The responses of British butterflies to four decades of climate change

Thesis submitted by

Louise Mair

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University of York
Biology Department

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Abstract

Species are responding to climate change by shifting their distributions polewards and/or uphill. However, the rates at which distributions are changing vary greatly among species. An understanding of how species' distributions are changing, and what drives the rate of distribution change, is necessary in order to identify which conservation strategies have the potential to facilitate range shifts and to prevent population and species losses.

I studied the responses of southerly-distributed butterflies in Britain to four decades of climate change. I found that not only did the rates of species' distribution area, northern range margin and abundance changes vary amongst species, but that rates of change also varied within species over time. Some of the variation in distribution change was explained by species' abundance trends; species required stable or increasing abundances in order to expand their distribution areas. Once species were expanding their range, however, the rate of expansion was affected by the amount of suitable habitat available in the landscape. The application of a simulation model, SPEED, to project species' distribution change supported these conclusions; all species modelled were capable of distribution expansion given sufficiently high population growth rate. Moreover, increased habitat availability allowed greater rates of distribution expansion.

The observed trend towards more negative abundance changes in recent years suggests that habitat quality has deteriorated. Results from this thesis showing that stable or increasing abundance trends are a prerequisite for distribution expansion imply that conservation strategies should focus on improving species' abundance trends through increasing habitat quality. Results also support the notion that conservation efforts aiming to protect and restore as much natural habitat as possible, in order to facilitate species' distribution expansion under climate change, are likely to be effective.

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This thesis involved collaboration with Jane Hill (JKH), Chris Thomas (CDT), Barbara Anderson (BJA), Calvin Dytham (CD), Richard Fox (RF), Marc Botham (MB), Tom Brereton (TB) and David Roy (DBR).

Chapter 2

This work was supervised by JHK and CDT. RF and MB provided data and comments on the manuscript, BJA formatted data. I carried out data analysis and wrote the manuscript. This work has been published in Global Change Biology, and the text, figures and tables are reproduced here verbatim, with some formatting changes made for inclusion in the thesis.

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Chapter 4

CDT, JHK and CD conceived and supervised this work. BJA and CD constructed and developed the model. CD and I tested the model. RF and DB provided data. BJA generated the climate suitability data used in the model. I ran the model and wrote the manuscript. This work has been submitted to Methods in Ecology and Evolution and the text, figures and tables are reproduced here verbatim, with some formatting changes made for inclusion in the thesis.

Anderson, B.J. Mair, L. Dytham, C. Thomas, C.D. & Hill, J.K. (under review) SPEED, a dynamic model for studying climate-driven range changes in species' distributions. *Methods in Ecology & Evolution*.

Chapter 5

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1 General Introduction

1.1 CLIMATE CHANGE AND SPECIES RESPONSES

Industrial activity over the last 150 years has led to higher concentrations of carbon dioxide CO_2 and methane CH_4 in the atmosphere than have been observed any time in the last 650,000 years (IPCC, 2007). This increased concentration of greenhouses gases (which also include nitrous oxide N_2O and CFCs) has led to increased global temperatures through radiative forcing. On average, global temperatures have increased by 0.13°C ±0.03°C per decade over the last 50 years (IPCC, 2007). The greatest increases in temperature have occurred at higher latitudes, and temperatures in the northern hemisphere over the last 50 years were likely higher than during any other 50 year period in the last 1300 years. This unprecedented rate of global warming is irrefutably linked to human activity (IPCC, 2007).

An overall increase in global temperatures is only one of a myriad of effects of anthropogenic climate change; there is also evidence for long term changes in large-scale atmospheric circulation systems. Regional changes in precipitation have been observed, with an increase in heavy precipitation events in some areas and more intense and longer droughts in others (Easterling *et al.*, 2000). There has also been a reduction in the number of extreme cold days, and an increase in the number of extreme warm days (IPCC, 2007).

In Britain, annual temperature increased by 0.47°C during the 20th century, and there has been an increase in climatic variability, with record-breaking periods of above-average temperatures, and periods of above- and below-average precipitation (Conway, 1998). Greenhouse gas emissions will continue into the future, although the scale of emissions will depend upon the global uptake of carbon reduction strategies, and therefore temperatures are predicted to continue to rise, along with an increase in the frequency of extreme weather events (IPCC, 2007). Globally, temperatures are predicted to increase by between 0.6°C in the best-case scenario and 4°C in the worst case by the year 2100 (relative to 1980-99; IPCC, 2007). In Britain, average annual temperatures may increase by around 3°C by 2100 (Conway, 1998).

These changes in temperature and precipitation have had a quantifiable effect on terrestrial plants and animals. Species' distributions are at least partly determined by climate and species are adapted to survive in particular climatic niches, whether that niche is determined by the species' physical tolerance, by the composition of resources within the climatic niche that the species exploits, or by the outcome of interspecific interactions under different climatic conditions. When faced with a changing climate, species have four options: they can (i) shift their distribution in order to maintain their climatic niche, (ii) alter their phenology in order to maintain their climatic niche without changing location, (iii) remain where they are and adjust to the climatic changes via phenotypic plasticity and/or genetic adaptation, or (iv) die out (Parmesan, 2006, Bellard *et al.*, 2012).

1.1.1 Distribution changes

Evidence from the fossil record suggests that in the past species responded to climate change by shifting their geographical distribution, rather than maintaining their range and evolving phenotypic adaptations (Coope & Wilkins, 1994, Davis & Shaw, 2001, Parmesan, 2006). Changes in species distributions in response to recent climate change have been observed in a wide range of taxa (Parmesan & Yohe, 2003, Root *et al.*, 2003, Hickling *et al.*, 2005, Walther, 2010) and there is evidence for distribution shifts polewards and/or uphill in both temperate (Hickling *et al.*, 2006, Frei *et al.*, 2010) and tropical regions (Chen *et al.*, 2009). Evidence of distributional responses has largely come from the detection of expansion at species' cool range margins (Parmesan & Yohe, 2003). Contraction at species' warm range margins has been detected (Franco *et al.*, 2006), although in some cases the extent of warm-edge contraction has been less than the extent of cool-edge expansion (Chen *et al.*, 2011b). Failure of species to expand at their cool leading-edge range margin may result in a reduction in overall range size if their warm trailing-edge range margin retreats (Wilson *et al.*, 2005, Parmesan, 2006).

There is large inter-specific variation in rates of climate-driven distribution change (Parmesan, 2006, le Roux & McGeoch, 2008, Chen *et al.*, 2011a, La Sorte & Jetz, 2012). Amongst those species that have shown distribution expansions, the rate of distribution change varied greatly (e.g. Parmesan *et al.*, 1999), but has generally lagged behind the rate of climate change (Menéndez *et al.*, 2006, Devictor *et al.*, 2008, Willis *et al.*, 2009a, Devictor *et al.*, 2012). While studies show a coherent signal of distribution shifts in response to climate change (Parmesan, 2006), not all species have been able to track recent climate change (Hill *et al.*, 2002). This is of particular concern as it is predicted that species will have to shift at faster rates under present-day climate change than they had to in post-glacial times (Malcolm *et al.*, 2002), although it has been suggested that some species are able to make use of temporary lulls in climate warming to 'catch up' with climate change (La Sorte & Jetz, 2012).

Such inter-specific variation in rates of distribution change is predicted to lead to the formation of non-analogous communities (Keith *et al.*, 2009), which are communities with a different species composition to those currently in existence. Changes in community composition have already been recorded in birds, butterflies (Devictor *et al.*, 2012) and plants (le Roux & McGeoch, 2008). The homogenisation of communities has also been observed, which has been attributed to the distribution expansion of generalist species and lack of expansion amongst specialist species (Davey *et al.*, 2012). The homogenisation of communities is predicted to be a widespread consequence of climate change, as generalists have shown a greater ability to shift their distribution in response to warming than have specialists across a range of taxa (Warren *et al.*, 2001, Menéndez *et al.*, 2006, Davey *et al.*, 2013).

1.1.2 Phenological changes

The advancement of species' first appearance and the lengthening of the growing or flight period in response to warming have been detected in both plants and animals (Peñuelas & Filella, 2001, Stefanescu *et al.*, 2003, Diamond *et al.*, 2011). However, phenological sensitivity in butterflies varies greatly between species and some species show little flexibility in their emergence timing (Hodgson *et al.*, 2011c). One possible explanation for this is that not all species' flight times are controlled by temperature alone; some species may rely more on photoperiod cues and therefore their emergence timing is expected to show little response to climate change (Valtonen *et al.*, 2011). Species traits may also be important, as earlier flying species and those that are less mobile showed greater temperature sensitivity than later flying and more mobile species of butterfly (Kharouba *et al.*, 2014), and species with narrower larval diet breadth and those that over-wintered as adults (rather than larvae or pupae) showed greater advances in first appearance (Diamond *et al.*, 2011). In European plants, species that showed the greatest phenological sensitivity to climate change were those which experienced the least variation in local spring temperatures (Wang *et al.*, 2014). This implies that species which experience large variation in spring temperatures rely on cues other than temperature and that conversely, those species with spring phenology cues most closely linked to temperature will show the greatest phenological changes in response to climate change.

It has been suggested that phenological plasticity has the potential to be of benefit to species under climate change, as earlier emergence could allow species to avoid adverse summer conditions such as drought (Cormont *et al.*, 2012). However the extent and scale of inter-specific variation in phenological responses to climate change has led to mismatches in the timing of emergence or flowering amongst species at different trophic levels, and it is predicted that this mismatch will be exacerbated as climate change continues into the future (Thackeray *et al.*, 2010). For example, the advancement of butterflies, bees and flowering plants in North America was found to be similar amongst the three taxa, but differed significantly from the advancement of birds, which showed a weaker response to temperature changes (Polgar *et al.*, 2013). Similarly, increasingly poor synchrony between the winter moth and oak trees in Europe has been recorded in recent years as temperature patterns have changed, indicating that it is not necessarily simply overall mean temperature changes that affect phenology, but that different patterns of change amongst seasonal temperatures are also likely to be important (Visser & Holleman, 2001). Interestingly, there is also research to suggest that phenological asynchrony may be the norm for some inter-specific interactions, but that the exacerbation of asynchrony by climate change may have negative impacts of species persistence (Singer & Parmesan, 2010). This highlights the difficulty of attributing phenological asynchrony to recent climate change, and emphasises the need for long term studies which are capable of detecting temporal trends and relating these to climatic changes.

1.1.3 In situ adaptation

It has been argued that observations of species' responses to recent climate change provide little evidence for any change in the absolute climatic tolerance of species (Parmesan, 2006, Berg *et al.*, 2010). However, Jump & Peñuelas, 2005 argue that the role of adaptation may have been underestimated, and that the pressure on species to adapt will be intense given that species may not be able to shift their distributions at a rate sufficient to keep up with rapid climate change. The existence of local adaptation within species provides evidence of genetic adaptation across space, and suggests that, given sufficient gene flow, species may be capable of adapting *in situ* to temporal changes in climate (Hoffmann & Sgro, 2011). Support for this comes from an experiment on a shrub species, which showed rapid genetic divergence in response to drought conditions (Jump *et al.*, 2008). It has also been suggested from a field study that temporal changes in gene frequency in the tree species *Fagus sylvatica* were likely in response to increasing temperatures (Jump *et al.*, 2006). However, despite this demonstrated capacity for an *in situ* response to climate change, populations of *F. sylvatica* were still being lost. The species was being out-competed at low altitudes by *Quercus ilex*, which has a higher recruitment rate, indicating that changing community structure can pose a threat to species' persistence under warmer climates (Peñuelas *et al.*, 2007). It may be that if the climate changes too quickly, the rate of species' evolution will not be fast enough to keep up (Hoffmann & Sgro, 2011).

1.1.4 Species extinctions due to climate change

Species distribution modelling has predicted global extinctions due to climate change (Thomas *et al.*, 2004), based on the premise that some species will suffer a reduction or complete loss of climatically-suitable area (Moritz & Agudo, 2013) and that the climate will change faster than many species can respond. Yet there is a lack of evidence in the fossil record for high extinction rates during the Quaternary period when the climate fluctuated (Coope & Wilkins, 1994). The extinction of local populations and the retraction of species' warm range margins have been observed, but attributing such losses to thermal intolerance is difficult (Thomas *et al.*, 2006). The link between local extinctions and anthropogenic climate change has been made in several cases; for most of these, the proximate causes of local extinctions were linked to species' interactions, particularly food supply, rather than directly to thermal intolerance (Cahill *et al.*, 2013). The mass extinctions observed amongst *Atelopus* frogs in the American tropics have been linked to outbreaks of chytrid fungus, which in turn have been linked to temperature changes (Pounds *et al.*, 2006). Thus the attribution of species' extinctions to climate change is not straight forward, and climate-driven changes to species' interactions may be of greater importance than thermal tolerance (Cahill *et al.*, 2013).

1.2 EXPLAINING VARIATION IN DISTRIBUITION CHANGES

Species' distribution changes are perhaps the most widely studied response to climate change and are the focus of this thesis. Inter-specific variation in rates of distribution change has been quantified across a wide range of taxa (e.g. Parmesan *et al.*, 1999, le Roux & McGeoch, 2008, La Sorte & Jetz, 2012) and studies have progressed on to attempts to explain this variation. This has involved the consideration of the rates of climate change and the sensitivity of species to climate, the influence of species-specific traits (such as reproductive rate, host-plant specificity and dispersal ability) and the structure of the landscape across which species have to (or fail to) expand.

1.2.1 Climate and species' distribution shifts

Species' distributions are expected to shift across space in order to track the species' shifting climatic niche. A fundamental element of a species' climatic niche is the temperature range which the species can tolerate, and therefore climate change research has largely focussed on how species have responded to temperature changes. Climate warming is not globally uniform and while the overall trend is for a shift polewards and/or uphill, individual species' range shifts often deviate from the simplistic expectation of a poleward direction (Burrows *et al.*, 2011) as isotherms do not necessarily show a clear northwards shift (Ohlemüller, 2011). Spatial and temporal variation in rates of warming affects the spatial and temporal rates of species' distribution change. For example, species of tropical moths experiencing higher levels of climate warming showed greater distribution shifts than species experiencing lower levels of warming (Chen *et al.*, 2011b) and a species of butterfly in Britain expanded more in warmer years then cooler ones (Bennie *et al.*, 2013). Thus there is strong evidence in these cases for a direct link between the rate of temperature change and the rate of species' distribution change. Such regional variation in climate change may have a negative impact on some species over the long term, however, as it is predicted to result in gaps in species' climate 'paths', which are the geographical routes along which a species' distribution is likely to shift in order to track the climate niche (Early & Sax, 2011). Spatial and temporal variation in temperature change is therefore likely to affect different species in different ways and species' responses to climate change have not been globally uniform (Parmesan, 2006).

Furthermore, species vary in their sensitivity to climate (Summers *et al.*, 2012), which suggests that not all distributional changes necessarily show strong associations with the rate of climate warming. Similarly, species' distributions are not necessarily at equilibrium with the current climate; the degree to which species' distributions are at equilibrium with the current climate is inversely related to their ability to track climate change (Araújo & Pearson, 2005). In general, across a range of species assemblages in Europe, co-variation between species composition and climate was highest in species assemblages with greater dispersal ability (Araújo & Pearson, 2005), indicating that climate is not the sole determinant of species' distributions (Thomas, 2010) and therefore is unlikely to be the sole determinant of species' distribution changes.

Temperature is unlikely to be the only climatic variable which determines species' distribution change. Precipitation changes in particular may also have an effect, and regional changes in temperature and precipitation are not necessarily complementary; for example increases in temperature in North America were shown to result in montane bird species moving upslope, while precipitation increases resulted in species moving downslope, leading to heterogeneous range shifts amongst species (Tingley *et al.*, 2012). Similarly there is evidence that changes in precipitation patterns have contributed to the decline of a previously successfully managed plant species (Krushelnycky *et al.*, 2013). The inclusion of precipitation change in models of projected range shifts can greatly alter results, with amphibian species especially predicted to experience severe declines under scenarios of reduced precipitation (McCain & Colwell, 2011). Species distribution changes will therefore be driven by changes to both the regional temperature and precipitation regimes, and the sensitivity of species to climatic change is likely to vary, resulting in considerable inter-specific variation in rates of distribution change (Deutsch *et al.*, 2008).

1.2.2 Species-specific traits

Although rates of range shifting are highly idiosyncratic, a trend that frequently emerges is that generalist species have expanded their distributions at faster rates than specialist species (Warren *et al.*, 2001, Mattila *et al.*, 2011). The faster rates of generalist species have been attributed to greater dispersal ability, allowing individuals to cross fragmented landscapes and colonise newly suitable habitat (Thomas *et al.*, 2001, Beaumont & Hughes, 2002), as well as to a greater availability of habitat within the landscape for generalist species (Menéndez *et al.*, 2007). Studies which have considered other species traits, such as flight period or diet breadth, have generally found weak relationships (Angert *et al.*, 2011, Reif & Flousek, 2012), and the conclusion is often reached that dispersal ability is a key determinant of the rate of distribution change (Pöyry *et al.*, 2009).

The most dispersive species are the most able to survive in increasingly fragmented landscapes (Thomas, 2000, Maes & Van Dyck, 2001) and it is this effect which is predicted lead to the homogenisation of communities; climate change is expected to produce communities dominated by mobile generalists which are better able to cope with the simultaneous pressures of climate and land use change (Warren *et al.*, 2001, Malcolm *et al.*, 2002).

The importance of dispersal for range expansion is emphasised in modelling studies, which predict that the persistence of species may critically depend on dispersal ability (Anderson *et al.*, 2012, Arribas *et al.*, 2012), because poorer dispersal ability can lead to greater reductions in species' range size (Jaeschke *et al.*, 2013). Evidence from empirical data is harder to obtain, given the difficulty involved in quantifying the dispersal ability of many species. However, the application of expert opinion to create a rank score of butterfly mobility allowed the importance of dispersal to be identified for range shifts in Australian butterflies (Pöyry *et al.*, 2009). Other studies have inferred the importance of dispersal ability for range shifting based on colonisation rates (Honnay *et al.*, 2002), and from the comparison of the velocity of climate change (which is the geographic shift in isotherms that indicates the speed at which a species must shift to keep up with climate change) against the velocity at which species are able to move given their dispersal ability (Schloss *et al.*, 2012).

Dispersal ability, however, is not a fixed trait (Phillips *et al.*, 2008) and has been shown to vary within species (Stevens *et al.*, 2010a). Colonising individuals at species' range margins are not a random subset of the species, but are those with increased colonisation ability. This is evident in insects in the greater investment in morphological features associated with flight in newly colonised sites than continuously occupied sites (Hill *et al.*, 1999a), and the greater frequency of dispersive, long-winged individuals in populations at the distribution margin compared to the distribution core (Simmons &

Thomas, 2004, Hill *et al.*, 2011). The evolution of dispersal ability at the range margin is the most commonly observed adaptation in species with expanding distributions (Hill *et al.*, 2011). Indeed, modelling work has predicted that populations at expanding range margins will evolve different dispersal strategies compared with populations at the distribution core and therefore it is the dispersal ability of the margin populations which will determine the rate of species range shifts (Dytham, 2009). However, modelling also predicts that although dispersal ability may increase at expanding range margins, continued habitat fragmentation has the potential to negate the benefits that increased dispersal ability could bring (Hughes *et al.*, 2007).

1.2.3 Landscape characteristics and range shifting

The advantage of increased dispersal ability is the capacity to colonise across fragmented landscapes, which implies that habitat availability and landscape structure are also important determinants of the rates of species' distribution expansion. Natural habitats are being increasingly lost and fragmented in human dominated landscapes (Haines-Young *et al.*, 2003), which causes species declines (Hanski, 2011) and is predicted to impede the ability of species to respond to climate change (Jump & Peñuelas, 2005, Wilson *et al.*, 2009).

Increased habitat availability should lead to larger population sizes, which reduce the risk of population extinction and also lead to the production of more dispersers for the colonisation of new habitat patches. Greater habitat availability in the landscape should also reduce dispersal mortality since dispersing individuals have a greater likelihood of finding a new suitable habitat patch, and this should in turn lead to increased colonisation success (King & With, 2002). The effect of habitat availability has been demonstrated in butterflies; a species was able to expand its distribution at a faster rate where habitat availability was greater (Hill *et al.*, 2001), and also in plants; higher colonisation rates were reported where habitat was more connected (Honnay *et al.*, 2002). Habitat restoration is predicted to increase the likelihood that species will persist under climate change by facilitating range expansion (Renton *et al.*, 2012).

How habitat should be protected or restored in terms of the optimal spatial structure to enhance species' distribution shifts has therefore become a focus for conservation. There is a difference between habitat availability (the amount of habitat in the landscape) and habitat connectivity (the configuration of habitat in the landscape or the degree of habitat fragmentation) (Harrison & Bruna, 1999, Fahrig, 2003) and the relative importance of habitat amount versus habitat connectivity in determining the rate of species' range shifts has been hotly debated (Hodgson *et al.*, 2009, Doerr *et al.*, 2011, Hodgson *et al.*, 2011a). There is some evidence to suggest that up to a certain threshold of habitat loss in a landscape, the amount of habitat remaining determines the species' distribution, and that beyond this threshold the degree of habitat fragmentation becomes important (Andren, 1994, King & With, 2002). However the implications of such a conclusion for species' range shifts are unclear, as greater habitat availability has the potential to increase species' persistence (Renton *et al.*, 2012), while greater connectivity through landscape features such as habitat 'stepping-stones' has the potential to increase rates of spread (Hodgson *et al.*, 2012). The effects of each of these measures can be difficult to disentangle, and studies attempting to separate out the effects and the importance of the two elements have reached different conclusions depending on the species and landscape studied, as well as the methodological approach taken (Ewers & Didham, 2006).

1.3 MODELLING SPECIES' DISTRIBUTION CHANGE

The implementation of effective conservation strategies under climate change is reliant upon an understanding of how species' distributions will change in response to climatic changes. Predictive distribution modelling has therefore been widely applied and has progressed rapidly as empirical evidence has accumulated and computational techniques have improved. Modelling is an essential tool in understanding species' responses to climate change, as it allows the exploration of a range of climate change scenarios, and the likely outcomes of different policy options. Species' distribution change can be predicted using empirical models (which are correlative models such as bioclimate envelope models; e.g. Erasmus *et al.*, 2002), mechanistic models (also called process-based models, e.g. Pearson *et al.*, 2014), or the more recently developed 'hybrid' models (e.g. Fordham *et al.*, 2013a), which incorporate aspects of both empirical and mechanistic models. The development of predictive distribution models, and the relative advantages and disadvantages of each of these approaches for predicting species' distribution change, are outlined below.

1.3.1 Bioclimate envelope modelling

The modelling of how species distributions are expected to change under climate change began at the most basic level with species' bioclimate envelopes, which are empirical models. The premise is that species' distributions are determined by climate and therefore by quantifying a species' climate envelope, which is the range of climatic parameters that the species can tolerate, and identifying how the current distribution of this envelope is expected to change under scenarios of future climate change, it is possible to predict whether a species is likely to experience an expansion in climatically suitable area, or a retraction (Thomas *et al.*, 2004, Huntley *et al.*, 2008). Using this approach it is possible to identify regions which are expected to suffer the greatest loss of biodiversity and the areas which could potentially receive the most new colonisers (Erasmus *et al.*, 2002). In Britain, climate envelope modelling has been used to predict the loss or gain of climate space for a range of species (Berry *et al.*, 2002), and has identified that montane species and habitats are particularly vulnerable to climate change (Berry *et al.*, 2003). It is also possible to use climate envelope modelling to estimate the rate of range shifting required by species to keep track of climate change, which can then be compared with estimated rates of species' dispersal, in order to determine likely changes in species' range sizes (Schloss *et al.*, 2012).

There are, however, a number of limitations to this approach. Climate envelope models make the assumptions firstly that species are at equilibrium with the current climate and secondly that climate is the main constraint on the species' distribution (Pearson & Dawson, 2003). However species' distributions are not necessarily at equilibrium with the climate, and are likely to be determined by a range of other influences, including interactions with other species and dispersal abilities (Davis *et al.*, 1998, Araújo & Pearson, 2005). A study of European birds found that the species-climate associations predicted from climate envelopes were no better than chance for just over half of species studied (Beale *et al.*, 2008), and it has been shown that modelling species which were not at equilibrium resulted in decreased prediction accuracy (Zurell *et al.*, 2009). Moreover, it has been suggested that the climate envelope approach is likely to overestimate the positive effects of climate change on species in temperate regions as it does not consider the negative impact of extreme climatic events on projected changes in species' distributions (WallisDeVries *et al.*, 2011). The application of climate envelopes should therefore not be indiscriminate and should be appropriate given the biology of the species and an understanding of the model limitations (Araújo & Peterson, 2012), as reasonable predictions can be made when the method is appropriately applied (Smith *et al.*, 2013).

1.3.2 Integration of habitat availability

A natural advance in predictive species' distribution modelling is the inclusion of habitat availability in bioclimate envelope models, which should improve the performance of climate-only models given that species cannot colonise where suitable habitat does not exist (Huntley *et al.*, 2010). The increasing availability of national land cover maps makes the incorporation of habitat into models feasible for many studies, and the integration of land cover data can significantly improve upon climate-only predictions of species' distributions (Pearson *et al.*, 2004). Indeed, it has been suggested that if the availability of habitat affects a species' distribution then land cover data should be used to improve model predictions, regardless of the fact that the questionable assumption may have to be made that land cover will not change over time as the climate changes (Stanton *et al.*, 2012). Where projections of land use change are possible, the inclusion of both climate and habitat change in models produces more reliable projections than climate or habitat change alone, and models considering both variables have been used to show that the species richness of bird communities in Europe was expected to decline under climate and land use change (Barbet-Massin *et al.*, 2012). Empirical models can therefore be improved by the inclusion of a greater range of environmental variables, which should capture more of the environmental determinants of species' distributions.

1.3.3 Integration of dispersal ability

Bioclimate envelope models which incorporate both climate and habitat may nevertheless make poor predictions because they fail to take account of species-specific dispersal ability, which affects the rate at which a species can spread across the landscape and therefore affects the extent to which a species can track its climatic niche (Mitikka *et al.*, 2008). The technique tends to assume two extremes of dispersal: either full dispersal (the species can colonise all areas with newly suitable climate), or no dispersal (the species can only remain in areas that continue to have suitable climate and cannot colonise any newly suitable areas) (e.g. Thomas *et al.*, 2004, Thuiller, 2004, Anderson *et al.*, 2012). Such an approach either vastly over- or under-estimates likely changes to species' distributions under climate and habitat change (except for in the case that the species' climate envelope disappears completely, as in many species' projections in Thomas *et al.*, 2004). As a result, climate envelope models have been advanced to incorporate more realistic dispersal abilities, by applying restrictions to the rate of spread or the distance over which spread can occur (e.g. Midgley *et al.*, 2006, Buse & Griebeler, 2011). In general, these models remain correlative, as a simple distance-based restriction is placed on the extent of projected spread. Therefore, although the incorporation of dispersal limitation requires a biological understanding of the likely species' dispersal ability, there is (often) not a mechanistic component to the model. Nevertheless, such models emphasise that the assumption of unlimited dispersal produces overly optimistic predictions for species' distribution change (Buse & Griebeler, 2011) and that including species-specific dispersal can result in predictions of range contraction rather than expansion under climate change (Jaeschke *et al.*, 2013). Thus the consideration of different dispersal scenarios demonstrates the strong effect that different dispersal assumptions can have upon predicted species' distributions, and highlights the importance of gaining a better understanding of species' dispersal abilities as well as the necessity to develop more realistic methods for incorporating these abilities into predictive distribution models (Engler *et al.*, 2009).

