change measure to estimate the change in range size of the vascular plant species in Britain over the last century. Previous comparative studies of plant distribution change in Britain have been geographically limited and, or have not accounted for phylogeny (Preston, 2000; Preston *et al.*, 2002a; Braithwaite *et al.*, 2006; Walker *et al.*, 2009), and therefore run the risk of increased type I error rates (Felsenstein, 1985; Harvey & Pagel, 1991; Purvis, 2008). In chapter three, I carried out a phylogenetically informed trait-based analysis of range change using some of the best plant distribution and trait data available in Europe, using a recently published, dated, species level plant phylogeny. I found that competitive habitat generalists out-performed habitat specialists, and attribute this result to the greater ability of generalists to adapt to environmental perturbation, and to the negative impact of agricultural intensification, in particular the loss of open, dry habitats characterised by nutrient poor soils.

A common goal of trait-based studies is to directly assist conservation practice, but they rarely meet this target and instead act as ‘calls to action’ highlighting biodiversity decline (Cardillo & Meijaard, 2011). One reason for this is that, although such studies explain biodiversity responses within their own datasets, they seldom test the predictive ability of their models by, for instance, assessing transferability of the results to new regions (Fisher & Owens, 2004; Pocock, 2010). In chapter four, I tested the ability of trait-based models to predict plant distribution change across seven geographic regions (Flanders and six regions in Britain) that varied in terms of land-cover and species composition. I discovered that transferability between regions was significantly positively related to land-cover similarity and not species compositional similarity, suggesting that trait-based studies maybe used to predict broad scale changes in new regions providing they share similar land cover characteristics.

In chapter five, I focussed on shifts in species range margins as opposed to overall change in range size. Poleward shifts in species distributions have been widely reported and are likely due to the shift in species’ climatic niches as a result of climate change (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Pöyry *et al.*, 2009; Chen *et al.*, 2011). Evidence suggests that certain character traits, such as good dispersal ability, allow species to track their climatic niche; species that lack this ability may be of conservation concern as they are lost from the now climatically unsuitable warmer range edge (Thomas *et al.*, 2004a; Perry *et al.*, 2005; Wilson *et al.*, 2005). Previous comparative studies of species range shift have primarily been restricted to birds and butterflies due to a lack of data for other taxonomic groups (Devictor *et al.*, 2008; La Sorte & Thompson III, 2007; Pöyry *et al.*, 2009; Mattila *et al.*, 2011). I tested the ability of traits that were derived from distribution data, alongside widely available land use and climate datasets, to explain variation in range shift across ten broad taxonomic groups in Britain. I discovered that distribution-based traits explain significant variation in species range shift, with a key result being a negative relationship between range shift and the marginality of the species habitat requirement. This result can be linked to the importance of habitat availability for range shift, with species' ability to track their climatic niche reliant on successful dispersal into the newly climatically available habitat patches.

Chapter six follows on closely by testing the difference in explanatory power of traits derived from distribution data to traditional life history traits for explaining variation in butterfly and plant range shifts. I discovered that models based on traits derived from distribution data can out-perform traditional comparative models based on life history traits. This highlights the value of distribution-based traits for comparative studies and in turn draws attention to the value of citizen science, particularly the data accumulated through public participation in biological recording for addressing ecological research questions that were previously unanswerable.

A limitation of the comparative trait-based approach is that the models do not directly test the impact of environmental change on species distribution patterns, but instead are used to infer potential impacts. In my final chapter, I addressed this limitation by conducting a spatial analysis of plant distribution change in Britain, examining the direct impact of land use and climate change on the spatial distribution of traits. A key discovery was the loss of species characterized by a preference for nitrogen poor soils in regions that had an increase in arable land cover. This finding supports the results from the trait-based analysis of plant range change in chapter three, highlighting the negative impact of agricultural intensification on nutrient poor habitat specialists, and demonstrates that trait-based analyses can be used to successfully infer drivers of species distribution change.

8.1 Limitations & Future Directions

To meet the assumptions of the statistical analysis techniques and the methods used to estimate distribution change, data were excluded from every study carried out in this thesis. As discussed in chapter two, limiting the data does not make full use of the available dataset, excluding potentially useful data, and the effort with which it was collected. A fruitful area for future research would be to quantitatively assess the different techniques used to estimate distribution change from atlas data while accounting for various data limitations. Such an assessment could simulate species distributions with increasing severity of the problems associated with atlas data, and then statistically test the accuracy of range change estimates of each technique. This study would build on my review in chapter two and would enable more robust method recommendations based on the quality of input data. This is an important area of research, given the increase in citizen science and the resulting rapid accumulation of species distribution data, as the ability to accurately estimate distribution change from this data would open up ample opportunity to address research question on many previously poorly studied taxonomic groups. Another negative aspect of limiting the data is that when limiting based on certain aspects of a grid cell (as was done in chapters 5 to 7), the final dataset used in the analysis can become restricted to just the small heavily-recorded regions. In Britain, this can often lead to trend estimates based purely on the south of England. During my analyses, I carefully chose intermediate levels of data restrictions to ensure my trend estimates were accurate while also retaining a broad study region.

In chapter two, I use a relative change index technique to measure range change while accounting for variation in recorder effort. I note that a relative change index measure may not enable equal opportunity to detect trait relationships that have resulted from an environmental change process that is acting equally across all species. For example, climate change may be considered an environmental process with widespread impacts. However, many studies have shown widespread variation in species responses to climate change, suggesting the relative change measures should still be able to detect the impact of climate change.

In chapter four, I found low r^2 values associated with my regional trait-based models of plant distribution change. Despite this low explanatory power I still discovered a significant relationship between transferability and land-use similarity. I believe that by reducing the noise in both the estimates of distribution change and species trait measurements, the predictive model r^2 values would improve, and consequently provide more compelling evidence that trait-based models can be used to predict change in new regions given similar land-use characteristics.

Chapters five and six examine variation in species range shift using trait-based comparative analyses. Although poleward range shifts are frequently reported in the literature as an impact of climate change on biodiversity, changes in phenology and behaviour, elevational shifts and phenotypic plasticity are also widely reported (Roy & Sparks, 2000; Hickling *et al.*, 2006; Phillimore *et al.*, 2010). An interesting next step would investigate whether species that show responses to environmental changes through one of those other mechanisms also exhibit shifts in their range, i.e. is the ability to adapt to environmental change consistent across all mechanisms of adaptation? Or are these other mechanisms associated with a different set of core traits?

8.2 Concluding Remarks

In this thesis, I discovered widespread variation in species response to environmental pressures and highlight the value of using species trait characteristics for understanding this variation. I examined environmental drivers of plant decline, and discovered land use change has had a greater impact on recent plant declines in Britain than climate change. I found cross-region transferability of trait-based models of range change was related to land cover similarity, and discovered that traits derived from distribution data were significant predictors of range shift across many taxonomic groups, out-performing traditional life history traits.

With the increase in public participation in biological recording and the associated increased availability of large scale distribution datasets, the future is bright for research into species distribution change. However, with the projected increase in climate and land use change, the future is far from bright for biodiversity in Britain.

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