1.3.4 Modelling species' population dynamics

The speed at which species' distributions can spread across the landscape will also be influenced by the species' population dynamics. Models which incorporate population dynamics into species distribution models are considered to be 'hybrids', as they incorporate both empirical and mechanistic modelling approaches. Hybrid models offer the advantage of considering both environmental variables, such as climate and habitat, and life-history traits, such as dispersal and population dynamics, and can be used to predict extinction risk and assess the likely efficacy of alternative management strategies (Fordham *et al.*, 2013a). Hybrid models differ from purely mechanistic models (which are process-based models that rely solely on biological assumptions and not empirical data) as they make species- and landscape-specific predictions of distribution change, while mechanistic models are largely used to test hypotheses based on general principles and biological concepts. For example, mechanistic models can be used to determine which life-history and spatial traits (e.g. occupied area) are related to extinction risk under climate change (Pearson *et al.*, 2014), while hybrid models can be applied to case studies in order to predict the likely distribution change of specific species under different climate change and management scenarios (Fordham *et al.*, 2013b).

Hybrid models can therefore advance our understanding of species' distribution change by allowing the affect of population dynamics to be explored. In one study, the application of a metapopulation model, which simulated a moving climate window across a structured landscape, indicated that K-selected (large-bodied) species were particularly vulnerable to climate change, and that the maximum rate of species distribution spread for any of the life history strategies studied was not fast enough to keep up with climate change, resulting in range contractions (Schippers *et al.*, 2011). Similar results were obtained in another study using metapopulation models, which also predicted that species distribution shifts would not be able to keep up with climate change, but that the rate of distribution spread could increase during periods of warming (Mustin *et al.*, 2009). The acceleration in distribution spread was attributed to the rate of species' distribution change initially lagging behind the rate of climate change; this resulted in conditions at the species distribution edge becoming closer to the optimal over time as the climate window moved faster than the species' distribution (Mustin *et al.*, 2009, Schippers *et al.*, 2011).

Studies have therefore moved beyond simple climate-envelope models to spatially explicit population models, which consider habitat availability, climatic suitability, dispersal ability and population dynamics (Keith *et al.*, 2008). Such fully integrated hybrid models provide more informative predictions of species' responses to climate change, but have three main challenges: (i) the assimilation of inputs across different temporal and spatial scales, (ii) quantification of uncertainty in model outputs, and (iii) balancing biological realism with model complexity and data availability (Huntley *et al.*, 2010). Therefore models of intermediate complexity will still prove crucial for species and habitats lacking detailed data (Huntley *et al.*, 2010).

1.4 THE IMPORTANCE OF UNDERSTANDING VARIATION IN RATES OF RANGE SHIFTING FOR CONSERVATION

Understanding how different species respond to climate change – and ascertaining which environmental and species traits drive the variation in response – is essential in order to develop effective climate change conservation policy. The knowledge that range shifting is a widespread species' response to climate change, and the supporting palaeo-ecological evidence for such a response in the past, has directed conservationists towards developing strategies that facilitate species range shifts (e.g. Williams *et al.*, 2005). The predicted formation of non-analogous communities under climate change, driven by different rates of distribution expansion amongst species, has directed conservation away from the preservation of existing community structures and instead towards the identification of vulnerable species or species groups (Thomas *et al.*, 2011a), and strategies for conserving as much biodiversity as possible (e.g. Wise *et al.*, 2012).

Identifying which species are the most vulnerable to climatic changes, and why, allows limited conservation resources to be efficiently targeted. The vulnerability of a species to climate change can be quantified as the interaction between species' exposure, sensitivity and adaptive capacity (Summers *et al.*, 2012). Exposure is determined by species' geographical distributions, sensitivity can be quantified as the likely changes to species' distributions in response to climate change and adaptive capacity can be estimated by assessing the species' ability to migrate in order to track climatic changes (Summers *et al.*, 2012). By quantifying these components, the species most vulnerable to climatic change can be identified. Conservation strategies can then be developed based upon an understanding of the species' traits, for example if a species has particularly poor dispersal ability then the maintenance of current populations and the creation of habitat corridors and networks to link current and future climatically-suitable geographic areas may provide the best prospects for species' persistence (Arribas *et al.*, 2012).

The threat to species and/or communities associated with particular habitat types can be assessed using bioclimate envelope modelling to determine whether the climatic niche is expected to shift to a geographical area without the species' associated habitat type. In particular, it is clear that species associated with montane habitats are likely to suffer substantial range size reductions as they are forced further uphill into increasingly smaller areas of habitat (Simmons *et al.*, 2004, Wilson *et al.*, 2005). Studies on tropical mountains have shown that despite some species expanding their upper boundaries at a faster rate than they have contracted at their lower boundaries, the area which the species occupied was nevertheless reduced due to the declining availability of land as elevation increased (Chen *et al.*, 2011b). Many montane species may therefore be consigned to extinction, given the limited possibility of dispersal to other suitable habitats (Williams *et al.*, 2003).

Nevertheless, predicting likely changes to species' distributions under climate change can have a wider application than simply forecasting doom and gloom scenarios. By predicting how species' distributions are likely to change, it is possible to assess whether current protected area networks are likely to continue to support biodiversity, and where new protected areas should be placed to maximise their conservation value. The efficacy of protected areas under future climate change is likely to vary substantially between geographic regions. In Sub-Saharan Africa, the Important Bird Area network is expected to maintain climatic suitability for ≥88% of priority birds by 2085 (Hole *et al.*, 2009). In contrast, more than 50% of the species of plants and vertebrates in a study in Europe were predicted to lose climatically suitability area within protected areas by 2080 (Araújo *et al.*, 2011). The appropriate designation of protected areas is a particularly important conservation strategy under climate change as evidence from both Britain and Tanzania showed that birds preferentially colonised protected areas during distribution expansion (Thomas *et al.*, 2012, Beale *et al.*, 2013, Hiley *et al.*, 2013). This implies that the higher quality of habitat inside protected areas increased colonisation success, and that protected areas can act as stepping stones for species expanding their distributions.

As well as the assessment of existing protected area networks, predictive modelling can help to identify how networks could be improved and where new protected areas should be located. By combining climate and land use change scenarios with estimates of species' dispersal abilities in predictive models, priority areas in Brazil were identified, which aimed to minimize the migration distance required for species forced to shift their distributions in response to climate change (Faleiro *et al.*, 2013). Of key importance in reducing the distance that species' will have to shift in response to climate change is the identification of climate refugia, which are microclimates that allow the persistence of species in areas where the climate has become largely unsuitable. It has been suggested that the existence of refugia may help to explain post-glacial expansion, as re-colonisation could have occurred over shorter distances if isolated populations were maintained within refugia (Pearson, 2006). If climate refugia can be successfully identified within species' current distributions, then areas of high quality habitat that are expected to experience less environmental change than the surrounding landscape can be protected, buffering species against climatic changes (Game *et al.*, 2011). The reconstructed demographic history and phylogeny of a bat species in Europe provided strong evidence for the persistence of the species in climate refugia during the Pleistocene glacial period, however projections of future climatic changes suggested that historical refugia are likely to become unsuitable and geographic barriers may limit dispersal to new refugia under contemporary climate change (Razgour *et al.*, 2013).

This last study highlights that in some cases, predictions for the future of species' distributions are bleak, and in such circumstances the controversial conservation strategy of species' translocations has been suggested (Early & Sax, 2011, Chauvenet *et al.*, 2013). The translocation of a species from an area in which it is expected to decline or die out, to a previously unoccupied area outside its potential dispersal range (where it is expected to persist based on the availability of suitable climate and habitat), is a contentious strategy because it goes against the pervasive thinking that introduced species are detrimental to the native flora and fauna of a biogeographic region (Minteer & Collins, 2010). One of the key arguments against undertaking species' translocations is that the impacts of introducing new species to an area are not fully understood nor are they necessarily predictable, and therefore it is a risk not worth taking (Ricciardi & Simberloff, 2009). However, the counter-argument is that conservationists need to move beyond regarding ecological communities as having a fixed state and should instead consider the conservation benefits of translocating species within broad biogeographical regions (Thomas, 2011). Indeed, by considering the ecological role that a translocated species could fulfil in a new region, it may be possible to change the rhetoric from the potential negative impacts of translocating species to the likely positive impacts of maintaining biodiversity and restoring ecosystem function (Lunt *et al.*, 2013).

Thus a greater understanding of how species have responded to climate change can inform conservation strategies by identifying the environmental and species constraints on distribution expansions. Vulnerable species and communities can then be identified and conservation resources directed towards the strategies most likely to succeed in facilitating distribution expansion or preventing distribution decline under future climate change.

1.5 THESIS OVERVIEW

The main aim of this thesis was to quantify and explain variation in species' distribution changes in response to climate change using both the analysis of citizen science data and the application of a newly-developed hybrid model to project species' distribution change. The thesis utilises butterflies in Britain as study species, and a key aspect of novelty in the research presented lies in the analysis of distribution and abundance changes across a large number of species within the taxon Lepidoptera.

1.5.1 Butterflies as study species

Butterflies provide a good model for studying responses to climate change as they are poikilothermic and their behaviour (Cormont *et al.*, 2011), abundance (Roy *et al.*, 2001) and distribution (Warren *et al.*, 2001) all respond to changes in climate. Butterflies in Britain encompass a wide range of dispersal abilities, from highly sedentary (e.g. *Plebejus argus*; Lewis *et al.*, 1997) to highly mobile (e.g. *Polygonia c-album*; Cowley *et al.*, 2001), as well as a broad range of habitat and host plant specialisations (Asher *et al.*, 2001). There is also large inter-specific variation in distribution size and northern range margin limits within Britain (Fox *et al.*, 2006). This diversity within the species group allows an examination of how species with different traits and life histories respond to climate change. Moreover, in Britain, data on species' abundances and distributions have been collected since the 1970s (Fox *et al.*, 2011), and there is therefore a large spatial and temporal dataset available, spanning four decades of climate change. Butterflies in Britain are therefore an ideal group for use in this study.

1.5.2 Knowledge gaps and thesis aims

Despite a wealth of studies on species' responses to climate change, there are still many gaps in our understanding, and the availability of national distribution and abundance data for butterflies, as well as detailed knowledge about species' life-histories, allows a range of approaches to be taken to address knowledge gaps using butterflies as study species.

Quantifying variation in species' responses to climate change is an important step in understanding how different species respond to climate change. As already detailed, inter-specific variation in distribution changes in response to climate change has been well documented (e.g. Parmesan *et al.*, 1999), however it is not known whether intra-specific variation in responses to climate change also exists. Throughout this thesis, intra-specific variation refers specifically to variation within species over time, in other words, temporal variation in the rates of distribution and/or abundance change within species. Temporal variation in species responses to climate change has received little attention so far, but is an important issue for understanding whether the drivers of species' distribution change vary over time, and also for informing projections of distribution change into the future. I therefore quantified both inter- and intra-specific variation in the distribution and abundance changes of southerly-distributed butterfly species in Britain. I also determined whether the responses of habitat generalist species differed from those of habitat specialists, and whether these differences were temporally consistent. The comparison of generalist and specialist species' responses should contribute to our understanding of how communities are expected to change as the climate changes, in particular whether generalists consistently show greater distribution expansion than specialists, and therefore the homogenisation of communities under climate change should be expected (Menéndez *et al.*, 2006).

Quantifying intra-specific variation in responses to climate change is a novel study in itself, but also paves the way for addressing potential determinants of rates of species' distribution change. Previous studies have shown that explaining variation in rates of responses to climate change is challenging, and there were only weak relationships between distribution change and a range of life-history variables (e.g.Angert *et al.*, 2011). There is therefore a lack of understanding of the determinants of rates of distribution change. I tackled this question by drawing together variables that have previously been shown to affect distribution change in separate studies, and analysing them simultaneously. Thus I determined how important species-specific habitat availability, dispersal ability and abundance changes were for explaining variation in rates of distribution change in southerly-distributed British butterflies. The potential explanatory variables examined were carefully chosen to reflect the interaction been species' life history traits and the landscape across which they were expanding (or failing to expand) their distribution. For example, while species' habitat specificity reflects the breadth of habitats a species can utilise, species' habitat availability reflects both the species' habitat associations and the amount of suitable habitat available in the landscape across which it has expanded its distribution. This study therefore holds novelty in the approach taken, with the aim of advancing upon previous studies by considering the potentially important interactions between species' life history and the landscape.

Such empirical analyses are essential for understanding species' responses to climate change, however they are inevitably limited by the spatial and temporal extent and the quality of available data. Consequently, models are widely used to project species' distribution change, as these allow a range of questions to be tackled. Much detail was given above on the advances made in predictive distribution modelling, and I highlighted that integrated 'hybrid' models are likely to be of great utility in understanding how species' distributions are likely to change in response to climate change (Huntley *et al.*, 2010). The development of flexible predictive models that can be applied to a range of species and landscapes is therefore an important progression, and so I tested the ability of a spatially-explicit individual-based model, SPEED, to project the distribution change of a southerly-distributed butterfly species (*Pararge aegeria*) in Britain. The model projects species' distribution change in relation to climate suitability, habitat availability, dispersal ability and population growth rate. The spatially explicit climate suitability and habitat availability components of the model are species-specific empirical components, while the dispersal ability and population growth rate components are mechanistic. The model is thus a hybrid which improves upon bioclimate-envelope modelling by considering the effects on distribution change of both species' life history and environmental variables (Huntley *et al.*, 2010). Hybrid models are an emerging field, and other examples exist of predictive models which couple species' distribution models (bioclimate envelopes) with population dynamic models. For example, hybrid models have been used to predict species' persistence under climate change in plants (Fordham *et al.*, 2012) and birds (Zurell *et al.*, 2012), and to assess the potential impact of assisted-colonisation on species' persistence (Regan *et al.*, 2012). In contrast to these examples, the model presented in this thesis was developed to be highly flexible and hold the potential to be applied to a wide range of species and landscapes, and this flexibility in itself is an advance in the field.

I used the model to further explore the effects of habitat, dispersal and population growth rate on rates of species' distribution change, which allowed a similar question to that posed above using empirical data, to be tested using a modelling framework. Specifically, I aimed to ascertain how population growth rate affects the relative importance of climate, habitat and dispersal for species' distribution change, as previous studies have suggested that population growth is likely to be an important determinant of distribution expansion (Willis *et al.*, 2009b). I applied the model to twenty-eight species of southerly-distributed butterflies in Britain, using species-specific climate suitability and habitat availability data, and varying the dispersal ability and population growth rate within each species. I therefore aimed to advance our understanding of the determinants of distribution expansion by modelling species' distribution change in relation to key lift-history traits and environmental variables. The application of a hybrid model allowed our mechanistic understanding of distribution change to be tested using spatially realistic habitat and climate data. Moreover, the flexibility of the model structure and the large amount of butterfly distribution and life-history data available meant that a large number of species' distributions could be projected (N = 28), and so it was possible to use relatively detailed species-specific data without being restricted to studying a small number of species. This highlights the advantage of hybrid models, which incorporate both empirical and mechanistic components and can therefore be adapted given different data availability and study aims.

1.5.3 Thesis structure and hypotheses

The thesis is constructed around four data chapters. Chapter 2 quantifies inter- and intra-specific variation in rates of distribution change, northern range margin shift and abundance change over time. I aimed to determine whether species' responses to climate change were temporally consistent, which is a question that has previously not been addressed. This chapter tests the hypotheses that (i) the rates of species responses to climate change are consistent over time, and (ii) the responses of generalist species differ from those of specialist species and this difference in maintained over time.

Chapter 3 aims to explain the intra- and inter-specific variation quantified in Chapter 2 by relating species' distribution changes to species-specific habitat availability, dispersal ability and abundance changes. This chapter aims to assess multiple potential determinants of distribution change simultaneously in order to elucidate the relative importance of each, bringing together variables that previous research has identified as likely or potential drivers of species' distribution change. I test the hypotheses that (i) changes in species' distribution areas are related to species-specific habitat availability, dispersal ability and abundance trends, and (ii) species' colonisation distances are related to species-specific habitat availability, dispersal ability and abundance trends. Species' colonisation distances are a novel metric developed in this chapter which provides an alternative measure of species' distribution spread, and which makes use of the high resolution butterfly distribution data that has been collected over the last two decades.

Chapter 4 describes a novel spatially-explicit, individual-based dynamic distribution model, SPEED, which projects species' distribution change in relation to climate suitability, habitat availability, dispersal ability and population growth rate. The model is a hybrid which incorporates both empirical (climate and habitat) and mechanistic (dispersal and population growth rate) components. The chapter describes the model and presents model sensitivity analyses using a butterfly species in Britain as an example. The chapter has been submitted to Methods in Ecology and Evolution and is reproduced here verbatim; the term 'hybrid' is not explicitly used, however both the empirical (referred to as statistical in the chapter) elements and mechanistic elements of the model are detailed.

Chapter 5 then applies the SPEED model described in Chapter 4 to twenty-eight species of southerly-distributed butterflies to examine the importance of population growth rate, habitat availability, climate suitability and dispersal ability for species' distribution expansion. I test the hypotheses that (i) all study species are capable of distribution expansion given high enough population growth rates, and (ii) the relative importance of habitat availability, climate suitability and dispersal ability for species' distribution expansion varies as the population growth rate is varied.

Finally, Chapter 6 draws together the results from all four data chapters, and outlines how they relate to the broader field of climate change research. I discuss the potential conservation implications of my results, the data limitations, and make suggestions for future work.

2 Temporal variation in responses of species to four decades of climate warming

Louise Mair[1]*, Chris D Thomas[1], Barbara J Anderson[1], Richard Fox[2], Marc Botham[3] & Jane K Hill[1]

[1]Department of Biology, Wentworth Way, University of York, York, YO10 5DD, UK.

[2] Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, BH20 5QP, UK.

[3] Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK.

*Corresponding author. Email: lm609@york.ac.uk, Tel: 01904 328645, Fax: 01904 328505.

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This chapter has been published in Global Change Biology, the text, figures and tables are reproduced here verbatim, with some formatting changes made for inclusion in the thesis.

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2.1 ABSTRACT

Many species are expanding at their leading-edge range boundaries in response to climate warming. Species are known to respond individualistically to climate change, but there has been little consideration of whether responses are consistent over time. We compared responses of 37 southerly-distributed British butterflies over two study periods, first between 1970-82 and 1995-99 and then between 1995-99 and 2005-09, when mean annual temperature increased regionally by 0.03 ^{0}C yr^{-1} (a significant rate of increase) and 0.01 ^{0}C yr^{-1} (a non-significant increase), respectively. Our study species might be expected to benefit from climate warming. We measured three responses to climate to investigate this; changes in range margin, distribution area and abundance. In general, the responses of species were inconsistent over time. Species that increased their distribution areas during the first period tended to do so again during the second period, but the relationship was weak. Change in range margins and abundance were not consistent. In addition, only 5/37 species showed qualitatively similar responses in all three response variables over time (three species increased and two species declined in all variables in both periods). Overall rates of range expansion and distribution area change were significantly greater in the second study period, despite the lower rate of warming, perhaps due to species exploiting climate-distribution lags remaining from the earlier, warmer period. However, there was a significantly greater decline in abundance during the second study period, so range expansions northwards were not necessarily accompanied by increases in distribution area and/or abundance. Hence species ranges have been thinning as they have expanded northwards. The idiosyncratic responses of these species likely reflect the balance of climatic and habitat drivers of species distribution and abundance changes.

2.2 INTRODUCTION

There is an increasingly large body of evidence documenting species range shifts in response to climate change (Parmesan & Yohe, 2003, Thomas, 2010, Walther, 2010, Chen *et al.*, 2011a). In temperate regions, expansion polewards at leading edge range margins has been recorded in many taxa including birds (Thomas & Lennon, 1999), butterflies (Parmesan, 1996, Hill *et al.*, 1999b, Parmesan *et al.*, 1999, Pöyry *et al.*, 2009), dragonflies and damselflies (Hickling *et al.*, 2005) and other taxa (Parmesan & Yohe, 2003, Root *et al.*, 2003, Hickling *et al.*, 2006). Expansion at upper elevation boundaries has also been recorded in both temperate (Forister *et al.*, 2010, Frei *et al.*, 2010, Maggini *et al.*, 2011) and tropical regions (Pounds *et al.*, 1999, Raxworthy *et al.*, 2008, Chen *et al.*, 2009).

To date, this burgeoning literature has concentrated on the average responses of species, establishing that the majority of species ranges have shifted to higher latitudes and elevations, and demonstrating that climate change is a major factor driving these changes in species distributions. Further understanding now requires evaluation of the extent to which response rates vary among species (Angert *et al.*, 2011), and over time, as climatic conditions vary. The palaeoecological literature generally argues that responses are species specific, and that rates of responses vary over time, but the spatial and temporal resolutions of these analyses are relatively coarse (Huntley, 1991, Davis & Shaw, 2001). There are already indications that current response rates vary among species (Parmesan, 2006, le Roux & McGeoch, 2008, Chen *et al.*, 2011a). For example, Parmesan *et al.* (1999) found that 63% of European butterflies had shifted their ranges northwards, but these shifts varied between 35 km and 240 km polewards for individual species. One explanation for variation in response rates is that expansion rates lag behind climate change (Menéndez *et al.*, 2006, Willis *et al.*, 2009a) and that some species have failed to track climate change because of the loss and fragmentation of habitat (Hill *et al.*, 2001). This explanation is plausible because habitat generalists, which can spread relatively easily through the landscape because of the high availability of their breeding habitats in the landscape and/or their high dispersal ability, have expanded their ranges more rapidly than specialists (Warren *et al.*, 2001). Butterflies do not occupy the entire range of their respective host plants (Quinn *et al.*, 1998) and therefore hold the potential to spread in response to climate change, thus the implication is that species will achieve their new potential distributions, given sufficient time for colonisation. However, an alternative explanation is that species apparently failing to respond to climate warming may not be “lagging” behind climate change but may be responding to other drivers, which act in conjunction with, or even over-ride, responses to climate (Chen *et al.*, 2011a).

Most studies of species’ range expansions have focussed on rates of change during a single time period, and there is little information on whether species show temporal variation in their rates of expansion. The rate of climate warming has varied over time (IPCC, 2007), and so rates of species range expansion might be expected to mirror this variation if range shifts are driven primarily by climate, such that range expansion will slow down or halt during periods of little or no warming. Alternatively, if species are lagging behind climate change, then species may continue expanding polewards or to higher elevations, even in periods of little or no warming.

In this study, we examined responses of species to climate change over different time periods in order to determine whether species show temporal variation in their response rates. Species may be responding in several ways and so we quantified rates of response to climate change according to three variables, by comparing change in (i) the location of the leading-edge (northern) range margin, (ii) distribution area, and (iii) population abundance. We analysed data for southerly-distributed British butterflies over the periods 1970-82 to 1995-99 and then 1995-99 to 2005-09 using the Butterflies for the New Millennium (BNM) and the UK Butterfly Monitoring Scheme (UKBMS) datasets. We related changes in these three variables to changes in mean annual temperature during the respective study periods, in order to evaluate whether species responses were related to climate change. We tested the hypotheses that (i) rates of species responses are consistent between the two study periods, (ii) the responses of generalist species differ from those of specialist species and this difference is maintained over time, and (iii) there are positive relationships among the three response variables (i.e. an increase in range margin shift is accompanied by an increase in population abundance and/or distribution area). We would expect to see positive relationships among response variables since range margin shifts (Parmesan *et al.* 1999), changes in distribution areas (Warren *et al.* 2001) and changes in abundance (Roy *et al.*, 2001) have all been found to show positive associations with climate warming. Moreover, a positive association between abundance and occupancy has been demonstrated both inter- and intra-specifically (Gaston *et al.*, 2000), and is has been shown in British butterflies that species which expanded their distribution also increased in abundance (Pollard *et al.*, 1995, Warren *et al.*, 2001).

2.3 MATERIALS AND METHODS

We analysed data for resident butterfly species which reach their northern range margin in Britain. Migrants and those present only in northern Britain were excluded, as were species present in Orkney and/or Shetland in 1970-82 (under the assumption that they could not expand any further north within Britain) and those present in fewer than ten 10km grid squares (as their northern range margin could not be measured using our methods). This resulted in 37 study species, each of which was classified as either a wider-countryside species (hereafter a 'generalist' for ease of reference) or specialist according to Asher *et al.* (2001) (for species list see Table A2). Data were grouped into three discrete time periods: 1970-82, 1995-99, and 2005-09 coinciding with the publication of national distribution atlases (Asher *et al.*, 2001, Fox *et al.*, 2006). Changes in species' distributions from 1970-82 to 1995-99 (the first study period) were compared with changes from 1995-99 to 2005-09 (the second study period). Annual temperature data from the Central England Temperature series were downloaded from the UK Met Office (http://www.metoffice.gov.uk). Regression analysis was used to determine the slope and significance of changes in temperature from 1970 to 1999 and from 1995 to 2009.

2.3.1 Butterfly datasets

2.3.1.1 Distribution data

Distribution data were obtained from Butterflies for the New Millennium (BNM; Asher *et al.*, 2001). Recording effort has varied greatly over time (10 fold increase from 1970-82 to 1995-99 and 1.5 fold increase from 1995-99 to 2005-09). To control for this variation in recorder effort, data were sub-sampled following Fox *et al.* (2006) in order to achieve spatially similar recording efforts in each time period.

Sub-sampling was repeated 100 times, and for each sub-sample, species presence/absence was determined at a 10km x 10km (hereafter “10km”) Ordnance Survey (OS) grid square resolution. Since each sub-sample produced a slightly different value for the location of each species’ northern range margin and distribution area (see description of their calculation below), the mean values of these variables for each species were used in subsequent analyses computing rates of change over time. It is expected that species distributions show temporal variation as new populations are established and old populations go extinct, therefore species distributions are likely to vary within the year-groups used in this analysis (e.g. within 1970-82). However, it is necessary to treat these year-groups as categorical due to the quality of the data, as the use of a single year would reflect the spatial recording effort of volunteers rather than the real species distributions.

2.3.1.2 Abundance data

Collated annual abundance indices for each species were obtained from the UK Butterfly Monitoring Scheme (UKBMS; Botham *et al.*, 2010) which started in 1976 with annual data available up to 2009. UKBMS data are compiled from transect data collected at selected sites across the UK, with >1000 monitored sites by 2009. Transects are walked once a week for up to 26 weeks per year between April and September and are carried out only in suitable conditions (Pollard & Yates, 1993). Species counts from individual sites are then collated to produce an annual abundance index for each species (Moss & Pollard, 1993). The methods used to collect abundance data have remained consistent over time and therefore this data holds no temporal bias.

2.3.2 Quantifying species responses to climate change

We computed three measures of species responses to climate warming; change in location of leading-edge (northern) range margin, change in distribution area and change in abundance. For each species, the location of the leading-edge range margin was calculated as the mean distance north of the 10 northern-most occupied 10 km grid squares (Warren *et al.*, 2001, Parmesan & Yohe, 2003, Hickling *et al.*, 2006). The change in range margin location (expressed in km yr^{-1}) was computed for each species for each of the two study periods. For each species, distribution area was calculated as the number of occupied 10km grid squares. Change in distribution area over each of the two study periods was expressed as the proportional change in the number of occupied 10km squares per year. Change in species abundance was calculated as the slope of the regression of $\log_{10}$ collated annual index against year (Pollard *et al.*, 1995, Warren *et al.*, 2001). This smoothes inter-annual variation in species abundance and allows changes in abundance to be described as percentage change per year. For each species, one slope value was calculated for 1976-1999 and another for 1995-2009, in order to encompass the time periods of the distribution data, as far as possible. Arguably, since the distribution data consists of year-groups (e.g. the start point is 1970-82, rather than simply 1970), slightly different time frames could be used to calculate abundance changes. For example, trends in abundance could be analysed from the mid-points of each year-group (i.e. 1976 to 1997, and 1997 to 2007 respectively), or from the end-points of each year-group (i.e. 1982 to 1999, and 1999 to 2009 respectively). We investigated the effect of using different start and end dates for calculating change in abundance (and also temperature), and found that while this produced different absolute rates of change in abundance and change in temperature, the direction of the trends remained the same, indicating that the exact time frames used had minimal impact on the results obtained.

2.3.3 Analysis of species' responses over time

We used regression analysis to examine the consistency of species' responses over time by plotting the change in each response variable during the first study period against the change in response variable during the second study period, where each data point is a species. If species have shown consistent responses over time then a regression slope of +1 is expected.

We also examined consistency in species response over time in relation to all three response measures simultaneously by categorising species' trends in range margin expansion, change in distribution area and change in abundance during each study period as either positive or negative. We also used linear regression to explore the relationship among rates of range margin shift, changes in distribution area and changes in abundance within each study period, in order to identify potential drivers of change.

2.4 RESULTS

We analysed 37 species, of which 17 were generalists and 20 were specialists (Asher *et al.*, 2001). There was more regional warming during the first study period than during the second study period. Mean annual temperature increased by 0.7°C from 9.5°C to 10.2°C in the first study period, at an average rate of 0.03° yr^{-1} (linear regression, b=0.026, $F_{1,28}$=6.235, r^2=0.15, P=0.02). Mean annual temperature increased less in the second study period, by only 0.1°C to 10.3°C, equivalent to an average increase of 0.01° yr^{-1}, a rate of change that was not significantly different from zero (b=0.013, $F_{1,13}$=0.301, r^2=-0.05, P=0.6).

During the first study period, the average trend for species' responses was a slight decrease in distribution area and contraction of the northern range margin, but an increase in abundance (Table 2.1). Even though there was less warming in the second period, rates of expansion north and changes in distribution area were significantly greater during the second study period (paired t-test comparing responses of species in the two study periods; range margin, t_{36}=2.86, P=0.007; distribution area, t_{36}=2.56, P=0.01). There was, however, a significant shift from increasing to declining abundances during the second study period compared with the first period (t_{36}=3.33, P=0.002). Nevertheless, large standard errors associated with the means indicate that there is a large amount of variation between species, and this should be borne in mind when interpreting these results.

Table 2.1 Mean responses and their associated standard errors of all species, and of generalist and specialist species separately, during the first and second study periods for change in northern range margin (km yr^{-1}), change in distribution area (proportional change in number of 10km grid squares occupied per year) and change in abundance (percentage change per year, from the regression slope of $\log_{10}$ abundance index against year).

		All species		Generalists		Specialists	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
1st study period	Range margin	-0.17	0.47	1.24	0.75	-1.37	0.46
	Distribution area	-0.011	0.003	0.003	0.004	-0.023	0.002
	Abundance	0.45	0.72	1.26	0.71	-0.24	1.18
2nd study period	Range margin	1.29	0.52	2.74	0.83	0.06	0.53
	Distribution area	-0.003	0.003	0.002	0.003	-0.007	0.005
	Abundance	-2.72	0.70	-3.01	1.02	-2.47	0.99

2.4.1 Consistency of species responses over time

The responses of species to climate warming in the first study period did not predict well their response during the second period. Rates of range expansion northwards showed a significant relationship between the two study periods (linear regression, $F_{1,35}$=9.77, r^2=0.19, P=0.004). However, this result was primarily due to an outlier that spread rapidly northwards in both study periods (*Polygonia c-album*, Fig 2.1a), and no significant relationship was evident when this species was excluded ($F_{1,34}$=2.11, r^2=0.03, P=0.1). Change in species' distribution area showed a positive relationship between study periods ($F_{1,35}$=9.16, r^2=0.18, P=0.005; Fig 2.1b), but changes in abundance were not related between study periods ($F_{1,35}$=0.44, r^2=0.02, P=0.5; Fig 2.1c).

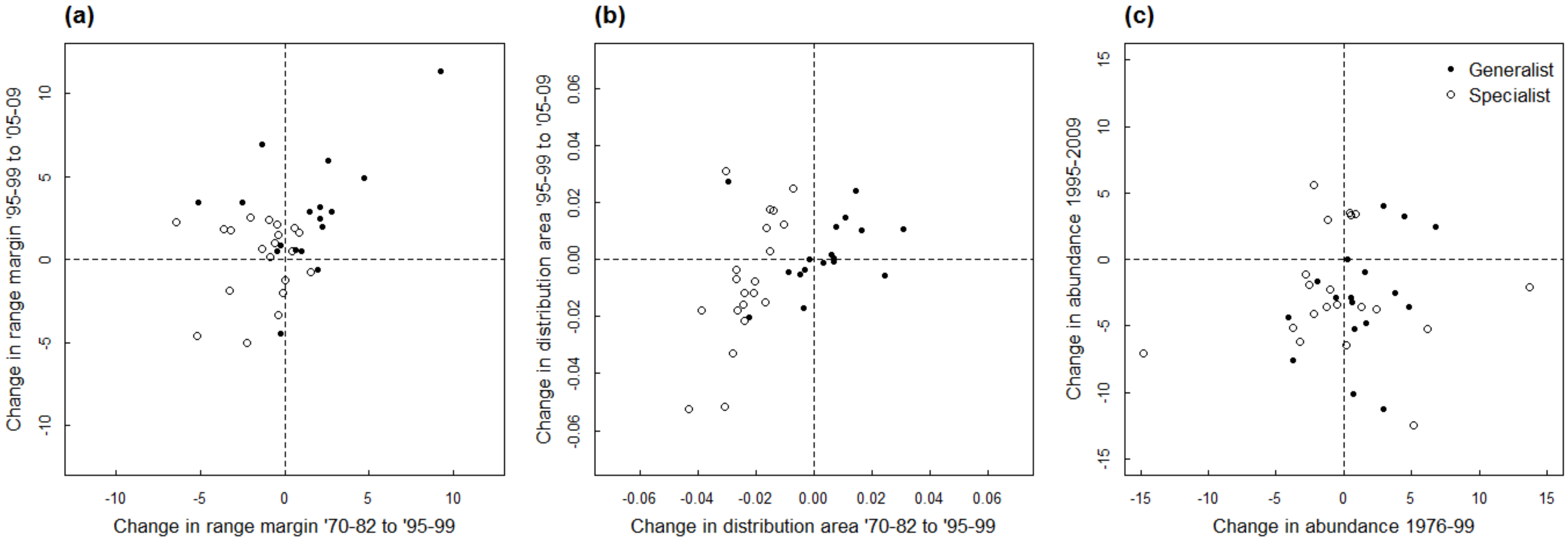

Figure 2.1. Consistency of species response in the second study period (1995-99 to 2005-09) plotted against response in the first study period (1970-82 to 1995-99) for **(a)** change in species' northern range margin (rate of change of the northern range margin in km yr^{-1}, *P. c-album* is an outlier) **(b)** change in species distribution area (mean proportional change in number of 10km grid squares occupied per year) and **(c)** change in species abundance (percentage change per year from the regression slope of $\log_{10}$ abundance index against year) for habitat generalists (solid symbols) and specialists (open symbols).

In order to compare responses of species for all three variables simultaneously, we converted changes in range margin, distribution area and abundance over time to categorical increase/decrease values. Table 2.2 highlights the lack of consistent responses of species over time using this method. Only five species (13.5%) showed qualitatively similar responses (either increase or decrease) to the three response variables over the two study periods. These were three generalists (*Aphantopus hyperantus*, *Pararge aegeria* and *Polygonia c-album*) with consistently positive trends in all three response variables, and two specialists (*Leptidea sinapis* and *Pyrgus malvae*) with consistently negative trends in all three response variables. All other species showed qualitatively inconsistent responses over time.

Table 2.2 Species' responses in the first and second study period, indicating whether species have increased (+) or decreased (–) in terms of change in distribution area, change in abundance, and change in northern range margin (+northwards shift, – southwards shift). G = habitat generalist, S = habitat specialist. Scientific names are those used in Fox *et al.* (2006). Vernacular names and values of change in response variables are given in Table A2.

Species	Habitat	Range Margin		Distribution area		Abundance	
		1st	2nd	1st	2nd	1st	2nd
Aphantopus hyperantus	G	+	+	+	+	+	+
Pararge aegeria	G	+	+	+	+	+	+
Polygonia c-album	G	+	+	+	+	+	+
Melanargia galathea	G	+	+	+	+	+	–
Plebeius (Aricia) agestis	G	+	+	+	+	+	–
Thymelicus lineola	G	+	+	+	+	+	–
Satyrium w-album	G	+	+	–	+	–	–
Limenitis camilla	S	+	+	–	+	–	–
Melitaea athalia	S	+	+	–	+	–	–
Thymelicus sylvestris	G	+	+	+	–	+	–
Gonepteryx rhamni	G	+	+	–	–	+	–
Plebeius argus	S	+	+	–	–	+	–
Polyommatus bellargus	S	–	+	–	+	+	+
Apatura iris	S	–	+	–	+	–	+
Hesperia comma	S	–	+	–	+	+	–
Celastrina argiolus	G	–	+	+	–	+	–
Pyronia tithonus	G	–	+	+	–	–	–
Euphydryas aurinia	S	–	+	–	–	–	+
Pieris rapae	G	–	+	–	–	+	–
Polyommatus coridon	S	–	+	–	–	+	–
Thecla betulae	S	–	+	–	–	+	–
Boloria euphrosyne	S	–	+	–	–	–	–
Boloria selene	S	–	+	–	–	–	–
Lasiommata megera	G	–	+	–	–	–	–
Neozephyrus quercus	G	–	+	–	–	–	–
Erynnis tages	S	–	+	–	–	–	–
Hipparchia semele	S	–	+	–	–	–	–
Anthocharis cardamines	G	+	–	+	+	+	–
Callophrys rubi	S	+	–	–	+	–	–
Cupido minimus	S	+	–	–	–	+	+
Ochlodes sylvanus (venata)	G	+	–	–	–	+	–
Argynnis paphia	S	–	–	–	+	+	+
Argynnis adippe	S	–	–	–	–	+	–
Hamearis lucina	S	–	–	–	–	+	–
Lycaena phlaeas	G	–	–	–	–	+	–
Leptidea sinapis	S	–	–	–	–	–	–
Pyrgus malvae	S	–	–	–	–	–	–

2.4.2 Relationships among response variables

Rates of marginal expansion northwards showed a significant positive relationship with changes in distribution area during the first and second study periods (linear regression; r^2=0.31, P<0.001, and r^2=0.15, P=0.01 respectively). The intercept of the relationship was not significantly different from zero for the first study period (intercept=0.49, t=0.85, P=0.4), but was for the second study period (intercept=1.58, t=2.95, P=0.005), indicating that during the second study period species range margins expanded northwards without any associated increase in species' distribution areas.

Changes in distribution area also showed a significant positive relationship with changes in abundance during the first and second study periods (r^2=0.16, P=0.008, and r^2=0.14, P=0.01 respectively). However, rates of range margin expansion showed no significant relationship with changes in abundance during the first or second study periods (r^2=0.0003, P=0.3, and r^2=0.008, P=0.4 respectively).

2.4.3 Responses of specialist and generalist species

Previous studies have shown that species responses to climate differ between generalist and specialist species. Our analyses confirmed that during the first study period, generalists were doing significantly better than specialists in terms of rates of expansion northwards (t-test, t_{27}=2.97, P=0.006) and changes in distribution areas (t_{25}=6.23, P<0.001; Fig 2.2a), but there was no significant difference in changes in abundance (t_{30}=1.09, P=0.3) (Table 2.1). During the second study period, generalists continued to spread northwards at significantly greater rates than specialists (t_{27}=2.72, P=0.01), but there was no longer a difference in terms of changes in distribution area (t_{30}=1.67, P=0.1; Fig 2.2b), and there was still no difference in terms of changes in abundance (t_{34}=0.38, P=0.7) (Table 2.1).

The lack of separation of generalists and specialists during the second study period is primarily due to different temporal trends in responses among generalists and specialists. Generalist species showed no significant difference between study periods in rates of range expansion northwards (paired t-test, t_{16}=1.84, P=0.08) or changes in distribution area (t_{16}=0.13, P=0.8), but did show a significant shift from increasing to decreasing abundances (t_{16}=4.28, P<0.001). In contrast, specialist species showed a significant increase in rates of expansion northwards (t_{19}=2.15, P=0.04) and changes in distribution area (t_{19}=3.90, P<0.001) but no significant difference between study periods in changes in abundance (t_{19}=1.45, P=0.1). Thus differences between generalists and specialists were less marked during the second study period.

The broad differences between specialists and generalists are illustrated by comparison of the specialist Grizzled Skipper (*Pyrgus malvae*), which declined in distribution area, abundance and northern range margin over both study periods, and the generalist Small Skipper (*Thymelicus sylvestris*), which expanded northwards during both study periods even though its distributional area and abundance declined slightly during the second study period (Fig 2.3).

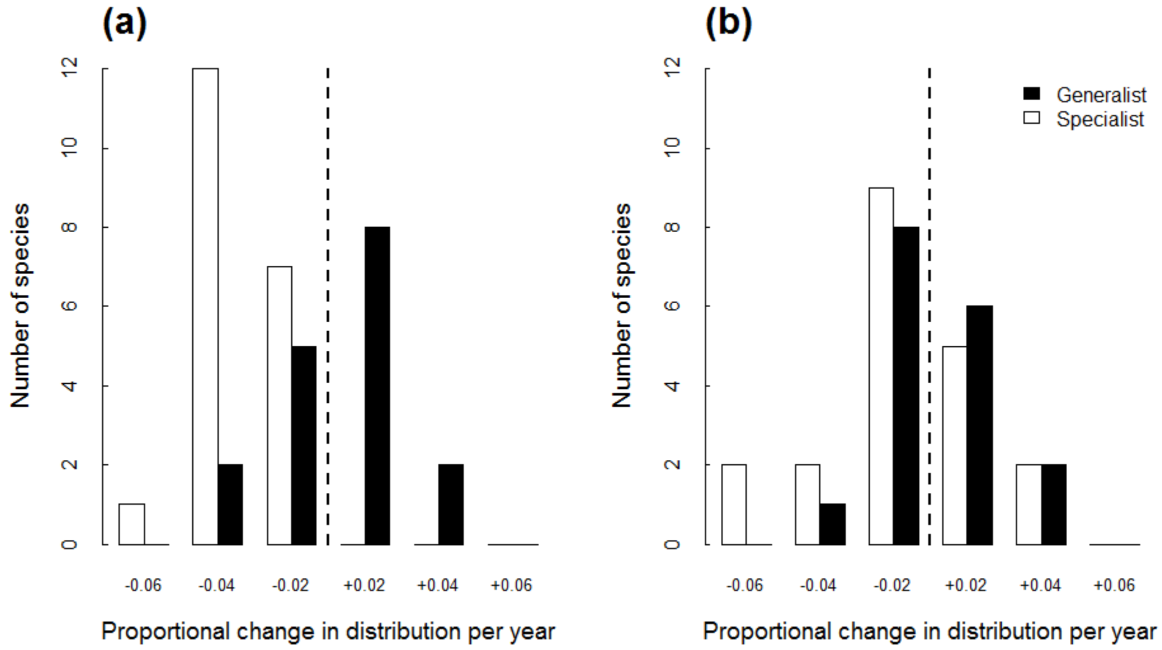

Figure 2.2.Change in species distribution area as the proportional change in number of 10km OS grid squares occupied per year for generalists (black bars) and specialists (white bars) (as defined by Asher *et al.* 2001) from **(a)** 1970-82 to 1995-99 and **(b)** 1995-99 to 2005-09.

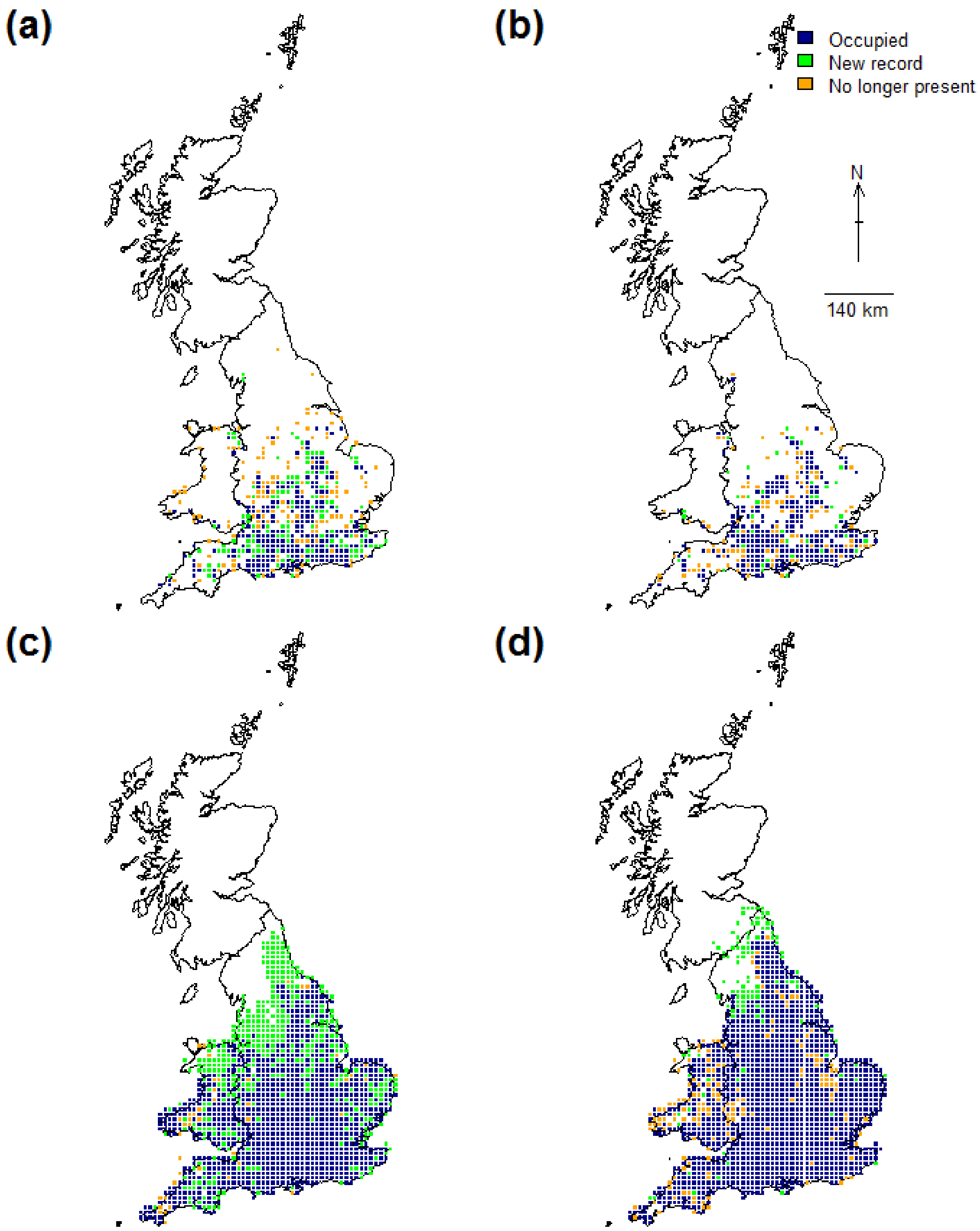

Figure 2.3. The change in distribution of two species which illustrate trends identified in Table 2.1. The Grizzled Skipper (*Pyrgus malvae*) has shown a decrease in distribution area and contraction south from both **(a)** 1970-82 to 1995-99; and **(b)** 1995-99 to 2005-09. The Small Skipper (*Thymelicus sylvestris*) increased its distribution area and expanded northward from **(c)** 1970-82 to 1995-99; and continued to expand northwards despite decreasing in distribution area and abundance from **(d)** 1995-99 to 2005-09. Blue squares (10km resolution) indicate currently and previously occupied squares, green squares are new records, and orange squares are location where the species was previously recorded but is not longer present.

2.5 DISCUSSION

2.5.1 Idiosyncratic species responses

We found that species responses to climate change were temporally variable. Although there was a weak positive relationship for change in distribution areas between study periods, there was no significant relationship for rate of expansion northwards or change in abundances. Furthermore, the qualitative analysis which categorised species responses as either increasing or decreasing indicated that only 13.5% (5/37) species showed qualitatively consistent responses over time. There are however, some broad trends in the analyses which may help to explain these idiosyncratic species responses.

Firstly, despite less warming during the second study period, species expanded northwards and increased their distribution areas at a significantly greater rate compared with the first study period. Indeed while the rate of temperature increase during the first study period was statistically significant, the lower rate of increase during the second study period was not significantly different from zero. This suggests that species may have been exploiting climate-distribution lags remaining from the earlier, warmer period and were not expanding at their maximum potential rates during the first study period (Menéndez *et al.*, 2006, Devictor *et al.*, 2012). The lack of relationship between study periods suggests that while overall species showed an increase in rates of expansion, temporal changes in individual rates were nevertheless idiosyncratic. The idiosyncratic responses of species were likely determined by species-specific factors such as spatial variation in habitat and host plant availability (Gutiérrez & Thomas, 2000, Hill *et al.*, 2001) and sensitivity to different climatic variables (Roy *et al.*, 2001).

Secondly, despite an increase in both rates of range margin shifts and changes in distribution areas during the second study period, there was evidence that range margin expansions were not necessarily accompanied by any associated increases in distribution areas. The significant intercept of the regression between range margins and distributions areas during the second study period indicates that the rates of range margin expansion exceeded the rates of distribution area changes, suggesting that as species range margins expanded northwards, their distributions thinned. This may reflect more scattered population distributions at species range margins (Brown *et al.*, 1996), but could also imply population losses within species ranges, suggesting that habitat loss and deterioration may be having negative effects on species distributions (Van Dyck *et al.*, 2009, Forister *et al.*, 2010).

Thirdly – and closely linked to the previous point – there was a significantly greater decline in species abundances during the second study period, and there was no evidence that the species which expanded northwards showed an increase in abundance. Declines in abundance tend to reflect environmental deterioration such as habitat loss and degradation as well as short-term climatic variation (Brereton *et al.*, 2011), while in contrast expansions northwards across human-modified and fragmented landscapes are more likely to be primarily driven by longer-term climatic changes (Thomas, 2010). Thus both the declines in abundances and the apparent thinning of species distributions during the second study period, support the suggestion that habitat changes are causing population losses within species ranges, but that climate change is nevertheless driving northwards expansion at species range margins. Species distributions and abundances thus reflect the cumulative impacts of both climatic and habitat variables (Hill *et al.*, 2002, Dieker *et al.*, 2011), and the individual nature of species requirements appears to have created individualistic responses to environmental change.

2.5.2 Responses of specialists and generalist species

Analysing generalist and specialist species separately further helps to explain the idiosyncratic nature of species responses. During the first study period, generalist species expanded their range margins and increased their distribution areas at significantly greater rates than specialists, as would be expected (Warren *et al.*, 2001, Jiguet *et al.*, 2007). However during the second study period, although generalists continued to expand northwards at greater rates than specialists, there was no difference between species groups in terms of changes in distribution areas. This is a result of the generalists showing little increase in distribution areas in either study period, combined with specialists showing significantly lower rates of decline in distribution areas in the second study period compared with the first. This may reflect some conservation successes for specialist species, which became evident in the later study period (Asher *et al.*, 2011, Fox *et al.*, 2011).

2.5.3 Conclusions

We conclude that the responses of British butterflies to climate change vary among species and within species over time, indicating that species respond in an individualistic way to both climatic and non-climatic drivers of distribution and abundance change. Northwards range margin expansions which are not always accompanied by increases in distribution areas and/or abundances suggest that some species’ distributions have thinned as the species have spread.

2.6 ACKNOWLEDGEMENTS

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3 Abundance changes and habitat availability drive species' responses to climate change

Louise Mair[1*], Jane K. Hill[1], Richard Fox[2], Marc Botham[3], Tom Brereton[2] & Chris D. Thomas[1]

[1]Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK.

[2]Butterfly Conservation, Manor Yard, East Lulworth, Wareham, BH20 5QP, Dorset, UK.

[3]Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford,
Wallingford, Oxfordshire, OX10 8BB, UK.

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3.1 ABSTRACT

There is little consensus as to why there is so much variation in the rates at which different species' geographic ranges expand in response to climate warming (Angert *et al.*, 2011, Mattila *et al.*, 2011). Here, we show for British butterfly species that the relative importance of species' abundance trends and habitat availability vary over time. Species with high habitat availability expanded more rapidly from the 1970s to mid-1990s, when abundances were generally stable, whereas habitat availability effects were confined to the subset of species with stable abundances from the mid-1990s to 2009, when abundance trends were generally declining. This suggests that stable (or positive) abundance trends are a prerequisite for range expansion. Given that species' abundance trends vary over time (Brereton *et al.*, 2011) for non-climatic as well as climatic reasons, assessment of abundance trends will help improve predictions of species' responses to climate change, and help understand the likely success of different conservation strategies for facilitating their expansions.

3.2 RESULTS AND DISCUSSION

Identifying species' traits associated with rapid range expansions in response to climate change provides insight into the conservation strategies most likely to be successful (Arribas *et al.*, 2012). However, such understanding may be difficult to attain, given that the ability of species' traits, such as reproductive rate, to explain responses to climate change is frequently low (Angert *et al.*, 2011). Previous studies suggest that the expansion of species' distributions across landscapes will depend on species' dispersal abilities (Warren *et al.*, 2001, Gaston & Blackburn, 2002, Mattila *et al.*, 2011), the availability of habitat (Hill *et al.*, 2002), and population abundance trends, which determine the supply of migrants to colonise new locations (Newton, 1997). Species' population and distribution trends will also be affected by interactions between traits and the environment, thus predictions of range expansions may be limited if habitat availability and population trends are not considered simultaneously. Furthermore, abundance trends vary over time (Brereton *et al.*, 2011), associated with variability in climate warming (Chen *et al.*, 2011a) and habitat quality and quantity (Eglington & Pearce-Higgins, 2012), so it might be expected that the relative importance of predictors of distribution changes also vary over time.

Here, we consider the roles of abundance trends, habitat availability and dispersal capacity in the range changes of 25 British butterfly species during two periods. Distribution changes were measured between blocks of time (1970-82 to 1995-99 and then 1995-99 to 2005-09) to ensure sufficient data to record distribution changes in a robust manner (1970-82, 1995-99 and 2005-09 represent periods with intensive recording; > 1,220,000 distribution records and > 262,000 abundance transect records). Butterflies are an ideal group for this analysis. Not only are there more long-term species-specific datasets than any other poikilothermic animal group worldwide, but most between-species variation in expansion rates exists within taxonomic groups rather than between groups (Chen *et al.*, 2011a) and so our conclusions are likely to be relevant to other taxa. Average annual temperature increased at a rate of 0.03 °C yr^{-1} in the first study period (1970-82 to 1995-99), and 0.01 °C yr^{-1} in the second (1995-99 to 2005-09). We expected the lower rate of temperature increase in the second period to have relatively little effect on rates of distribution change due to climate distribution lags (Devictor *et al.*, 2012, La Sorte & Jetz, 2012), and indeed species showed idiosyncratic responses to climate warming; some expanded their ranges in both periods, some in only one period, and some retracted in both periods (Mair *et al.*, 2012) (Table A3.3.1).

We studied 25 southerly-distributed butterfly species which have the potential to extend their distributions under climate change (migrants, northern and ubiquitous species were excluded, further exclusions were due to insufficient data). We quantified changes in distribution area using the Butterflies for the New Millennium (BNM) dataset (Asher *et al.*, 2001) as the percentage change in the number of 10 km grid squares occupied per year, to account for the different lengths of study periods and different initial species' range sizes. Changes in abundance were calculated using the UK Butterfly Monitoring Scheme (UKBMS) transect dataset (Botham *et al.*, 2010) by regressing abundance indices from continuously occupied transect sites (sites at which a species was present every year during the study period) against year (Pollard *et al.*, 1995), to give percentage change in abundance per year for each species. We used a rank mobility score (Cowley *et al.*, 2001) to represent species dispersal ability (derived from expert opinion). Habitat availability was calculated by combining remote-sensed land cover (Fuller *et al.*, 2002, Morton *et al.*, 2011) estimates with expert assessments of species' habitat associations (Asher *et al.*, 2001) (see Appendix 3). We only considered the availability of habitat in the 10 km grid squares which the species colonised during each period, thus focussing measures on those areas where species' distributions were changing. It was not possible to quantify landscape change over time because annual habitat data are not available and the categorisation of land cover data in the two study periods has changed (Morton *et al.*, 2011). We employed an information-theoretic approach to identify the best models for explaining distribution changes. For each study period separately, we constructed general linear models to assess distribution changes against all three variables (abundance trends, habitat availability, dispersal ability) including their interactions, and AICc values and Akaike weights were used to determine the best fitting models. When ΔAICc < 2, models are considered to be of equal strength (Burnham & Anderson, 2002) so model averaging was used. (Incorporation of phylogenetic correlations did not improve the fit of models so we do not present phylogenetic analyses; see Appendix 3).

In the earlier period, nine species expanded their distribution area (mean change = 0.8% yr^{-1} ±0.1 s.e.m.) and 16 species retracted (mean change = -2% yr^{-1} ±0.2 s.e.m.). The abundance trends of species were generally stable in permanently occupied sites (mean abundance change = -0.5% yr^{-1} ±1.75 s.e.m.). The best fitting models included habitat availability and dispersal ability, but not abundance (Table 3.1a). Habitat availability was the most important explanatory variable (R^2 = 0.35, Table A3.3.4a); range expansions were greatest for species with high habitat availability (Fig 3.1a). Dispersal ability was much less important, and in models where it was included it showed a negative relationship. This unexpected relationship suggests that once habitat availability was accounted for, less dispersive species did not fare any worse than more dispersive species.

In the later study period, 11 species extended their ranges (mean change = 1.4% yr^{-1} ±0.3 s.e.m.) and 14 species retracted (mean change = -0.8% yr^{-1} ±0.1 s.e.m.), during a period when overall abundance trends were negative (mean change = -6.99% yr^{-1} ±3.04 s.e.m.). In contrast to the first period, the best fitting model included only abundance (Table 3.1a; Fig 3.1b). Distribution change showed a positive association with abundance change (R^2 = 0.15, Table A3.3.4b); species which retracted their ranges showed larger declines in abundance (mean abundance change = -11.47% yr^{-1} ±4.23 s.e.m), whereas species with expanding ranges showed considerably smaller declines or had stable abundances (mean change = -2.39% yr^{-1} ±2.92 s.e.m). Thus there was little consistency in the responses of species over the two study periods (Mair *et al.*, 2012), and the importance of habitat availability as a determinant of range expansion also varied over time, associated with abundance trends. We found little evidence that dispersal was important, which supports other studies indicating that species' traits are poor predictors of distribution changes (Angert *et al.*, 2011), and our results suggest that the importance of species' traits may be context-specific.

Table 3.1. Average model parameter estimates, standard errors and relative importance of variables.

Model variables	Estimate	Unconditional S.E.	Relative importance*
a Change in distribution (abundance from continuously-occupied sites)			
1970-82 to 1995-99			
Habitat availability	1.835	0.584	1
Dispersal ability	-0.659	0.715	0.28
1995-99 to 2005-09			
Change in abundance	1.427	0.631	1
b Change in distribution (abundance from all sites)			
1970-82 to 1995-99			
Change in abundance	1.996	0.531	1
Habitat availability	2.059	0.626	1
Abundance x habitat	1.670	0.803	0.61
Dispersal ability	-0.873	0.531	0.68
Abundance x dispersal	1.858	1.017	0.21
1995-99 to 2005-09			
Change in abundance	1.258	0.442	1
c Median colonisation distance			
1995-99 to 2005-09			
Habitat availability	3.802	1.045	1

a response variable is change in distribution area (using species' abundances from only continuously-occupied transect sites)

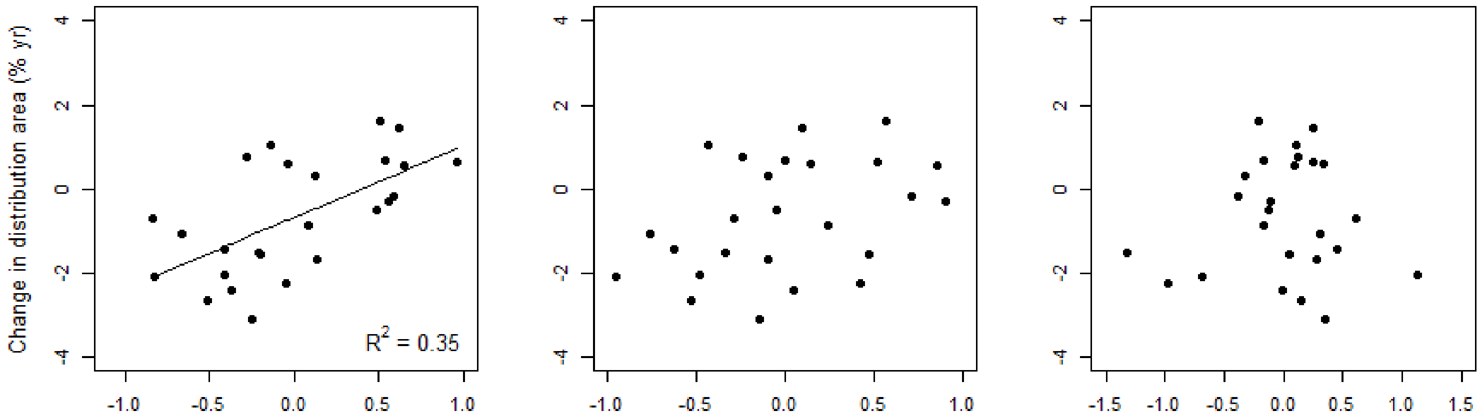
b response variable is change in distribution area (using species' abundances from all sites including those that were colonised during the study period)

c response variable is median colonisation distances

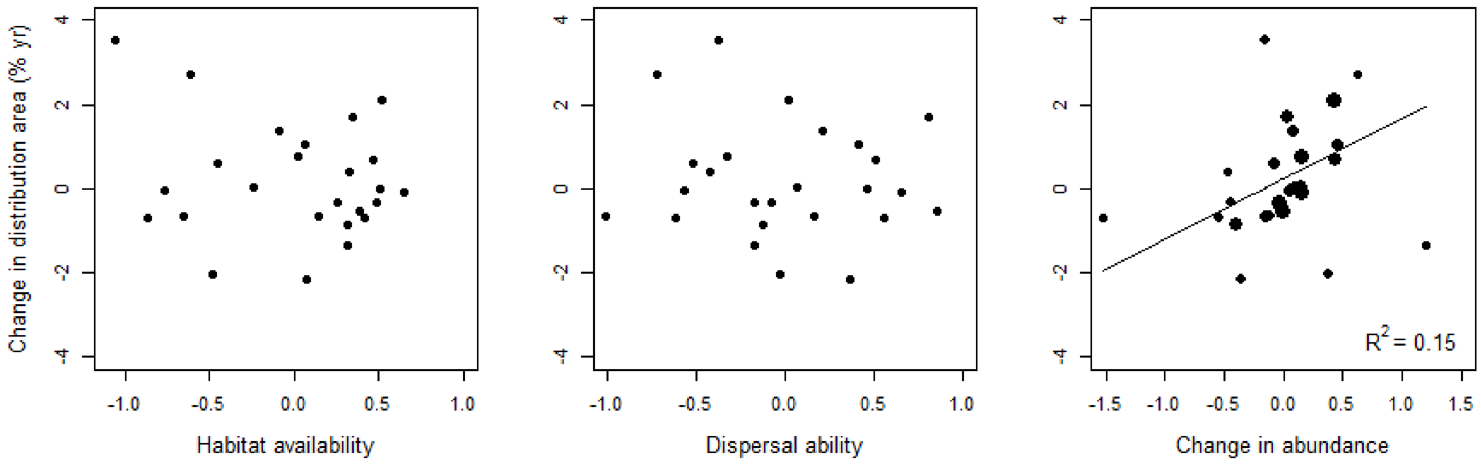
* Relative importance of variables of 1 indicates that the variable was present in all top models, or was the only variable when model averaging was not necessary because the difference in AICc between the first and second highest ranking models was > 2 (Tables A3.3.4 and A3.3.6).

Figure 3.1. Change in species distribution area in relation to habitat availability, dispersal ability and change in abundance (at continuously-occupied transect sites). Distribution change is plotted against standardized variables: $\log_{10}$ habitat availability index, rank order dispersal ability and change in abundance (% yr^{-1}) for **a** the first study period (1970-82 to 1995-99) and **b** the second study period (1995-99 to 2005-09). Solid line is the fitted relationship for the most important explanatory variable (Table 3.1). The size of points reflects weighting in analyses involving abundance change (weight = 1/S.E. abundance), which improved the model fit for the second period, but not the first.

a 1970-82 to 1995-99



b 1995-99 to 2005-09



Previous research has found a strong relationship between abundance changes and distribution changes (Pollard *et al.*, 1995, Warren *et al.*, 2001) and we show that abundance trends are important for determining whether or not species expand their range. The absence of abundance as an important predictor of distribution changes in the best fitting models in the first study period may be because we analysed abundance trends only at continuously occupied sites. When data for transect sites colonised during the first period were also included in estimates of species' abundance trends, abundance was positively related to change in distribution area, suggesting that increased overall abundance was a consequence rather than a cause of expansion (Table 3.1b). This implies that species with generally stable abundances in long-established populations exhibit density-dependent, positive population growth at newly-colonised sites (Nee *et al.*, 1991). In contrast, species with steeply-declining abundances in long-established sites would be unlikely to produce many migrants and may show negative population growth at newly-colonised sites, and hence fail to establish and expand their ranges (Conrad *et al.*, 2001).

We further tested these determinants of distribution changes by examining factors associated with colonisation in the subset of species that expanded their ranges in the second study period (N = 11 species; see Fig 3.2 and Appendix 3). We found that habitat availability was the most important explanatory variable of median colonisation distance ($R^2 = 0.55$, Table A3.3.6), and that dispersal ability and abundance trends were not important (Table 3.1c; Fig 3.3). Thus for the subset of species in the second period with stable abundances and expanding ranges, species with greater habitat availability colonised over longer distances, in agreement with our findings in the first period and supporting the notion that species' traits (e.g. dispersal ability), other than those that affect habitat availability, may be poor predictors of distribution change (Angert *et al.*, 2011). For declining species the null model was best, as was expected because colonisation is not usually an important feature of declining distributions.

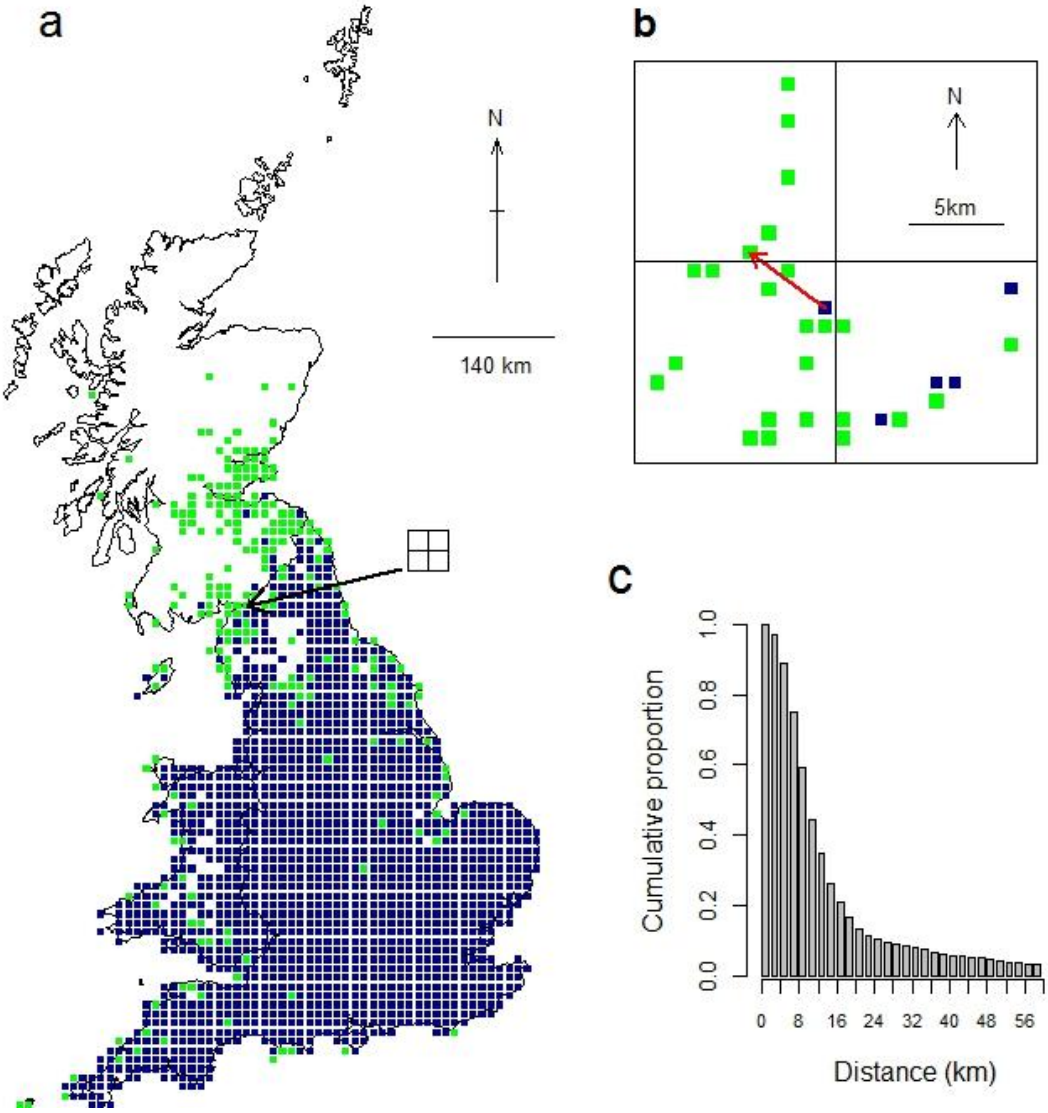


Figure 3.2. The distribution and colonisation distances of *Polygonnia c-album*. **a** The change in distribution of the butterfly from 1995-99 to 2005-09 (10 km resolution). Blue squares = occupied in 1995-99, green squares = colonised in 2005-09. **b** A selection of the distribution data at 1km resolution, showing presence in 1995-99 (blue squares) and new records in 2005-09 (green squares). The distances from new locations at the species distribution edge (defined as 10km squares which were unoccupied in 1995-99 but colonised in 2005-09) to the nearest existing records (red arrow) were found, and used to compute **c** colonisation distance distributions.

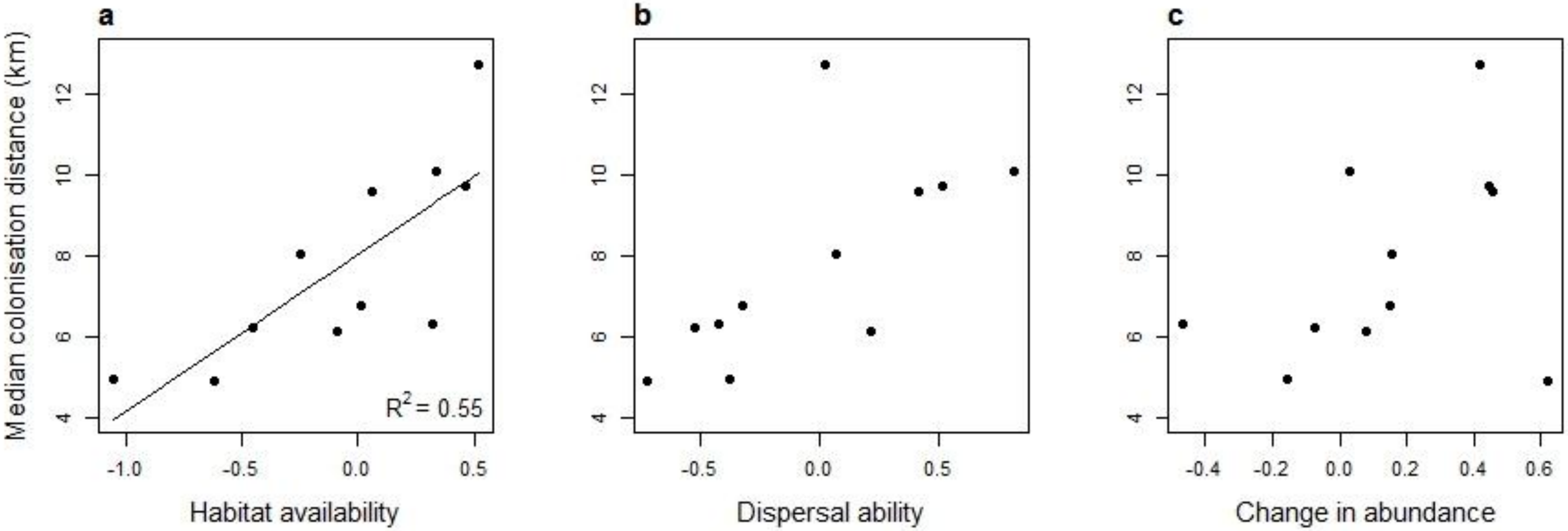


Figure 3.3. Colonisation distance for distribution-expanding species in relation to habitat availability, dispersal ability and change in abundance. Median colonisation distance (km) is plotted against standardized **a** $\log_{10}$ habitat availability index, **b** rank order dispersal ability and **c** change in abundance (% yr^{-1}, at continuously-occupied transect sites) for the second study period (1995-99 to 2005-09). Solid line is the fitted relationship for the most important explanatory variable (Table 3.1).

Our results suggest that positive or stable abundance trends are a prerequisite for species range expansion (Willis *et al.*, 2009b), enabling species to establish populations in new sites. Once these conditions are met, habitat availability, which arises from the interaction between a species' niche-related traits and the environment, becomes a limiting factor. During the first study period, when abundance trends generally were not limiting, habitat availability was the most important determinant of range expansion (10 km grid resolution data). During the second period, when declining abundance trends limited expansion, habitat availability had no predictive power, but was the most important explanatory variable for the subset of species with expanding distributions and stable abundance trends (for colonisation distances estimated at 1 km grid resolution).

We conclude that drivers of range expansion in response to climate warming vary over time and that species' abundance patterns are crucial to interpreting these responses. It is unclear why the abundances of many butterfly species have declined in Britain, but the abundances of many other taxa are also declining (McRae *et al.*, 2012). Current evidence suggests that many species fail to expand because of lack of suitable habitat (Hill *et al.*, 2002), and so habitat connectivity should be improved (Lawton *et al.*, 2010). Our results strongly support this conclusion for the subset of species with stable abundances whose ranges are already expanding, and management such as habitat restoration may increase their rates of expansion (Davies *et al.*, 2005). However this type of habitat management is likely to prove ineffective for species with declining abundances. We conclude that conservation management to stabilise and increase abundance trends within the core of species' ranges is required (e.g. improving habitat quality), and that habitat creation to increase the number of species extending their range margins polewards will only be effective once species' abundance trends are stable or increasing.

3.3 METHODS SUMMARY

Change in species' distribution area was the percentage change in the number of 10 km x 10 km grid squares occupied. Sub-sampling was carried out on the dataset to account for the temporal increase in recording effort using established methods to give similar number of records and spatial coverage over time (Fox *et al.*, 2006) (see Appendix 3).

A rank mobility score (Cowley *et al.*, 2001) based on expert opinion was used to represent species' dispersal ability. Habitat availability was quantified separately for the two study periods as the proportion of each species' breeding habitat in the landscape using LCM2000 (Fuller *et al.*,

2002) and LCM2007 (Morton *et al.*, 2011) 25m resolution raster datasets respectively. Landcover categories relevant to species breeding habitat were identified using expert opinion (Asher *et al.*, 2001), and weighted based on the frequency with which species distribution records were associated with that landcover type (see Appendix 3). Change in abundance from the UKBMS transect dataset was calculated for continuously-occupied transect sites, but subsequent analyses also included recently-colonised sites (see main text). To estimate change in abundance for each species, $\log_{10}$ abundance index was regressed against year (Pollard *et al.*, 1995), with transect site as a random variable.

For each species during the second study period, we quantified colonisation distances from the BNM dataset (1 km grid resolution). The distances and frequencies of newly colonised sites (new 1 km grid square records in 2005-09) from the nearest occupied sites (existing 1 km records in 1995-99; Fig. 3.2 and Fig. A3.2.1) were computed. We included only colonisations at species' distribution edges (10 km squares which were unoccupied in 1995-99 but colonised by 2005-09; N = 12234 colonisations). Inverse power functions were fitted to the colonisation-distance distributions for each species, and the median distances from the fitted curves were used in analyses (Table A3.3.5).

Annual temperature data from the Central England Temperature series were downloaded from the UK Met Office (http://www.metoffice.gov.uk) to compute temperature change.

3.4 ACKNOWLEDGEMENTS

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3.5 AUTHOR CONTRIBUTIONS

JKH and CDT conceived and supervised the study and edited the manuscript. RF, MB and TB provided data and edited the manuscript. LM analysed the data and wrote the manuscript.

4 SPEED, a dynamic model for studying climate-driven range changes in relation to habitat availability

Barbara J. Anderson[1,2], Louise Mair[1], Calvin Dytham[1], Richard Fox[3], David B. Roy[4], Chris D. Thomas[1], Jane K. Hill[1]

[1] Department of Biology, Wentworth Way, University of York, York YO10 5DD, UK

[2] Landcare Research, Private Bag 1930, Dunedin 9045, New Zealand

[3] Butterfly Conservation, 3 Manor Yard, East Lulworth, Dorset BH20 5QP, UK

[4] Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK

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4.1 SUMMARY

1. Dynamic models relating species' distributions to climate and habitat availability are required in order to improve our projections of how species' ranges may shift in future. We have developed a spatially-explicit, individual (agent)-based dynamic model ('SPEED') that includes dispersal, as well as population dynamics mediated by climate suitability and habitat availability, to simulate distributions in realistic landscapes.

2. We describe SPEED and demonstrate its practical application. At each time step in the model, individuals are born, disperse, reproduce and die, and these population dynamics are determined by habitat availability and temporal variation in local climate suitability. We describe the model inputs, operation, and outputs.

3. We illustrate the model's performance by simulating range changes over three decades in *Pararge aegeria* (speckled wood butterfly). We seeded the model with the species' historical (1970s) distribution in Britain, and SPEED successfully simulated the observed range expansion of *P. aegeria* at a 1 km grid resolution over 34 years of climate change. For *Pararge aegeria*, SPEED was most sensitive to variation in maximum population growth rate, which primarily affected the rate of expansion (27% reduction in predicted range extent for 25% reduction in population growth rate), and was less sensitive to variation in dispersal ability or carrying capacity.

4. There is an urgent need to develop dynamic models that can simulate species' range changes, and that incorporate spatial and temporal variation in climate change and habitat availability. SPEED can be used to examine recent range changes and also to project future changes. SPEED is parameterised with data that are becoming increasingly available and SPEED has the potential to be widely used in studies examining both habitat-change and climate-driven range expansion and retraction.

Keywords: Agent-based models; Species distribution models; Individual-based models; Lepidoptera; invasion; dispersal.

4.2 INTRODUCTION

The geographic distributions of species are at least partly determined by climatic factors and recent climate change has resulted in species shifting their ranges to higher latitudes and uphill to track climate (Parmesan & Yohe, 2003, Chen *et al.*, 2011a). However, the responses of species to climate change are idiosyncratic (le Roux & McGeoch, 2008) and rates of range shift also vary within species ranges (Hill *et al.*, 2001) and over time (Mair *et al.*, 2012); although the factors driving variation in species' responses are poorly understood (Angert *et al.*, 2011). Thus, there is a need to develop better methods for studying changes in species' ranges, in order to examine the relative importance of climate versus other factors on rates of range shifting, and to evaluate how species' ranges may change in the future.

Previous methods for studying climate impacts on species' ranges, and for projecting future distributions under climate change, have used static 'climate envelope' models to describe species' distributions (e.g. Thuiller, 2004). These static models normally express dispersal as one of two extremes, either 'no dispersal' where the species are assumed to occupy only those areas of the species' current distribution that remain climatically suitable in future, or 'unlimited dispersal' where species are assumed to colonise all climatically-suitable areas in future (Hill *et al.*, 2002). Given that neither of these two dispersal scenarios is likely to be realistic, there is a need to develop dynamic models that incorporate species' dispersal ability (Hill *et al.*, 2001) and which can be used to study range expansion across patchy landscapes (Willis *et al.*, 2009b). Furthermore, given that dispersal is essentially a stochastic process where the probability of dispersing is partially dependent on the number of propagules available for dispersal, such models need to incorporate population dynamics.

Here, we describe an individual-based distribution model ('SPEED') which integrates spatially explicit environmental modelling with population dynamic and dispersal processes. SPEED includes statistical and mechanistic components by combining a static climate-envelope statistical model with a dynamic stochastic mechanistic population model. SPEED improves upon existing models in several ways; for example, SPEED links species' population dynamics to climate suitability and habitat availability, individuals disperse in continuous space, and SPEED can include a realistically large number of individuals, thereby allowing stochastic, rare dispersal events at range margins to be modelled. SPEED can model the expansion or retraction of species across extensive realistic landscapes, incorporating species' dispersal ability and combining annual variability in local climate with concomitant changes in population dynamics. The incorporation of fine scale spatial and temporal data allows SPEED to project species range changes across landscapes that reflect the climatic and habitat heterogeneity of modern landscapes. For example, previous models have projected range changes assuming climate is uniformly favourable (Hill *et al.*, 2001, Willis *et al.*, 2009b), or based on decadal averaged climate data (Anderson *et al.*, 2009), conditions that imply a degree of environmental smoothing that is unrealistic compared to the life span most individuals are likely to experience (WallisDeVries *et al.*, 2011). In addition, climate smoothing may have a large impact on the expansion or retraction of species when there is an underlying trend in climate suitability. For example, several 'good' years in succession might allow a population to increase sufficiently to overcome a physical barrier or region of largely unsuitable habitat, while several 'bad' years might drive a population locally extinct even while mean climatic conditions would indicate persistence (Bennie *et al.*, 2013, Estay *et al.*, 2014). Such patterns may not be simulated with smoothed data, which may be unrealistic given annual variability and its effect on population growth (Roy *et al.*, 2001), yet can be included within SPEED.

The key characteristics of the SPEED model are:

1. Individuals are located in continuous space and population dynamics are explicitly linked to local habitat availability and temporal variation in climate suitability;
2. Individuals disperse across heterogeneous landscapes comprising grid-based datasets for habitat availability (e.g. our illustrative example uses remotely-sensed land cover data, but other data such as topography, host plant, or other species' distributions could also be included) and climate suitability (here downscaled from species distribution-climate envelope models, but could also be based on other environmental surfaces, such as those based on physiological and microclimate models);
3. SPEED can be run at fine resolution over large areas for huge populations (e.g. Britain at 1 ha grid resolution for more than one billion individuals) using a standard PC with 32GB RAM;
4. Model gridded outputs include both distribution and local abundance data.

We describe the SPEED model and then illustrate its utility by modelling recent range expansion of *Pararge aegeria* (speckled wood butterfly) in Britain over three decades. The butterfly reaches a (northern) leading-edge range margin in Britain, and it has been expanding its range northwards to higher latitudes since the 1940s (Asher *et al.*, 2001), making it an ideal species for studying climate-driven range changes (Hill *et al.*, 2001). In addition, the butterfly is predominantly a woodland species, especially at its range margin (Asher *et al.*, 2001), and this habitat can be mapped readily from land cover data. The butterfly develops through several generations a year

(Pollard *et al.*, 1996), depending on temperature, but in this paper we run the model on an annual basis and incorporate population dynamic data based on annual measures. We illustrate the basic features of SPEED by simulating range expansion of *P. aegeria* in Britain from 1970 to 2004. These dates were chosen because they correspond to dates when national butterfly distributional atlases and surveys were carried out (Heath *et al.*, 1984, Fox *et al.*, 2006). In order to illustrate SPEED's properties further, we investigate the sensitivity of SPEED to assumptions of species' dispersal ability, local population carrying capacity and reproductive rate for *P. aegeria* in Britain.

4.3 MATERIALS & METHODS

4.3.1. The SPEED model

SPEED is an individual-based, spatially-explicit model where individuals are born, disperse, reproduce and die, and population dynamics are related to the local environment. Carrying capacity is determined by the amount of each type of suitable habitat available locally and reproductive rate by local climate suitability (Fig 4.1). Each individual experiences the surrounding population density, local habitat and climatic environments (at spatial scales of m, ha or km, as appropriate), with the climatic conditions adjusted at each time step (annual in our example, although any relevant time step can be used). These data are combined within the model to determine the likelihood of survival to reproduction, and number of offspring produced. Thus SPEED integrates four major drivers of species' range shifts: population dynamics (carrying capacity and reproductive rate), habitat availability, climate suitability, and dispersal. We describe methods for computing these parameters, and sources of data. Access to the executable for running SPEED, the parameter list and user manual for running the model are provided in the Supplementary Information, and other data sets are available from the sources we cite.

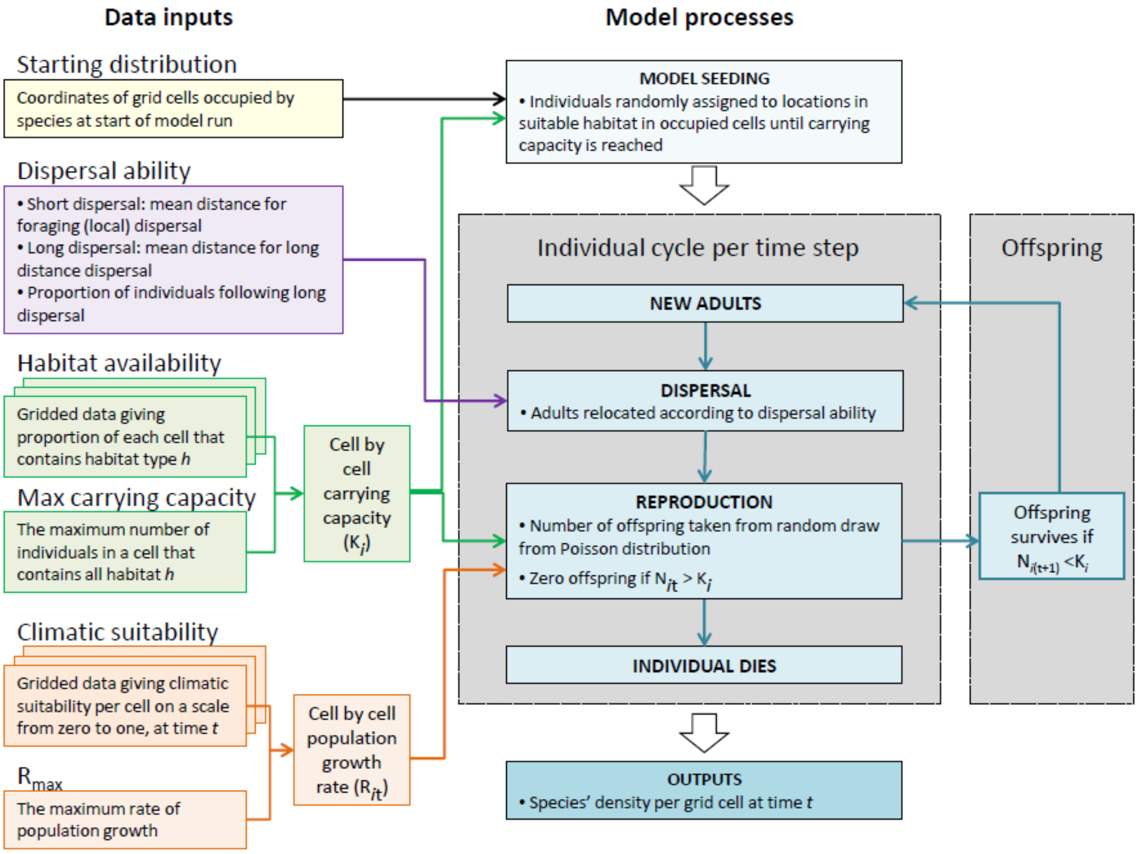


Figure 4.1. The structure of the SPEED model. The data required to run the model are detailed under 'Data Inputs' and arrows indicate how the data feed into the model processes. K_i denotes the cell-specific carrying capacity. N_{it} denotes the number of individuals in a cell (i) at time (t).

4.3.1.1 Mapping climate suitability

Any climate suitability surfaces can be used as inputs to SPEED, scaled from zero (unsuitable) to one (optimum) and inputted as gridded data at a resolution appropriate to the simulation. In our example, climate suitability was incorporated from climate envelope models at a 10 km grid square resolution and was varied annually.

4.3.1.2 Rate of reproduction

SPEED requires an estimate of the maximum population growth rate (R_{max}). Reproduction occurs in the SPEED model as a single event per time step (in the case of *P. aegeria* we have used an annual time step). The actual reproductive rate achieved is assumed in SPEED to be dependent on climate suitability, derived from the climate suitability layer. This allows the reproductive rate to vary both spatially and temporally, as individuals in different cells (spatial) or different time steps (temporal) experience different climatic conditions. The relationship between climatic suitability and population growth is defined as follows. We assumed that the realised population growth rate (R) increases linearly between two climatic thresholds: the minimum climate suitability for reproductive replacement (the 'break-even' point, where R = 1) and the optimum climate suitability (where R_{max} is achieved and beyond which there is no further increase in reproductive rate; See Fig A4.1). The optimum climate suitability (where R_{max} is achieved) can be specified by the user, or (as in our example using *P. aegeria*) can be taken as the maximum climate suitability observed in any grid cell within the study landscape at the start of the simulation. In our example, we assumed that the 'break-even' point (where R = 1) occurred when climate suitability values were equal to the AUC (Area Under the receiver operating characteristic Curve) threshold value generated from the species' observed starting distribution (1970-1982 distribution in Britain) and its projected probability of occurrence, based on a downscaled projection from a continental European climate-distribution model (see below). When climate suitability is lower than the 'break-even' point, R declines linearly to zero when climate suitability is zero (Fig. A4.1). In order to include a stochastic element representing natural variation in success and failure, the number of offspring produced by each individual is taken from a random draw of a Poisson distribution with a mean (*mu*) equal to the estimated reproductive rate (R) per grid cell (Travis & Dytham, 1999).

4.3.1.3 Determining habitat availability and carrying capacity

Carrying capacity (K) is determined by the amount of habitat available locally and the relative suitability of that habitat. SPEED requires an input surface of habitat availability, which could be based on field surveys or remotely-sensed data, at a spatial resolution appropriate to the study organism and which can be at a different resolution than climate suitability. Habitat availability data give the proportion of each grid cell that contains habitat suitable for reproduction. A maximum grid cell carrying capacity is set, which is the maximum number of individuals a grid cell can support if it contains 100% suitable habitat. The specific carrying capacity of each individual grid cell is calculated by multiplying the proportion of suitable habitat within the cell by the maximum carrying capacity.

Multiple habitat types can be incorporated into SPEED, and each habitat type can be weighted, assuming the modelled species may reach different densities in different habitat types. In this case, each habitat type is assigned a proportional value, which reflects the densities reached in that habitat type relative to the maximum density achieved in the most suitable habitat. When multiple habitat types are used, the cell-specific carrying capacity is the sum of the carrying capacities for each habitat type present in that cell (based on the area of each habitat type and the relative density of the species in each).

4.3.1.4 Dispersal ability

SPEED includes three dispersal parameters, although the modular structure of the programme would allow other dispersal functions to be incorporated. Two negative exponential dispersal kernels describe short-distance and long-distance dispersal, which together capture short-distance routine movements (e.g. foraging) and also longer-distance movements resulting in displacement (e.g. Van Dyck & Baguette, 2005). The third dispersal parameter quantifies the proportion of individuals allocated to long-distance versus short-distance dispersal. Thus dispersal is incorporated in SPEED as short distance dispersal, long distance dispersal, and the proportion of dispersing individuals allocated to long-distance dispersal (ranging between 0 = all short distance and 1 = all long distance). At each time step of the model, an individual disperses a random distance in a random direction in continuous space according to the long-distance or short-distance dispersal kernel it is allocated to.

4.3.2. Running and testing the SPEED model

4.3.2.1 Climate suitability for Pararge aegeria

For our illustrative example, we derived the climate suitability surfaces for *Pararge aegeria* for each year following the method of Carroll *et al.* (2009). Annual climate suitability maps for *P. aegeria* in Britain were generated for each year from 1970 to 2004 using a Generalised Additive

Model (GAM) (Hastie & Tibshirani, 1990). The GAM was built using European butterfly distribution data for *P. aegeria* (Carroll *et al.*, 2009) and European climate data (http://www.alarmproject.net/alarm; Fernández-Chacón *et al.*, 2014), but excluding UK data (see below). The GAM was then used to produce annual climate suitability maps for *P. aegeria* in Britain at 10 km grid resolution (Fig 4.2a). All spatial analyses to manipulate climate data were conducted in ArcMap version 9.3 (ESRI, Redlands, California, USA).

The European presence–absence data for *P. aegeria* were taken from Kudrna, 2002) and aggregated to the Atlas Florae Europaeae (AFE) 50 km grid. To reduce the impact of false absences, grid cells that were under-sampled were removed prior to analyses (including Russia, Belarus, Ukraine, Moldova and Turkey; based on Luoto & Heikkinen, 2008). Only distribution records between 1950 and 2000 were included to generate the climate envelope. We excluded British records for *P. aegeria* to reduce dependence of projections of climatic suitability for Britain on these training data.

European climate data for the climate 'normal' period of 1961–1990 at a 10 minute latitude-longitude grid resolution were generated by the FP5 ATEAM project (New *et al.*, 2002, Schröter *et al.*, 2005). We used these data to generate three bioclimatic variables (50 km grid resolution) that have been shown to be important to butterfly growth and survival; mean temperature of the coldest month (MTCO) associated with overwintering survival, annual growing degree days above 5 °C (GDD5) associated with larval development, and precipitation during the warmest six months (PPT6; Hill *et al.*, 1999b).

To project climate suitability for *P. aegeria* in Britain, data for the three bioclimate variables for Britain at a 10 km Ordnance Survey grid resolution were derived from CRU ts2.1 and CRU 61-90 climate datasets (Barrow *et al.*, 1993). This involved the anomalies at 0.5 deg grid resolution being interpolated onto the UK Ordnance Survey 10 km grid and combined with the TIGER climate data (Hill, 1995) from mean elevations within grid cells. Projections from the GAM using these finer scale climate data were generated to determine annual climate suitability in Britain for *P. aegeria* at a 10 km grid resolution for each year from 1970 to 2004. Climate suitability was mapped on a scale from zero (unsuitable) to one (optimum) (Fig 4.2a). The climate in Britain generally improved for *P. aegeria* over the 34 yr study period (Fig A4.2a&b), although there was some fluctuation, with 1974 having the least suitable climate and 2003 the most suitable for *P. aegeria* (Fig A4.2c&d).

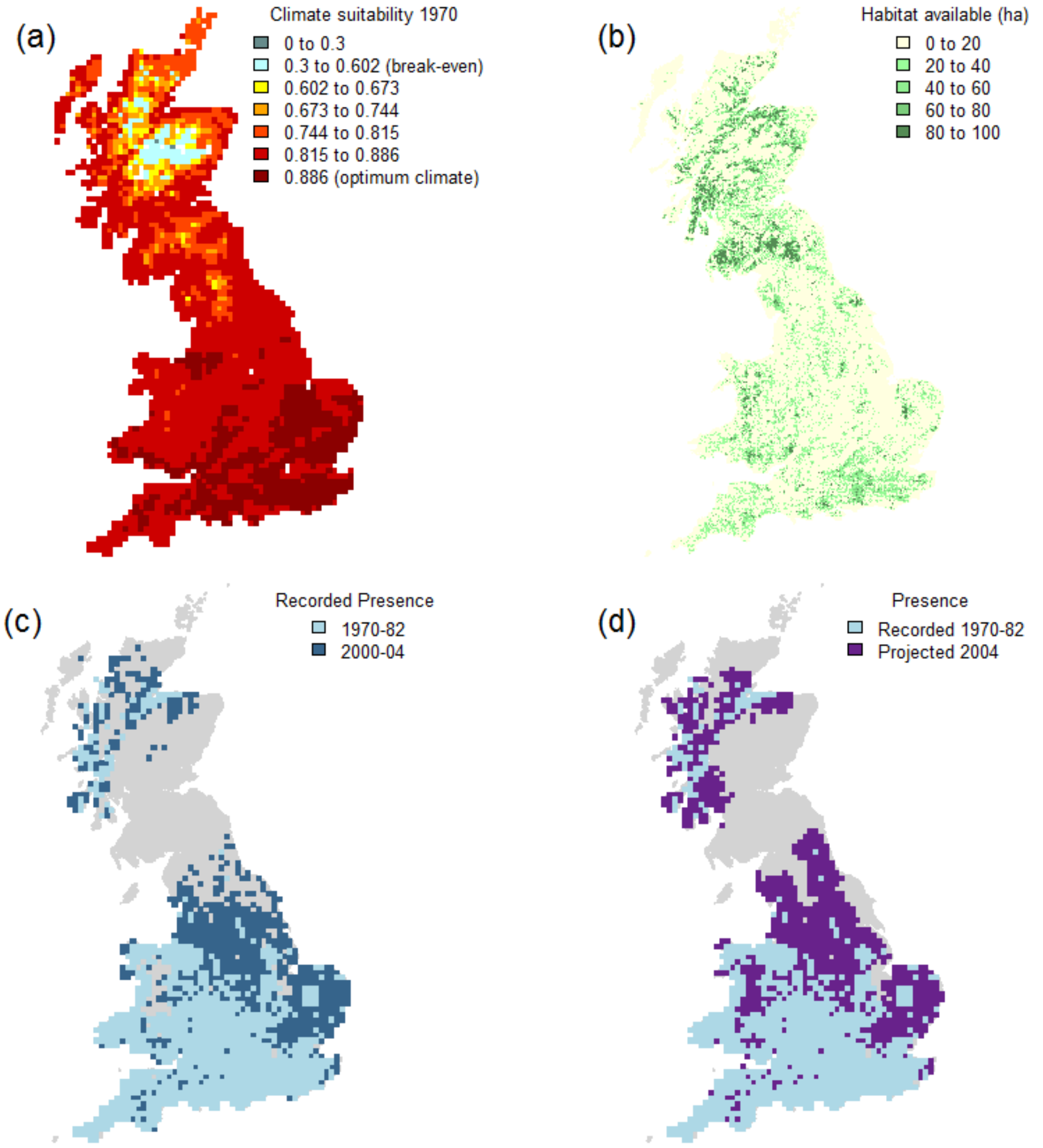


Figure 4.2. We illustrate SPEED by simulating range expansion in exemplar butterfly species, *Pararge aegeria* in the UK. **(a)** Climate suitability in 1970, from 0 = unsuitable, to 1 = suitable, **(b)** habitat availability at 1 km resolution (availability of deciduous and coniferous woodland from LCM2007), **(c)** observed distribution change for *P. aegeria* (1970 to 2004; light blue recorded as present in both 1970-82 and 2000-04 periods; dark blue cells show 'colonised' cells where the species was not recorded in 1907-82, but was present by 2000-04), and **(d)** distribution change predicted by SPEED (1970 to 2004; purple cells show the area of predicted colonisation), using the parameter specifications in Table 4.1 (Variation 0).

4.3.2.2 Reproductive rate

For *P. aegeria* in 1970, maximum climate suitability in Britain was 0.882 and the maximum population growth rate was R_{max} = 1.5 for any cells with a climatic suitability of 0.882 or above in subsequent years. Willis *et al.* (2009b) report the intrinsic rate of increase (r) to be 0.405 for *P. aegeria*, and we used the equation $r = \ln(R)$ to generate R_{max}. For *P. aegeria*, the population growth rate, R, is set to R=1 at a climate suitability value of 0.602, which is the suitability value that corresponded to the AUC threshold for the species' observed starting (1970-1982) distribution in Britain and the projected probability of occurrence for this same period based on our downscaled European GAM.

4.3.2.3 Habitat availability and carrying capacity

We incorporated habitat availability for *P. aegeria* into SPEED as gridded land cover data, based on analysis of remotely-sensed data, which distinguish different habitat types in Britain (LCM2007; Morton *et al.*, 2011). We selected 25 m resolution UK land cover data LCM2007 as the land cover map most likely to represent habitat availability at the end of the model run in 2004. It would potentially be possible to input annual land use surfaces into SPEED, were these available for a study species. *Pararge aegeria* occurs in deciduous and coniferous woodland (Hill *et al.*, 2001), and so these two land cover types were used to determine habitat availability.

We computed the mean density of *P. aegeria* using count data (based on 26 weekly surveys from April to September each year since 1976) from the UK Butterfly Monitoring Scheme transects (UKBMS, Botham *et al.*, 2010) for 339 geo-referenced transects where the species was present in at least one year during the study period (Oliver *et al.*, 2009). Density (adult *P. aegeria* counted per m^2 of habitat) was calculated separately for deciduous and coniferous woodland habitat types, by matching transect section data with the LCM2007 land cover surfaces and dividing butterfly abundance by the area of the transect within that habitat type (assuming that transects are 5 m wide and that each adult butterfly lives on average for one week). Density estimates were averaged across all years that each transect was recorded (maximum 35 years as the UKBMS started in 1976).

Our analyses of UKBMS transect data produced average *P. aegeria* density estimates of 12252 km^2 in deciduous woodland and 2157 km^2 in coniferous woodland. These mean densities of *P. aegeria* in each habitat were multiplied by the amount of deciduous and coniferous woodland habitat available per 1 km grid cell (summed from LCM2007 data available at 25m resolution), and summed to give an overall carrying capacity for each 1 km grid cell across Britain. Fig 4.2b shows the availability of suitable ('woodland') habitat for *P. aegeria* in Britain at a 1 km grid square resolution. Once a 1 km grid cell is at carrying capacity, new individuals either disperse or die (dispersal occurs from all occupied cells, regardless of whether or not they have reached carrying capacity, see below).

4.3.2.4 Dispersal ability

Empirical dispersal data are not available for *P. aegeria*. Thus the mean of the short-distance negative exponential kernel was set at 100 m and the mean of the long-distance negative exponential kernel was set at 5000 m to span the likely dispersal ability of relatively mobile butterflies such as *P. aegeria*.

4.3.2.5 Running the model

SPEED is seeded with individuals placed at random within grid cells recorded occupied at the start of the modelling period. We seeded the model with *P. aegeria* records from 1970-82 (10 km grid resolution; Fox *et al.*, 2006; Fig 4.2c). This time period corresponds to the first intensive recording period for British butterflies (Heath *et al.*, 1984), and represents the likely distribution of *P. aegeria* at this time. Individuals were assigned to random locations (at 1 m resolution) within the 10 km grid squares with butterfly records (928 grid squares in total) until the maximum density was reached within the available habitat. We incorporated habitat availability (1 km grid resolution) and climate suitability (10 km grid resolution) and used SPEED to simulate changes to the distribution of *P. aegeria* in Britain from 1970 to 2004, comparing the final modelled distribution in 2004 to the actually distribution of the species recorded in 2000-04 (Fig 4.2c).

We further explored the properties of SPEED by examining the sensitivity of the model to changes in parameter values by manipulating carrying capacity (K), maximum population growth rate (R_{max}) and dispersal ability (Table 4.1). We first ran SPEED with 2% of individuals following long distance dispersal, a relatively low estimate according to Stevens *et al.* (2013), which produced a mean dispersal distance of 296 m. We set population growth rate of R =1.5 (taken from an intrinsic rate of increase (r) = 0.405; calculated in Willis *et al.* (2009b), and K = 12000 individuals per 1 km grid square of suitable habitat (as calculated above and rounded to the nearest thousand). We then re-ran the model varying the mean dispersal distance, the maximum population growth rate (R) and the carrying capacity (K) each by ±5%, ±10%, ±15%, ±20% and ±25% (Table 4.1). Parameters were varied separately and we did not examine interaction effects. All models were run for 34 years (from 1970 to 2004), and we compared model outputs with the recorded distribution of *P. aegeria* in 2000-04. For each combination of parameters we ran the model five times to account for model stochasticity.

4.3.2.6 Detection thresholds of model outputs

We explored a range of detection thresholds for transforming butterfly densities produced from model outputs to presence/absence data. The threshold densities applied were 0.1%, 0.5%, 1%, 5% and 10% of the maximum density (1,200,000 individuals per 10 km grid square if 100% of the grid square was suitable habitat). We found little difference in predicted distribution size as the threshold was increased from 0.1% to 1%, but a dramatic decrease when the threshold was increased from 1% to 5% (Fig A4.3 & Table A4.1). We therefore selected a detection threshold of 1% of the maximum density (12,000 individuals per 10 km grid square) to compare model simulations with observed distribution in 2004.

Table 4.1. Parameters used for our example species, *Pararge aegeria*. We first ran the model using parameter values taken from available datasets (see methods), and then varied these by ±5%, ±10%, ±15%, ±20% and ±25%. For dispersal, variation in the mean dispersal distance was achieved by adjusting the proportion of individuals (Prop_LDdisp) following long distance (*versus* short distance) dispersal kernel (keeping the negative exponential short distance and long distance dispersal means constant at 100 m and 5000 m respectively). For population growth and carrying capacity respectively, we varied R_{max} and K.

	Variation										
Parameter	- 25%	- 20%	- 15%	- 10%	- 5%	0	+ 5%	+ 10%	+ 15%	+ 20%	+25%
Prop_LDdisp	0.010	0.012	0.014	0.016	0.018	0.020	0.022	0.024	0.026	0.028	0.030
Mean dispersal distance (m)	148.5	158.4	168.3	178.2	188.1	198	207.9	217.8	227.7	237.6	247.5
R_{max}	1.124	1.199	1.274	1.349	1.424	1.499	1.574	1.649	1.723	1.799	1.874
K	9,000	9,600	10,200	10,800	11,400	12,000	12,600	13,200	13,800	14,400	15,000

4.4. RESULTS

We used SPEED to simulate range expansion by a butterfly in Britain over a 34 year period of climate change. The model handled over two hundred million individuals (mean of 209,968,249 individuals in 2004) spread over more than 130,000 1 km grid cells.

Empirical data show that the distribution of *P. aegeria* expanded northwards in Britain between 1970-82 and 2000-04 (Fig 4.2c; 928 10 km grid squares occupied in 1970-82, increasing to 1546 10 km grid squares occupied in 2000-04; Fox *et al.*, 2006), and SPEED simulated this expansion (1693 10 km grid squares simulated occupied in 2004, starting with 928 occupied in 1970; AUC = 0.90, sensitivity = 0.92, specificity = 0.75 and prevalence = 0.59; Fig 4.2d).

There are stochastic components of SPEED (number of offspring produced, distance and direction dispersed), but there was very little stochasticity in the model outputs (Fig. 4.3), presumably because of the very large numbers of individuals simulated. Of the three biological processes (K, R_{max}, dispersal) that comprise SPEED, our exemplar species showed the greatest sensitivity to variation in maximum population growth rate and was less sensitive to dispersal ability and carrying capacity for the range of values modelled (Fig. 4.3). Varying the maximum population growth rate ($R_{max)}$ by ± 25% produced the greatest variation in distribution area (Fig 4.4a-c), but varying the mean dispersal distance by ± 25% produced little variation in the 2004 distribution area or densities (Fig 4.4d,b,e). Varying carrying capacity by ± 25% resulted in variation in the densities of *P. aegeria* achieved but made little difference to the predicted distribution extent (Fig 4.4f,b,g).

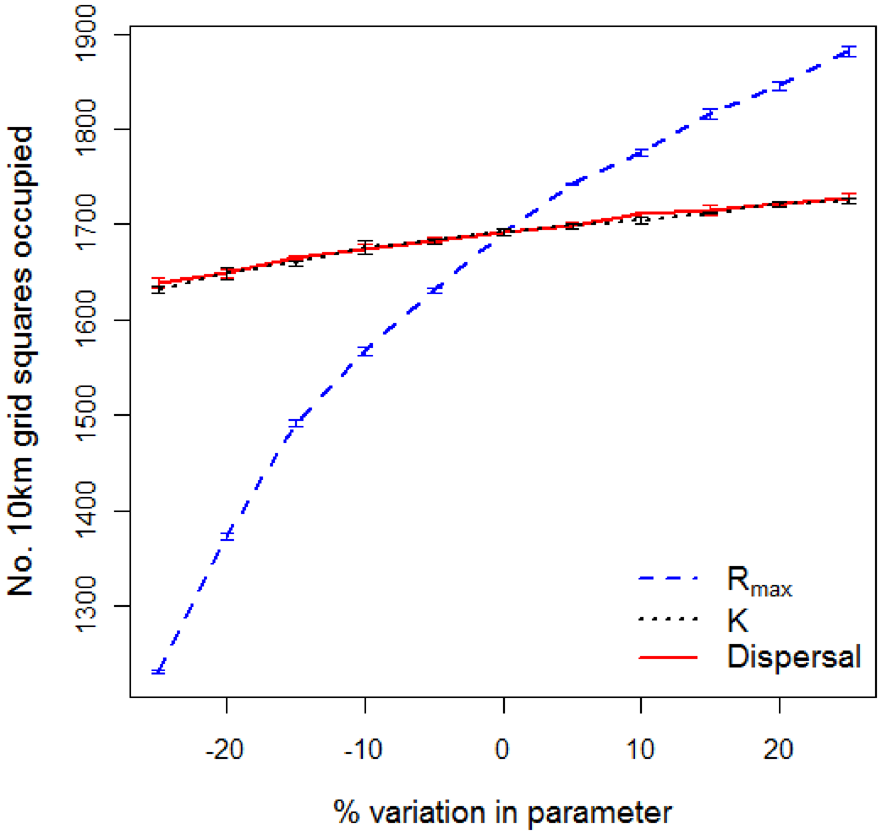


Figure 4.3. The sensitivity of the modelled distribution size (number of 10 km grid squares ±2 S.E. in 2004) of *P. aegeria* to maximum population growth (R_{max}), mean dispersal distance (Dispersal) and carrying capacity (K). Each parameter was varied by ±5%, ±10%, ±15%, ±20% and ±25% around the values shown in Table 4.1. A detection threshold of >12000 individuals per 10 km grid square was used to determine presence.

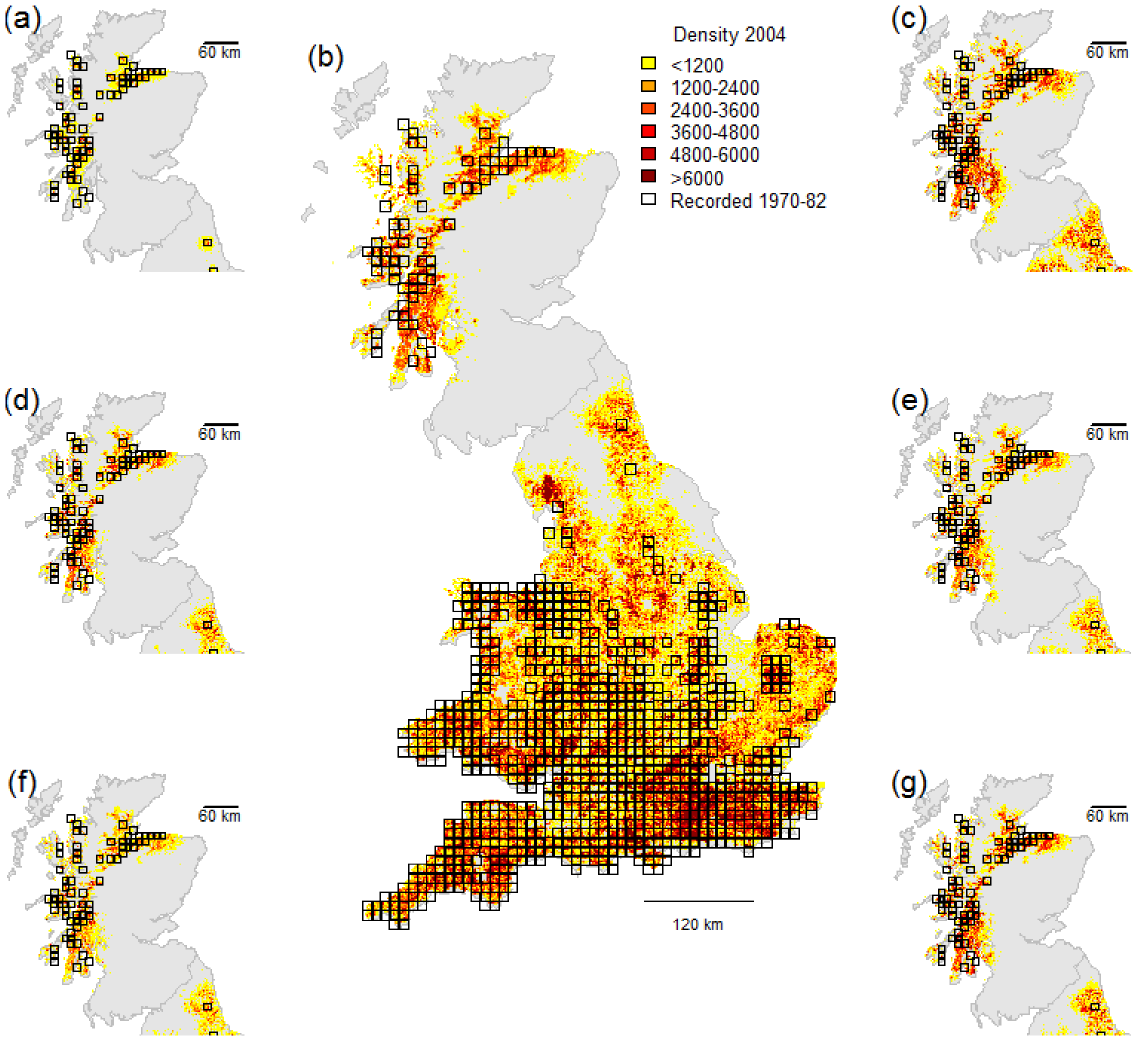


Figure 4.4. The predicted distribution extent of *P. aegeria* in 2004 at a 1 km grid square resolution. The central map of Britain **(b)** shows the starting distribution in 1970 (open 10 km grid cells), and the predicted population modelled densities at 1 km resolution in 2004, using our central parameter estimates (zero variation in Table 4.1). The remaining maps show predicted 2004 densities in Scotland when three key parameters are varied by ±25%: **(a,c)** varying maximum population growth rate by ±25%, **(d,e)** dispersal varied by ±25% and **(f,g)** carrying capacity varied by ±25% (see Table 4.1). A detection threshold of >120 individuals per 1 km grid square was applied (1% of the maximum cell carrying capacity).

4.5 DISCUSSION

SPEED incorporates species-specific climatic suitability, habitat availability, population dynamics and dispersal ability, and is capable of handling over two hundred million individuals on a standard PC equipped with 32 GB RAM (an unoptimised model run handling over two hundred million individuals spread over >130,000 1 km grid cells took ~25 minutes on a standard PC). The availability of the types of data required for this model is increasing with the use of remote-sensing for mapping land cover and the rapid development of species' climate-niche models. With the exception of information on dispersal, variables and their parameter values were available for our exemplar species from existing data sets, although most parameters can be estimated from expert opinion provided that habitat maps and climatic data are available. The model is also flexible in the spatial and temporal resolution of data that can be used.

SPEED successfully modelled range expansion in *P. aegeria*, and for the range of values we examined, SPEED showed greatest sensitivity to variation in maximum population growth rate. The population dynamics included within SPEED are intentionally simplified, but could include more detailed demographics such as multiple generations per year (e.g. Hodgson *et al.*, 2011c) and density dependent effects. Outputs from SPEED support previous work that has emphasised the importance of population dynamics in determining rates of species' range shifting (Willis *et al.*, 2009b, Fordham *et al.*, 2013b, Mair *et al.*, 2014), although the parameter space for a wider range of species needs exploring. For example, varying dispersal ability by ± 25% did not encompass the full range of variation in dispersal observed in non-migratory Lepidoptera (Botham *et al.*, 2010, Stevens *et al.*, 2010b). Thus, our sensitivity analyses should primarily be interpreted as explorations of SPEED, and illustrations of its properties.

A key improvement of the SPEED model over previous models is the spatially explicit structure of the relationship between the population dynamics (reproductive rate and carrying capacity) of the species and the environment (climate suitability and habitat availability). This means that the species' population dynamics can vary in both space and time, explicitly incorporating gradients and changes in the environment. This in turn allows for greater exploration of the manner in which climate change and habitat availability interact with population dynamics and dispersal ability to affect the distribution and abundance of species. For our exemplar study species, we assumed a linear relationship between reproductive rate and climate suitability, with no density dependence and no interaction between habitat availability and climate suitability, but the modular nature of

SPEED means more complex relationships could be implemented if necessary (e.g. Kearney & Porter, 2009, Oswald *et al.*, 2011).

A key component of SPEED is the wide range of dispersal values that can be modelled, by altering the short and long dispersal kernels, as well as the proportion of individuals undertaking long versus short distance dispersal. The dispersal components within SPEED relocate each individual from its birth location to that of reproduction, enabling the incorporation of a variety of different dispersal functions to be included as appropriate. Advancing from very basic dispersal scenarios of either no or full dispersal (Hill *et al.*, 1999b, Hill *et al.*, 2002) to species-specific dispersal will produce much more informative predictions of species' distribution shifts under climate change (Midgley *et al.*, 2006, Anderson *et al.*, 2012), as shown in recent studies (Buse & Griebeler, 2011, Jaeschke *et al.*, 2013), particularly in fragmented landscapes (Hughes *et al.*, 2007, Dytham, 2009). Thus we anticipate that SPEED will produce more robust projections of species' responses to climate change.

SPEED improves upon existing predictive distribution models by incorporating climatic suitability, habitat availability, population growth rate and dispersal ability in a spatially-explicit, individual-based dynamic model. Inclusion of population dynamic processes provides greater insight into the determinants of the distribution changes already observed and increases the utility of future predictions (Leroux *et al.*, 2013). The flexibility of the SPEED model allows it to be tailored to different temporal and spatial data resolutions and to different taxonomic groups, and thus SPEED will be useful for studying range expansions, contractions and invasions in many different types of species across different landscapes.

4.6 ACKNOWLEDGEMENTS

We thank the large number of volunteer recorders contributing GB butterfly occurrence records and data to the UKBMS. These datasets are operated by Butterfly Conservation and the NERC Centre for Ecology & Hydrology, and financially supported by a consortium of government agencies. BJA was supported by NERC grant NE/FO18606/1. LM was supported by NERC grant NE/H00940X/1.

4.7 AUTHOR CONTRIBUTIONS

CDT, JKH & CD conceived and supervised the project and edited the manuscript. BJA & CD constructed and developed the model. CD & LM tested the model. LM wrote the manuscript. BJA edited the manuscript and prepared the model manual. RF & DBR provided data and comments on the manuscript.

4.8 DATA ACCESSIBILITY

The SPEED model requires gridded habitat and climate data, as well as species' starting distribution data (or predicted starting distribution where data are incomplete but sufficient to model); these data can be obtained from a wide range of sources and need not be the same as has been used in the specific example presented in this paper. The data we used in this example were obtained from the following sources:

- European and UK climate data: data freely available (with appropriate acknowledgement) from http://www.alarmproject.net/climate/climate/

- Land cover data (LCM2007): licensed data available from http://www.ceh.ac.uk/landcovermap2007.html (DOI: http://doi.org/10.5285/a382af78-129e-4326-a561-d3034b72c4a3)

- British butterfly distribution data, gathered by the Butterflies for the New Millennium recording scheme, are held by Butterfly Conservation and the Centre for Ecology & Hydrology, and are available through http://butterfly-conservation.org/111/butterflies-for-the-new-millennium.html and http://data.nbn.org.uk (contact: Richard Fox, rfox@butterfly-conservation.org)

- British butterfly abundance data are held by the Centre for Ecology & Hydrology and Butterfly Conservation, and are available through http://www.ukbms.org/Obtaining.aspx (contact: Marc Botham, ukbms@ceh.ac.uk)

- European butterfly species' distribution data: taken from Kudrna, O. (2002) The distribution atlas of European butterflies. *Oedippus,* **20,** 1-343

- Model execution file: available on Google Drive (see below)

- R scripts: available on Google Drive (see below)

All files and information required to run SPEED are publically available at https://drive.google.com/folderview?id=0B0SdcsEswe_lQ3QzUVVkMTN2Tkk&usp=sharing

We have also provided dummy data for a starting distribution, habitat availability and climate suitability for an imaginary ‘species’ in order that readers can examine how the SPEED model runs. Please note these data files are not actual distribution data sets, and are not the data sets used in this paper, which are available from sources listed above. We also provide outputs from using these dummy data so readers can check the model is running correctly.

5 Modelling the role of climate suitability, population growth rate, habitat and dispersal in determining species' range expansion

5.1 ABSTRACT

There is considerable variation in the responses of species to recent climate change. Analysis of empirical data suggests that stable and/or increasing abundance trends are a prerequisite for range expansion, but the relative importance of population growth rates in the context of variation in climate suitability, habitat availability and dispersal ability are unclear. I used a novel distribution model (SPEED) to examine range expansion of 28 species of southerly-distributed butterflies in Britain. SPEED is a spatially-explicit individual-based hybrid model, which includes species-specific climate suitability and habitat availability, and I varied maximum population growth rate and dispersal ability of each species, in order to examine their relative importance on rates of range expansion.

Model outputs showed that all species were capable of increasing their distribution area given sufficiently high population growth rate, but that range expansion was limited to species with greater habitat availability and greater climatic suitability when population growth rate was low. However both habitat and climate became less important determinants of variation in distribution change, and dispersal ability became more important, as population growth rate increased.

I found that an increase in habitat availability always increased range expansion, but increased dispersal ability only increased range expansion when population growth rate, habitat availability and/or climate suitability were high. My results emphasise that measures to increase population growth rates will be important if conservation efforts are to facilitate species' distribution expansions. Increased habitat availability should also facilitate range expansion under climate change, particularly for those species with low population growth rate and/or at the cool limit of their climatic tolerance.

5.2 INTRODUCTION

Species' responses to climate change are idiosyncratic (Parmesan, 2006), and large inter- and intra-specific variation in the rates of species' range shifting has been observed (le Roux & McGeoch, 2008, Mair *et al.*, 2012). The results presented in Chapter 3 suggested that a greater understanding of the variation in rates of distribution change could be gained from consideration of species' abundance trends, as stable or increasing abundances were found to be a necessity for distribution expansion (Mair *et al.*, 2014). However, studies have also shown that increased habitat availability can result in more rapid range expansion (Hill *et al.*, 2001), that species have expanded more rapidly where the climate has warmed more (Chen *et al.*, 2011a), and that greater dispersal ability is correlated with faster rates of range expansion (Warren *et al.*, 2001). Considering all these potential constraints on species' distribution expansion simultaneously requires large amounts of spatial and temporal data, and as a result it can be difficult to disentangle the effects of population trends, climate, habitat and dispersal on distribution change using empirical data (e.g. Warren *et al.*, 2001). Species' distribution modelling therefore provides an ideal opportunity to explore these constraints; modelling can be used to project species distributions into the future under different climate change scenarios (e.g. Barbet-Massin *et al.*, 2012), and also to understand how habitat availability (e.g. Collingham & Huntley, 2000), dispersal ability (e.g. Anderson *et al.*, 2009) and population dynamics (e.g.Fordham *et al.*, 2013b) affect species' responses to climate change.

Previous modelling work, which has incorporated dispersal limitations into bioclimate envelopes, has shown that assumptions about species' dispersal ability can have a major impact on the projected extent of distribution expansion or decline (Anderson *et al.*, 2012, Fordham *et al.*, 2012, Jaeschke *et al.*, 2013) and that increased dispersal ability has the potential to increase the rate of expansion at the leading range-edge (Anderson *et al.*, 2009). There is, however, sparse direct evidence from empirical studies that greater dispersal ability results in greater range expansion (Kharouba *et al.*, 2013), and analysis of the relationship between species' traits and distribution expansion indicates that dispersal ability has weak explanatory power (Angert *et al.*, 2011). Therefore further modelling studies which incorporate multiple aspects of species life-history and environmental traits may help to elucidate the conditions under which dispersal ability is an important determinant of the rate of distribution change.

Population dynamics has also shown to be an important life history trait which affects projections of species' distribution change (Keith *et al.*, 2008). Incorporation of population dynamics into bioclimate envelope models has led to a new generation of predictive models termed 'hybrids', which incorporate empirical components (such as climate and habitat) and mechanistic components (such as dispersal and population dynamics) (Keith *et al.*, 2008). It has already been shown using mechanistic models that under some conditions population dynamics may be more important for distribution expansion that habitat availability (Willis *et al.*, 2009b), and hybrid models have advanced upon this understanding by combining empirical and mechanistic components to show that the likelihood of range expansion in some species may depend upon interactions between climate-dependent mortality and population dynamics, an effect that bioclimate envelope models alone could not predict (Fordham *et al.*, 2013b). Indeed, consideration of population dynamics can improve our ability to predict extinction risk, while consideration of both habitat and dispersal can provide informative predictions of distribution change at range margins (Fordham *et al.*, 2012), indicating that multiple aspects of species life-history and environmental variables should be considered simultaneously (Huntley *et al.*, 2010).

Species distribution modelling has thus progressed rapidly as the need for increased complexity has been recognised. There are many alternative methods of incorporating dispersal ability, habitat availability and population dynamics into species distribution models (Guisan & Thuiller, 2005, Engler *et al.*, 2012), however fully integrated 'hybrid' models are the ideal that consider all of these variables together with climate change (Huntley *et al.*, 2010). Therefore in this study, I apply a newly-developed hybrid model (SPEED) which incorporates climate, habitat, dispersal and population dynamics (Chapter 4). SPEED is a spatially-explicit individual-based model which integrates the spatial distribution of species-specific annual climate suitability with species' habitat availability. The maximum population growth rate can be manipulated and the model utilises dispersal parameters that can account for both short-distance foraging movements and longer-distance displacement movements.

My aim was to examine the extent to which stable or increasing population trends are a prerequisite for distribution expansion, and to ascertain the relative importance of habitat availability, local climate variation and dispersal ability in determining the rate of distribution change as population growth rate varies. I used the SPEED model to project distribution changes for 28 species of southerly-distributed butterflies in Britain from 1970 to 2004. I included information on species-specific annual climate suitability and habitat availability, and varied dispersal ability and maximum population growth rate for each species (within bounds that are realistic for butterflies) in order to test the hypotheses that (i) all species are capable of distribution expansion given a sufficiently high population growth rate, and (ii) the relative importance of habitat availability and dispersal ability for distribution expansion vary according to population growth rate.

5.3 METHODS

SPEED is a spatially-explicit, individual based dynamic model which has been described in detail in Chapter 4. In brief, the model tracks individuals of a species across space (1 km grid) and time (generation). In each time step (a year), individuals are born, disperse, reproduce and then die. The carrying capacity of a cell is determined by habitat availability (represented at 1 km grid resolution; measured from the higher resolution cover of different land uses, appropriate to each species, within each 1 km cell). The maximum population growth rate (R_{max}, the maximum number of offspring per individual) can be varied, but the realised population growth rate in each 1 km cell is determined by its climatic suitability (based on the species-specific climate suitability of the 10 km grid cell within which the 1 km cell lies). Dispersal ability is determined by the combination of the three dispersal parameters (a short-distance kernel, a long-distance kernel and the proportion of individuals following each). Although the model is individual-based, it behaves in a largely deterministic way due to the large number of individuals modelled (Chapter 4). It can simulate distribution changes over > 130,000 km^2 for > 200,000,000 individuals.

5.3.1 Species selection and model parameterisation

I was primarily interested in species with the potential to expand their distributions in response to climate change, and so I only modelled southerly-distributed species (Table A5.1.1). Thus northern species, migrants and ubiquitous species were excluded (for a species to be considered ubiquitous it must have at least one 10 km resolution record in every 100 km grid square of mainland Britain in 1970-82, according to distributions in Asher *et al.*, 2001). Further criteria for species selection are described below.

Climate suitability, habitat availability and the initial distribution of occupied areas (used to seed the model) are all species-specific parameters. Maximum carrying capacity was kept the same across species, and dispersal ability and maximum population growth rate (R_{max}) were varied in the same way among species to examine their impact on range expansion. Parameterisation of each variable is described below.

5.3.1.1 Climate suitability

Species' climate envelopes were determined using European climate and species' distribution data (excluding Britain) and the annual climate suitability for each species was then projected for Britain at a 10 km grid resolution (see Chapter 4 for details), providing species-specific annual gridded data at 10 km grid resolution. Species were excluded from the analysis if it was not possible to determine the availability of suitable climate in Britain from European distribution data (five species excluded, see below). For each species, climate suitability was projected on a scale from zero (unsuitable) to one (suitable), and a 'climate threshold' was identified for each species, which was the minimum climatic suitability value at which a species was expected to achieve reproductive replacement (i.e. $R = 1$). I would expect that species' populations would occur only where climate suitability was projected to be at or above the climate threshold (as below this threshold populations are expected to decline). I would also expect that some species may fail to occupy all areas in Britain which are predicted to be climatically suitable (e.g. due to limited habitat availability, inter-specific interactions and/or dispersal constraints). I therefore determined the climate envelope fit for each species in Britain using sensitivity measures, where sensitivity quantifies the proportion of the observed distribution of a given species projected to be at, or above, the climate threshold, but this measure does not consider the proportion of unoccupied but climatically suitable squares. Thus the sensitivity measure assumes that a species must have suitable climate where it is present, but suitable climate may also exist where the species is absent. For each species, I calculated the mean projected climate suitability of each 10 km grid cell in Britain for the period 1970-82 and used the observed species distribution in 1970-82 to calculate the sensitivity of each species' climate layer (i.e. the proportion of occupied 10 km grid squares which had a projected climate suitability that was at or above the climate threshold). I then excluded four species (*Aricia agestis, Melanargia galathea, Polyommatus bellargus* and *Polyommatus coridon*) with a sensitivity of < 0.6, for which many of the observed distribution records in 1970-82 fell outside the region predicted to be climatically suitable. This suggests that the climate models for these four species were unreliable. A fifth species, *Melitaea cinxia*, was excluded as the majority of its populations occur on islands/coasts (Isle of Wight, Guernsey and Alderney; Asher *et al.*, 2001) which were not adequately covered by the climate data. The remaining 28 species (Table A5.1.1) had a sensitivity of > 0.8 (27/28 remaining species had a sensitivity of > 0.95), indicating that the climate models parameterised from their European (excluding Britain) distributions gave an accurate representation of the regions that were climatically suitable for them in Britain in the 1970s.

5.3.1.2 Habitat availability

Habitat availability was determined from Land Cover Map 2007 (Morton *et al.*, 2011) using species-specific habitat associations identified in Chapter 3 (see Appendix 3) and assuming that each species was able to reach its maximum density in each habitat type it used (following population growth). Species' habitat availability (quantified as the proportion of 25 m grid squares in the 100 km squares of the species' distribution containing suitable habitat, to avoid computing habitat availability beyond the species' current range) varied among the 28 study species. An overall mean of 0.0712 (7%; median = 0.0648) of the land surface was deemed suitable, averaged across species, ranging from a minimum of 0.0004 (0.04% of land surface deemed suitable for *Thymelicus acteon*) to a maximum of 0.1828 (18% of land surface deemed suitable for *Gonepteryx rhamni*).

5.3.1.3 Initial distribution area for seeding models

Species' seed distributions were the observed distribution in 1970-82 at a 10 km resolution. Each model run was seeded by randomly allocating individuals to 1 km grid cells containing suitable habitat until 70% of the maximum density was reached within the 1 km grid. This was an arbitrary threshold selected to allow the population in each seeded cell to either increase or decrease (rather than already be at maximum carrying capacity) at the start of the model run.

5.3.1.4 Carrying capacity

I set the maximum grid cell carrying capacity at 1000 individuals (this was a trade-off between high densities to promote population persistence and low densities to promote faster model runs). This was kept constant across all species for all analyses.

5.3.1.5 Population growth rate

I varied the maximum population growth rate (R_{max}) in the same way for each species. From published literature the intrinsic rate of population increase (r) has been calculated to be between 0.2 and 0.4 for three generalist butterfly species in Britain (*Pararge aegeria*, *Aphantopus hyperantus* and *Pyronia tithonus*; Willis *et al.* (2009b). Since $R = e^r$, I varied the intrinsic rate of population increase (r) from 0 to 1.5 at intervals of 0.1, and calculated the corresponding R_{max} values (i.e. R_{max} varied from 1.0 to 4.48). This provided a range of R_{max} values that probably encompassed the likely range of R_{max} values among the butterfly study species, and allowed the exploration of extremes as well as more realistic values (Table 5.1).

5.3.1.6 Dispersal ability

I also varied dispersal in the same way for each species. I set short-distance dispersal to a mean distance of 100 m and long-distance dispersal to a mean of 5000 m, and examined the effect of dispersal by varying the proportion of individuals following long distance dispersal. The dispersal ability selected for my initial analysis was the proportion of individuals following long distance dispersal = 0.01 (i.e. 1% of individuals showing displacement movement), and I varied dispersal through 0.0001, 0.001, 0.01 and 0.1 allocated to long-distance dispersal for further analyses (Table 5.1). This captured a range of dispersal abilities from highly sedentary (0.0001; 0.01% of individuals showing long-distance movement) to highly mobile (0.1; 10% of individuals showing long-distance movement). The aim was to encompass a similar magnitude of variation in dispersal ability as existed in species-specific habitat availability (habitat availability varied from 0.04% through to 18% of land surface containing suitable habitat, see above), in order to allow as direct a comparison as possible between the two variables.

Table 5.1. The range of values used to parameterize the model for all 28 study species (listed in Table A5.1).

Parameter	Value
Maximum density in 1 km grid cells that contain all suitable habitat	1000
Short distance dispersal mean	100m
Long distance dispersal mean	5000m
Proportion following long-distance dispersal	0.0001, 0.001, 0.01, 0.1
Density of seeded cells	0.7 x max density
R_{max}	1.00, 1.11, 1.22, 1.35, 1.49, 1.65, 1.82, 2.01, 2.23, 2.46, 2.72, 3.00, 3.32, 3.67, 4.06, 4.48 (corresponding to values of *r* ranging from 0 to 1.5 at intervals of 0.1)

5.3.2 Model outputs

Models were run for 35 years (from 1970 to 2004), with species-specific annual climate data at a 10 km grid resolution and species-specific habitat availability data at 1 km grid resolution. The model outputs the location of 1 random individual in every 1000 individuals each year, which is a detection threshold that was developed to simulate the random nature of recording effort in real data. I used these data to generate species' presence/absence data at a 10 km grid square resolution in order to quantify distribution change after 35 years of the model. I quantified distribution change as the percentage change in the number of 10 km grid squares simulated occupied by a species between 1970 and 2004. I elected to use the simulated 1970 distribution (the projected distribution after a single year of model run) rather than the observed 1970-82 distribution which was used to seed the model in order to account for any discrepancies between habitat availability according to land cover data and the real distribution of habitat (Morton *et al.*, 2011). Such discrepancies might result in some grid cells of a species' observed 1970-82 distribution containing no suitable habitat according to the land cover data; these cells therefore could not be seeded with any individuals, resulting in initial species' distributions in the model being slightly different to the observed distributions.

5.3.3 Assessing the minimum population growth rate required for species' distribution expansion (hypothesis 1)

In order to examine how population growth rate affected species' distribution expansion, I ran the model varying the maximum population growth rate (R_{max}) between 1.00 and 4.48 for each species (Table 5.1), keeping all other parameters constant (for dispersal the proportion following long distance was set at 0.01 for all species). I then found the lowest value of R_{max} at which each species first showed distribution expansion, defined as a positive distribution change from 1970 to 2004. To identify the species-specific characteristics which determined the minimum value of R_{max} required for distribution expansion, I used linear models with habitat availability, climatic suitability and the starting distribution area as potential explanatory variables. I quantified habitat availability as the proportion of species-specific suitable habitat available in the landscape (as described above). To quantify climatic suitability, I calculated for each year the proportion of 10 km grid squares in the landscape which were at or above the species' climate threshold (the climatic suitability at which the species achieves reproductive replacement), and then took the mean proportion over all years of the model run (Table A5.1.1). I quantified the starting distribution area as the number of 10 km grid squares simulated occupied by the species in the model run in 1970.

5.3.4 Examining the relative importance of habitat, climate and dispersal as population growth rate is varied (hypothesis 2)

To test the relative importance of habitat availability and dispersal ability as population growth rate varied, I ran models for each study species at four different dispersal abilities for each level of R_{max} (from 1.0 to 4.48), keeping all other parameters constant (Table 5.1; 64 models per species). In order to quantify how the importance of habitat availability, climatic suitability, dispersal ability and starting distribution area changed as R_{max} varied, I fitted General Linear Mixed-Effects Models (GLMMs) for each value of R_{max} separately. The response variable was percentage change in distribution area from 1970 to 2004, with species identity included as a random variable and habitat availability, dispersal ability, climatic suitability and starting distribution area as fixed factors. I used Analysis of Variance of the GLMMs to obtain Sums of Squares for each explanatory variable (habitat availability, dispersal ability, climatic suitability and starting distribution area), from which I calculated the percentage of variation explained by each variable for each value of R_{max}.

I then used a multi-model inference approach to ascertain the importance and the direction of any interactions between dispersal ability, habitat availability, climate suitability and starting distribution area in determining the rate of distribution change as R_{max} was varied. For each value of R_{max} separately, I built a global GLMM, which included all two-way interactions, with species identity included as a random variable. I applied the *dredge* function in the R package *MuMIn* (R Core Team, 2012) to find the best-fitting model. The best fitting model was defined as having $\Delta AICc > 2$. Model averaging was used when $\Delta AICc < 2$ because the models can be considered of equal weight (Burnham & Anderson, 2002).

5.3.5 Exemplar species

I selected three exemplar species to illustrate model outputs, and to show how differences in habitat availability and climate suitability among species affect model inputs and to give a comparison of observed distribution change against projected distribution change for a selection of species. The species *Thymelicus lineola, Pyronia tithonus* and *Pararge aegaria* were selected to encompass a range of initial distribution areas, habitat availabilities and climatic suitabilities.

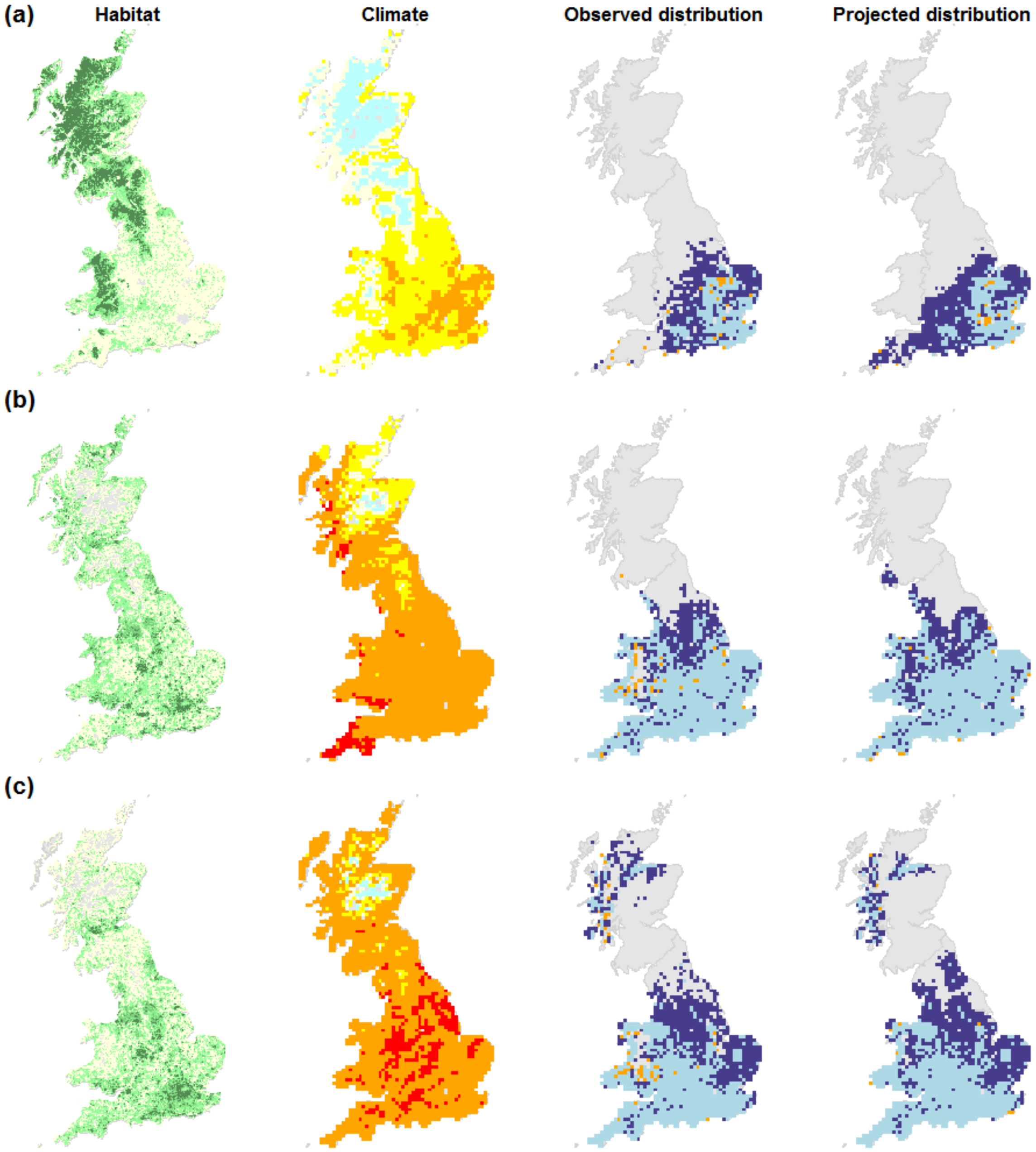
(i) *Thymelicus lineola* (Essex skipper) occurs in south-east Britain and is associated with a number of different grassland types (Asher *et al.*, 2001). This species has the smallest starting distribution area and lowest habitat availability of the three exemplar species (habitat availability = 0.033

within its distribution bounds; Fig 5.1a), and has moderate to high climate suitability across its range (average climate suitability (calculated as described above) = 0.733; Fig 5.1a).

(ii) *Pyronia tithonus* (gatekeeper) occurs over most of southern Britain and utilises grassland habitats (Asher *et al.*, 2001). The species has greater habitat availability than *T. lineola* as it utilises different grassland types (habitat availability = 0.097; Fig 5.1b) and the majority of Britain was predicted to contain highly suitable climate for this species in 2004 (average climate suitability = 0.895; Fig 5.1b).

(iii) *Pararge aegaria* (speckled wood butterfly) occurs across England and in northern Scotland, and is associated with woodland edges and clearings (Asher *et al.*, 2001). The species has the largest starting distribution area and highest habitat availability of the three exemplar species (habitat availability = 0.116; Fig 5.1c) and the majority of Britain was predicted to have high climatic suitability for the species in 2004, with some areas reaching the optimum climatic suitability for the species (average climate suitability = 0.970; Fig 5.1c).

Figure 5.1. Habitat availability, climatic suitability (in 2004), observed distribution change from 1970-82 to 2000-04, and projected distribution change from 1970 to 2004 for **(a)** *Thymelicus lineola* (Essex skipper; projections obtained using R_{max} = 2.2 and proportion of individuals following long distance dispersal = 0.01) **(b)** *Pyronia tithonus* (gatekeeper; R_{max} = 1.5 and proportion of individuals following long distance dispersal = 0.01) **(c)** *Pararge aegaria* (speckled wood; R_{max} = 1.5 and proportion of individuals following long distance dispersal = 0.01). Habitat availability ranges from <20% (light yellow) to >80% (dark green) per 1 km grid square. Climate suitability ranges from unsuitable (blue) through minimally suitable (yellow; the minimum climatic suitability required for reproductive replacement) to optimal (red; the climatic suitability at which species reach maximum population growth rate) at 10 km grid resolution. Observed and projected distribution change are at 10 km grid resolution; light blue = occupied in 1970 and 2004, dark blue = colonised by 2004, orange = occupied in 1970 but extinct by 2004.


(a)
Habitat
Climate
Observed distribution
Projected distribution
(b)
(c)

5.4 RESULTS

I ran the SPEED model for 28 southerly-distributed British butterfly species from 1970 to 2004. Fig 5.1 illustrates observed distributions in 2000-04 with the SPEED model projections of distributions in 2004 for the three exemplar species. All three species expanded their distribution areas from 1970-82 to 2000-04 (Fox *et al.*, 2006; Fig 5.1) and these expansion patterns were simulated well by SPEED (*Thymelicus lineola*, the best-fitting model, AUC (Area Under the receiver operating characteristic Curve) = 0.89, sensitivity = 0.87, specificity = 0.91; Fig 5.1a; *Pyronia tithonus*, AUC = 0.92, sensitivity = 0.95, specificity = 0.89; Fig 5.1b; *Pararge aegaria*, AUC = 0.87, sensitivity = 0.91, specificity = 0.81; Fig 5.1c).

5.4.1 Assessing the minimum population growth rate required for species' distribution expansion (hypothesis 1)

I found that all 28 study species were capable of expanding their distribution area, based on species' current habitat availability and climate suitability, provided that they had a sufficiently high maximum population growth rate (R_{max}). At the minimum value of R_{max} applied (R_{max}=1, which is reproductive replacement) a total of 13/28 species were able to show a slight expansion in their distribution area. However, for the remaining 15/28 species, declines in range size were simulated at R_{max}=1. All species showed increasingly greater simulated distribution expansions as R_{max} was increased (Fig 5.2a). For all species, I also calculated the change in total population size to examine how abundance varied with distribution size (% yr^{-1}, using linear regression of change in total population size relative to the first year of the model run against year). At R_{max}=1, the total population size declined in all species (Fig 5.2b), although most species were able to show a population increase at R_{max}=1.11 (Fig 5.2b). Thus despite overall population declines in all species at R_{max}=1, 46% of study species expanded their distribution areas, as individuals dispersed away from their starting distributions.

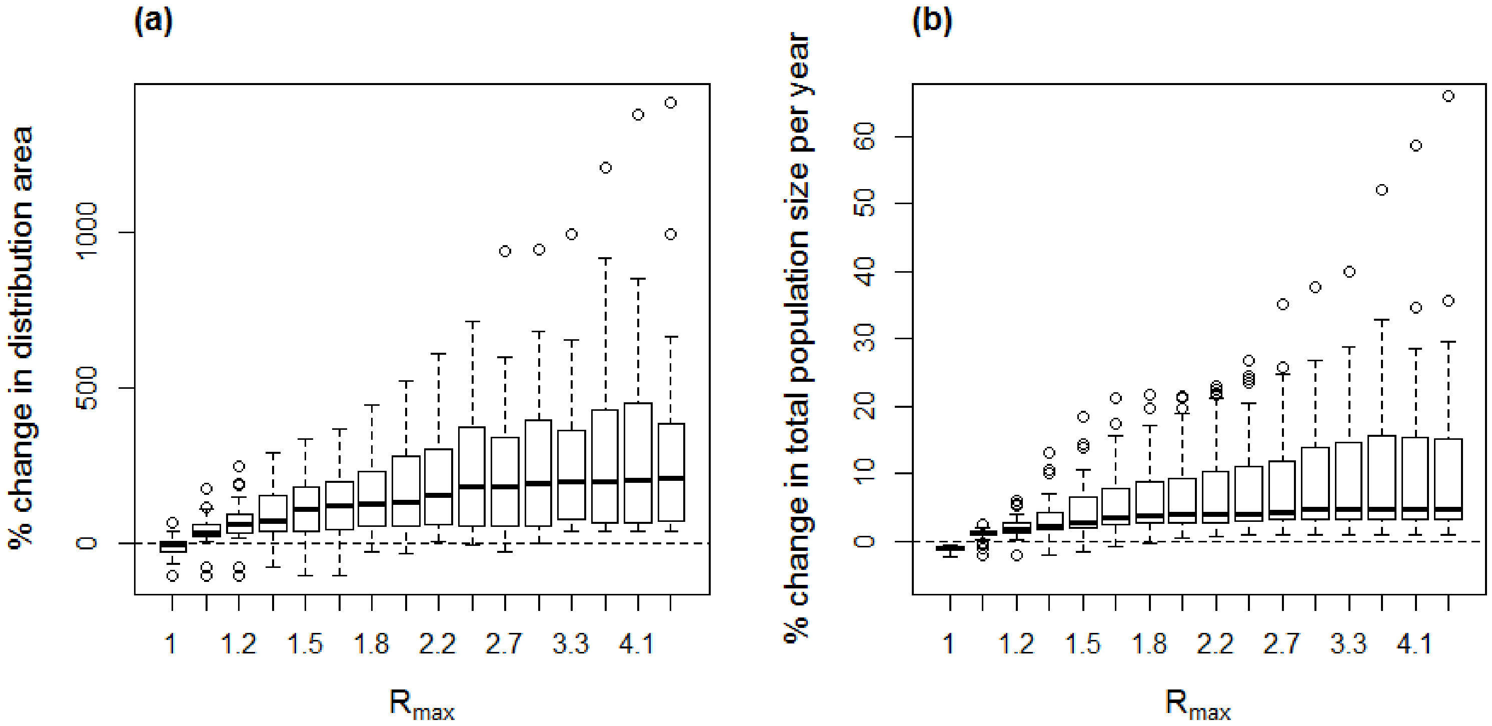


Figure 5.2. Simulated change in **(a)** the distribution area (percentage change in the number of 10km grid squares occupied), and **(b)** the total population size (percentage change in the total number of individuals per year), of 28 study species from 1970 to 2004 when the maximum population growth rate was varied from R_{max} = 1 to 4.5. The dashed black horizontal line indicates where change = 0.

The exemplar species illustrate the variation amongst species in relationships with R_{max}. *Thymelicus lineola* (the species with the smallest starting distribution area and lowest habitat availability of the three exemplars) showed distribution decline when R_{max} = 1.0 but expanded rapidly as R_{max} increased (Fig 5.3a & 5.4a). *Pyronia tithonus* showed a slight distribution decline when R_{max} = 1.0 and expanded as R_{max} was increased, but showed little benefit from increasing R_{max} much above 1.6 (Fig 5.3b & 5.4b), indicating that other constraints were in operation at higher values. *Pararge aegeria* (the species with the greatest habitat availability and climate suitability) showed slight distribution expansion at R_{max} = 1.0 and then expanded as R_{max} increased, showing the most benefit of increased population growth rate at low values of R_{max} but continuing to benefit from an increase in population growth rate throughout the range of values explored (Fig 5.3c & 5.4c). Thus the parameters that differed among the study species (species-specific habitat availability, climate suitability and starting distribution area) likely produced inter-specific variation in the response to increased population growth rate.

I ascertained which variables determined the threshold population growth rate required for distribution expansion using a linear model, with the minimum value of R_{max} at which each species showed distribution expansion, against habitat availability, climate suitability and starting distribution area. Species that were able to expand their distributions at low values of R_{max} had greater habitat availability (model R^2=0.60, slope estimate = -0.89, P=0.04) and greater climatic suitability (estimate = -0.55, P<0.001), but there was no effect of starting distribution area (P=0.6; Table A5.1.2a). I also applied a linear model to population change, and found that the only significant limitation on the minimum value of R_{max} at which overall population increase could occur was climatic suitability (linear model, model R^2=0.69, estimate = -0.20, P<0.001; Table A5.1.2b).

This is illustrated in the exemplar species, where only *P. aegeria* was projected to expand its distribution area when R_{max} = 1.0 (Fig 5.3), and this species had greater climatic suitability and habitat availability than either *T. lineola* or *P. tithonus* (Fig 5.1).

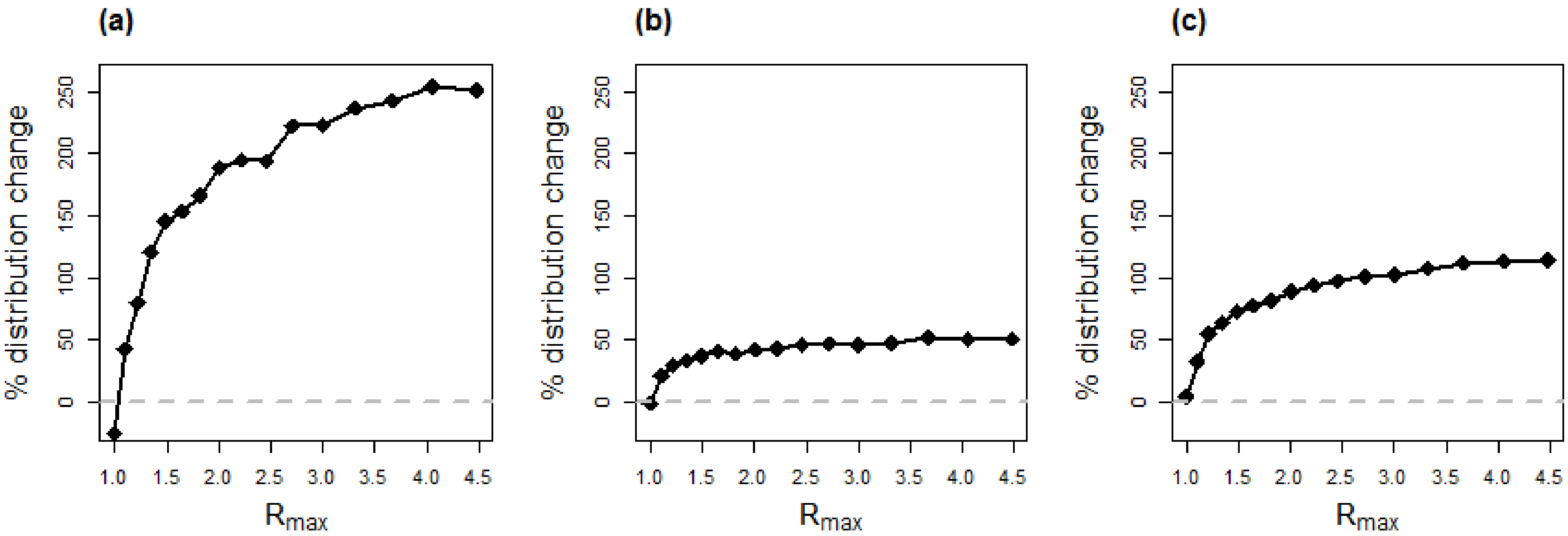


Figure 5.3. The change in distribution (percentage change in number of 10km grid squares occupied) from 1970 to 2004 for **(a)** *Thymelicus lineola*, **(b)** *Pyronia tithonus*, and **(c)** *Pararge aegeria*, as the maximum population growth rate (R_{max}) was varied. The dashed grey line indicates where distribution change = 0.

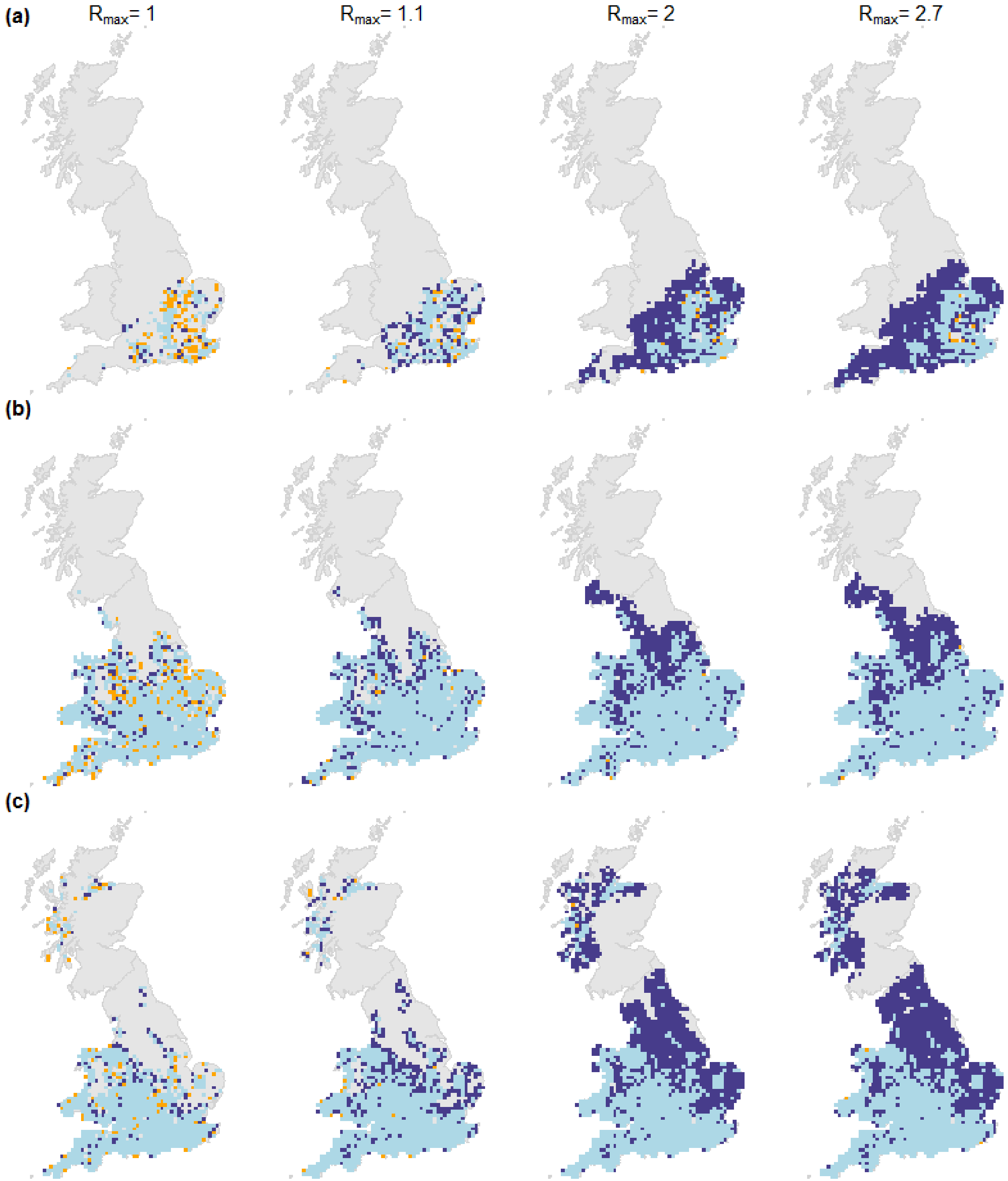


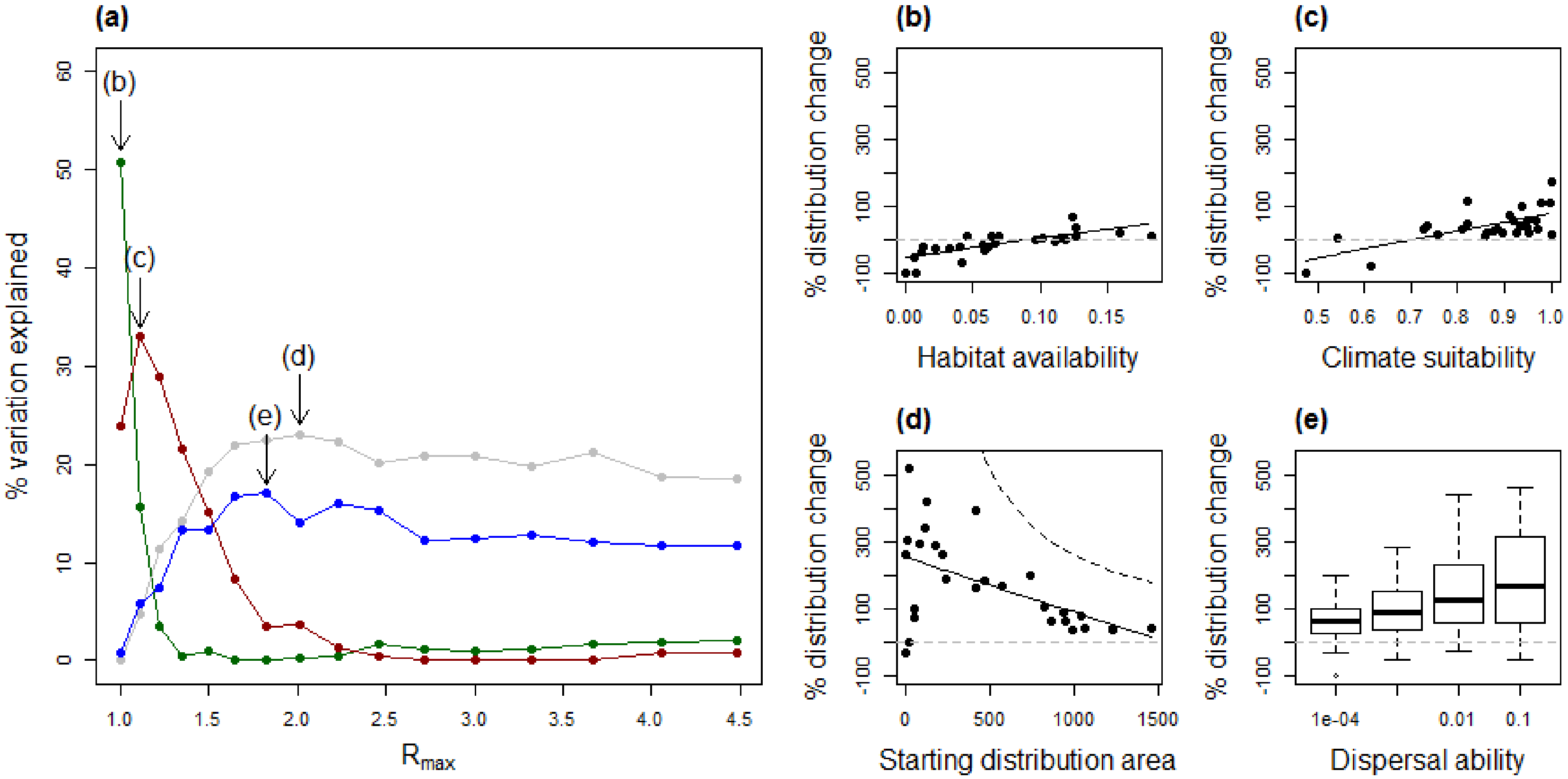
Figure 5.4. Simulated change in distribution at 10 km grid square resolution from 1970 to 2004 for **(a)** *Thymelicus lineola*, **(b)** *Pyronia tithonus*, and **(c)** *Pararge aegeria*, when R_{max}=1, 1.1, 2.0 and 2.7. Light blue = occupied in 1970 and 2004, dark blue = colonised by 2004, orange = occupied in 1970 but extinct by 2004.

5.4.2 Examining the relative importance of habitat, climate and dispersal as population growth rate is varied (hypothesis 2)

I ran the SPEED model varying both the R_{max} and dispersal ability of each species, keeping all other parameters constant. I used GLMMs to quantify how much of the variation in distribution change was explained by habitat availability, climatic suitability, dispersal ability and starting distribution area at each value of R_{max}. The importance of each variable changed as R_{max} was varied (Fig 5.5a). When $R_{max} = 1$, habitat availability explained the most variation in change in distribution area (green line in Fig 5.5a). The importance of habitat availability quickly declined as R_{max} increased, with dispersal ability (blue line in Fig 5.5a) explaining relatively more variation at higher values of R_{max}. Climate suitability (red line in Fig 5.5a) was important at low values of R_{max}, but its importance declined as R_{max} increased. The starting distribution area (grey line in Fig 5.5a) explained little variation at low values of R_{max} but explained more variation as R_{max} was increased.

In order to demonstrate the direction of the effect that each explanatory variable had on distribution expansion (e.g. if there was a positive or a negative relationship between habitat availability and distribution expansion), I selected the value of R_{max} at which the effect of each variable was strongest, and plotted species' change in distribution area against the explanatory variable. For the analyses of the effects of habitat, climate and starting distribution area, I selected a moderate dispersal ability (proportion far = 0.01) so that each species was represented by a single value. Species with greater habitat availability and greater climatic suitability showed greater distribution expansion (Fig 5.5b-c). In general, species with smaller starting distribution areas expanded by a larger relative percent than species with bigger starting distribution areas, although there were some species with a small starting distribution area which showed relatively little expansion (Fig 5.5d). Lower expansion in species with larger starting distributions may partly be due to the finite area available for expansion in Britain; the dotted line in Fig 5.5d shows the maximum expansion possible, for species with different original range sizes. Increased dispersal ability also resulted in greater distribution expansion (Fig 5.5e).

Figure 5.5. The relative importance of habitat, climate, dispersal and starting distribution area on predicted distribution change as the maximum population growth rate (R_{max}) is varied. **(a)** The percentage of variation in change in distribution area explained by habitat availability (green), climatic suitability (red), dispersal ability (blue) and starting distribution area (grey) as R_{max} was varied. The value of R_{max} at which each variable had the greatest effect was then select to show the effect of **(b)** habitat availability, **(c)** climate suitability, **(d)** starting distribution area, and **(e)** dispersal ability, on predicted distribution change. In (b-d) the dispersal ability selected was 1% of individuals following long distance dispersal (see Table 5.1). In (d) the dashed line indicates the maximum expansion possible for each starting distribution area. Solid line indicates the significant relationship between each variable and the percentage change in projected distribution area from 1970 to 2004.


(a)
% variation explained
0
10
20
30
40
50
60
(b)
(c)
(d)
(e)
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
R_{max}
(b)
% distribution change
-100
100
300
500
0.00
0.05
0.10
0.15
Habitat availability
(c)
% distribution change
-100
100
300
500
0.5
0.6
0.7
0.8
0.9
1.0
Climate suitability
(d)
% distribution change
-100
100
300
500
0
500
1000
1500
Starting distribution area
(e)
% distribution change
-100
100
300
500
1e-04
0.01
0.1
Dispersal ability

The exemplar species illustrate the benefits of increased dispersal ability given a relatively high population growth rate. I mapped projected distribution change for each of these three exemplar species when R_{max} = 1.82 (the value of R_{max} at which the effect of dispersal was greatest; Fig 5.5a) for each of the four levels of dispersal ability (Fig 5.6). All three species showed greater distribution expansion with increased dispersal ability. The comparatively strongest effect of increased dispersal ability amongst the exemplar species was found in projections for *T. lineola*, which showed a more than three-fold increase in distribution expansion going from the lowest to the highest dispersal ability, with distribution expansion increasing from 65% to 249% (Fig 5.6a). The influence of dispersal was relatively smaller for the other two exemplars. The projected distribution expansion for *P. tithonus* was 26% at the lowest dispersal and this increased to 44% at the highest dispersal (Fig 5.6b). For *P. aegeria* projected distribution expansion increased from 40% to 97% (Fig 5.6c).

In order to ascertain the importance and direction of any interactive effects between explanatory variables (e.g. do species with greater habitat availability benefit more from increased dispersal than species with low habitat availability), I applied a multi-model inference approach to each value of R_{max} separately. Inspection of interaction terms in the best-fit models highlighted two key results (see Table A5.1.3, Fig A5.2.1 and Appendix 5.3 for full results). Firstly, increased dispersal ability did not necessarily result in increased distribution expansion; greater dispersal ability actually resulted in larger distribution retraction when R_{max} and habitat availability were low, associated with increased mortality due to dispersal. Secondly, species with greater habitat availability showed relatively larger increases in distribution expansion, given higher climate suitability or higher dispersal ability, compared to species with low habitat availability.

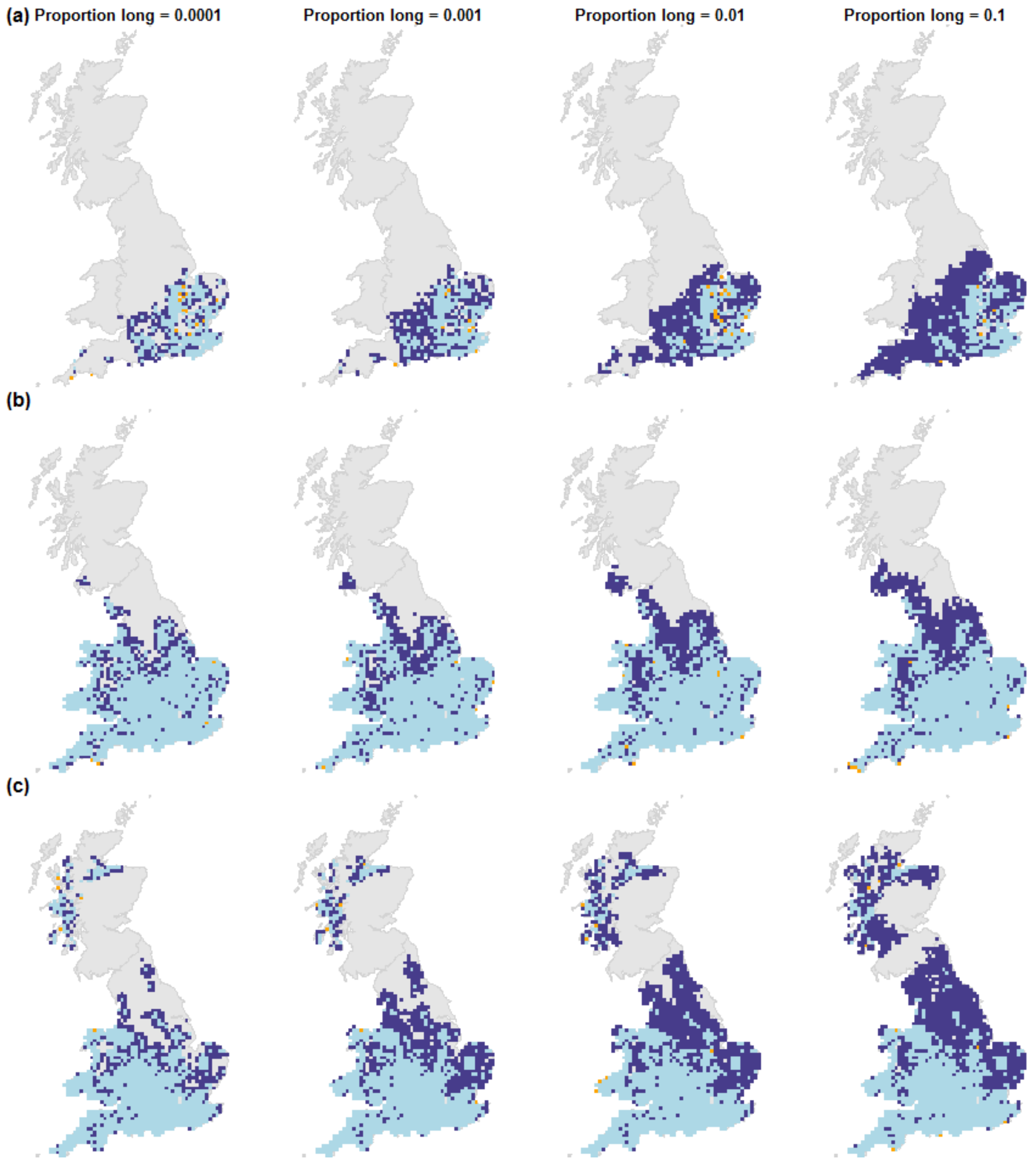


Figure 5.6. Change in distribution at 10 km grid square resolution from 1970 to 2004 for **(a)** *Thymelicus lineola*, **(b)** *Pyronia tithonus*, and **(c)** *Pararge aegeria*, when R_{max} = 1.82 and proportion of individuals following long-distance dispersal (‘proportion far’) = 0.0001, 0.001, 0.01 and 0.1. Light blue = occupied in 1970 and 2004, dark blue = colonised by 2004, orange = occupied in 1970 but extinct by 2004.

5.5 DISCUSSION

I used a spatially-explicit individual-based dynamic model, SPEED, to explore the effects of climate suitability, habitat availability, population growth rate and dispersal ability on projected distribution expansion from 1970 to 2004 for 28 species of southerly-distributed British butterflies. Results revealed that, for the range of parameters explored, all species of butterfly were capable of distribution expansion, given a high enough population growth rate. This indicates that, for all species, climatically suitable, unoccupied habitat existed in the landscape (given the relatively coarse land cover data available), and that this habitat could be colonised during the course of the model run given a sufficiently high population growth rate. Population growth is therefore an important component of species' distribution expansion (Mair *et al.*, 2014), as increased population growth rate facilitated distribution expansion even amongst species with low habitat availability or climatic suitability.

Species which were able to expand their distribution areas at low population growth rate had greater habitat availability and greater climatic suitability than species which required high population growth rate to expand. The effect of habitat availability is likely the result of larger population sizes in cells with more habitat (since cell carrying capacity is determined by habitat availability in the model) which provides more propagules for dispersal, and also a greater success rate during dispersal, as individuals which fail to locate suitable habitat die. Realised population growth rate in the model increases with climate suitability, thus the effect of climate is likely directly linked to population growth in occupied cells, as cells with greater climatic suitability have higher reproductive rates. The model assumptions are based on an ecological understanding of species' population dynamics, and there is evidence from the direct comparison of micro-climate modelling predictions with field data that more favourable climatic conditions can result in higher local population sizes, rates of colonisation and longer colonisation distances (Bennie *et al.*, 2013). There is also a wealth of evidence for the importance of habitat availability for species' distribution expansion (Collingham & Huntley, 2000, Hill *et al.*, 2001, Hodgson *et al.*, 2012). The model therefore produces biologically intuitive results and highlights the importance of population growth for species' distribution expansion.

5.5.1 Relative importance of habitat, climate and dispersal as population growth rate is varied

The relative importance of habitat, climate, dispersal and the size of the starting (seeded) distribution area for range expansion changed as the maximum reproductive rate was varied. At reproductive replacement (the lowest reproductive rate I applied), habitat availability was the most important determinant of distribution expansion; species with greater habitat availability were able to expand their distribution areas despite showing population decline within their range. When population growth rate was increased above reproductive replacement, climate suitability became the most important variable, but the importance of habitat and climate both quickly dropped off as population growth rate was increased further. This suggests that given a sufficiently high population growth rate, species were able to overcome the barriers of low habitat availability and low climate suitability to expand their distributions. Such a scenario may be overly optimistic for real species, however, given that realised population growth rates are unlikely to be very high in small habitat patches or where the climate is only marginally suitable (Thomas *et al.*, 1999), and that species with the most specialised habitat requirements only occupy a subset of the land within each land cover class that is assigned to them. Thus I conclude that the real effects of variation in habitat availability may be greater than those evident from the model. Starting distribution area became more important as population growth rate was increased, suggesting that the availability of unoccupied habitat in the landscape became limiting once the number of propagules available for colonisation was no longer a constraint.

Greater habitat availability and greater climatic suitability consistently had a positive effect on the rate of distribution expansion, however interactions between these variables, and with dispersal, were more complex as maximum population growth rate was varied. In general, species with low climate suitability were predicted to benefit more from increased habitat availability were than species with high climate suitability. This is again likely to be due to greater habitat availability resulting in larger population sizes in the model, which reduces the likelihood of population extinction and provides propagules for dispersal (Thomas *et al.*, 2011b), which is of greater advantage when realised reproductive rate is low (as is the case in the model when climatic suitability is low). At low population growth rate, increased dispersal ability was only beneficial given high habitat availability and climate suitability, and even then the benefit of increased dispersal ability was relatively less than at high population growth rates. This result agrees well with previous research which suggests that species which occur in highly fragmented, rare habitat tend to be sedentary due to high dispersal mortality (Ravenscroft, 1990, Travis & Dytham, 1999), and implies that increased dispersal ability is only an advantage given sufficient habitat availability.

These results may help to explain why analyses in Chapter 3 found a significant effect of habitat availability on the rate of species' distribution expansion, but no significant effect of dispersal (Mair *et al.*, 2014). Given that a strong effect of dispersal ability was only observed at high population growth rates, it may be that for the empirical data analysed in Chapter 3, species were not achieving a sufficiently high population growth rate for any effect of dispersal ability to be detected. Furthermore, the SPEED model outputs showed that habitat availability was of particular importance at low population growth rates (and low climate suitability), and the empirical data in Chapter 3 showed a significant positive relationship between habitat availability and distribution expansion. Taken together I conclude that these results suggest that species in Chapter 3 may have been achieving only low population growth rates. Results also suggest that while increased dispersal ability may increase the rate of distribution expansion amongst expanding species, dispersal ability does not affect which species do or do not expand their distributions in the first place. Other modelling studies which have highlighted the importance of dispersal ability in determining the rate of distribution expansion have generally not incorporated population dynamics or have assumed positive population growth (e.g. Hughes *et al.*, 2007, Engler *et al.*, 2009, Jaeschke *et al.*, 2013). Model outputs in this study demonstrate the advantages of integrated models which allow the interactions between species' life history traits to be explored (Huntley *et al.*, 2010), and which help to bridge the gap between observations of real species and model predictions made using theoretical species and landscapes.

5.5.2 Implications for conservation under climate change

The importance of positive population growth rate for species' distribution expansion is clear, particularly for species with limited habitat availability or those near the edge of their climatic tolerance. These findings suggest that one of the key strategies in climate change conservation should be the management of natural habitats to increase species' population growth rates. Habitat quality can be improved to encourage species' population growth and facilitate population recovery (Brereton *et al.*, 2008), which should in turn encourage distribution expansion (Mair *et al.*, 2014). Stable or increasing population abundances are important for species' persistence in general and have long been a focus for conservation, yet the importance of population trends for species' distribution expansion has largely been overlooked in the climate change literature.

My results suggest that, alongside strategies to increase species' population growth rates, conservation management should also be applied to increase the amount of suitable habitat in the landscape, in order to improve colonisation success rate (Hill *et al.*, 1999b, Hill *et al.*, 2001). A contentious point in the conservation debate concerning habitat availability is the relative importance of the absolute amount versus the connectivity of suitable habitat (Doerr *et al.*, 2011, Hodgson *et al.*, 2011a). However, working from the idea that for a given landscape, the greater the dispersal ability of a species the more connected it perceives that landscape to be (Tischendorf & Fahring, 2000), these results suggest that habitat amount is more important than connectivity at low reproductive rates, as an increased dispersal ability did not provide any benefits when maximum population growth rate was low.

5.5.3 Conclusions

The SPEED model has provided a useful tool for exploring the relative importance of, and interactions between, climate, habitat, population growth rate and dispersal for species' distribution expansion under climate change. These environmental and species-specific traits vary through space and time, with the result that the limitations on species' distribution expansion are context-dependent. For example, increased dispersal ability may only enhance distribution expansion providing a range of conditions are met; these conditions are likely to include good habitat availability, high climatic suitability and high population growth rates, but the balance between these conditions will depend on the species and landscape in question. Nevertheless it is possible to make some general inferences from these results. I conclude that more positive population growth should increase the likelihood that a species will be able to expand its distribution under climate change, and that increased habitat availability is always beneficial, particularly for species with low population growth rate or on the edge of their climatic tolerance. Conservation management to facilitate species' range shifts under climate change requires measures to improve population growth rates and increase habitat availability.

6 General Discussion

6.1 SUMMARY OF RESULTS

The overall objective of this thesis was to quantify and explain inter-specific variation in the responses of southerly-distributed butterflies in Britain to climate change. I did this using the analysis of empirical data on species' distribution and abundance changes, and predictive distribution modelling.

I firstly quantified changes in species' distribution area, northern range margin and abundance over two consecutive time periods, to ascertain whether species' responses to climate change showed temporal consistency over the past four decades. I found that, amongst southerly-distributed butterflies in Britain, not only was there large inter-specific variation in distribution and abundance changes in response to climate change, which has been documented in other studies (e.g. le Roux & McGeoch, 2008, La Sorte & Jetz, 2012), but there was also intra-specific temporal variation (Chapter 2). Thus, species which showed increases in distribution or abundance in one time period did not necessarily continue to show increases in the next time period. I also found that despite a smaller increase in temperature during the second time period studied, species' northern range margins on average shifted north more rapidly than during the first time period. This suggests that species may have been taking advantage of a climate-distribution lag (Menéndez *et al.*, 2006, Lindström *et al.*, 2013). However, abundance changes showed the opposite trend, with species on average showing greater abundance declines during the second study period. This implies a deterioration of environmental conditions for many species and there was evidence of population losses within species' ranges during the second period. Distribution and abundance changes were correlated amongst species during both time periods, indicating that species with more positive abundance trends expanded their distribution areas, while species with more negative trends showed distribution declines.

In order to explain some of the variation found amongst southerly-distributed butterflies in Britain, I related changes in species' distribution area to species-specific habitat availability, dispersal ability and changes in abundance at core sites. Results indicated that only those species with stable or increasing abundance trends at core sites were able to expand their distribution areas, but that amongst those species with stable abundances, habitat availability was the most important determinant of the rate of distribution expansion (Chapter 3). These findings suggest that there are two key drivers of distribution change, abundance changes and habitat availability, both of which could potentially be enhanced to facilitate range expansion given appropriate conservation management strategies.

A greater understanding of species' responses to climate change can be gained from predictive species' distribution modelling, and I therefore tested the ability of a novel model, SPEED, to project the distribution change of *Pararge aegeria*, an expanding species of butterfly in Britain. SPEED is a spatially-explicit individual-based model. It is a hybrid model which projects species' distribution changes in relation to climate and habitat, which are species-specific empirical components, and dispersal ability and population growth rate, which are mechanistic components. Distribution change of *Pararge aegeria* was simulated using SPEED from 1970 to 2004, and the model output was compared to the observed distribution; the resulting AUC, specificity and sensitivity measures indicated that the projections from SPEED were good representations of recent changes in *P. aegeria*'s distribution in Britain (Chapter 4). SPEED therefore represents an advance in the newly emerging field of hybrid modelling, as it incorporates the variables and processes which are considered to be key to understanding species' distribution change (Huntley *et al.*, 2010), and moreover it is a flexible model with the potential to be applied to a wide range of species and landscapes.

I then used the SPEED model to explore the conclusions from my analysis of empirical data in Chapter 3; namely that population trends limit distribution spread, and that habitat availability is an important determinant of the rate of distribution expansion. The model simulations of 28 southerly-distributed butterflies in Britain indicated that all species studied were capable of distribution expansion, given sufficiently high population growth rates (Chapter 5). Thus unoccupied but suitable habitat was available for all in the landscapes into which expansion could occur under favourable conditions. As would be expected, species with greater climatic suitability were able to expand more, and climate suitability was particularly important when population growth rate was low. Modelling results also indicated that an increase in habitat availability was always advantageous for range expansion, regardless of the climatic suitability, dispersal ability or population growth rate. Species with greater habitat availability were less likely to undergo distribution declines when population growth rate was low, and were able to show greater distribution expansions when population growth rate was high.

6.2 DEVELOPING A BETTER UNDERSTANDING OF INTRA- AND INTER-SPECIFIC VARIATION IN RESPONSES TO CLIMATE CHANGE

The existence of intra- and inter-specific variation in species' distribution change in response to climate change indicates that the drivers of species' distribution change vary both among species and within species over time. The results presented in this thesis can be drawn together to give an overall picture of how species' distribution changes vary, and the environmental and species' traits that drive this variation.

The most significant conclusion reached from analyses in this thesis is that species' abundance trends were of over-riding importance in determining distribution change. In my analyses of empirical data (Chapter 3), range expansion was confined to the subset of species with stable or increasing abundance trends. The application of the SPEED model to project distribution change amongst southerly-distributed species (Chapter 5) provided a different approach to assessing the determinants of distribution change, and results emphasised the importance of population growth rate for distribution expansion. SPEED model projections demonstrated that increased population growth rates allowed species to overcome the limitations of low habitat availability and/or low dispersal ability. The importance of population growth for distribution expansion has been shown in other studies (e.g. Willis *et al.*, 2009b), and the work presented here suggests that population growth is likely to be the most important determinant of whether or not a species expands its distribution area in response to climate change. Species' abundance trends vary over time (Chapter 2), therefore understanding the drivers of population change will be necessary to identify which conservation strategies are required to improve abundance trends and facilitate species' distribution expansion.

The second conclusion is that habitat availability is an important determinant of the rate of distribution expansion. Amongst those species which did show positive abundance trends, the rate of distribution expansion depended upon the species-specific habitat availability (Chapter 3). This substantiates the suggestion that the greater habitat availability of generalist compared to specialist species contributed to the faster rates of distribution expansion observed amongst generalist species (in the analysis of temporal variation in species' distribution change; Chapter 2). Other studies have also made the inference that differences in habitat availability between generalist and specialist species contribute to observed differences in rates of distribution expansion (e.g. Warren *et al.*, 2001, Davey *et al.*, 2012) and my results provide evidence for their conclusions. Results of the SPEED model also identified habitat availability as an important determinant of distribution change, particularly at low population growth rates (Chapter 5). Thus increased habitat availability not only facilitated distribution spread but also helped to prevent distribution decline, because larger areas of habitat supported more individuals, which reduced the risk of population extinction.

It is clear that inter-specific variation in habitat availability contributes to the variation among species in rates of distribution expansion, and species' habitat availability is also likely to vary over time as habitat is lost or restored. Furthermore it has been shown that species habitat associations are likely to vary in response to environmental change. Butterfly species in Britain were shown to make use of a wider range of habitat types during warmer years, yet, despite an increase in average temperatures over time, the overall trend was towards narrower habitat breadths (Oliver *et al.*, 2012). It was suggested that this narrowing of habitat breadths was due to habitat deterioration, and therefore there are likely to be multiple drivers of species' habitat associations, which will in turn affect species' habitat availability.

The third conclusion is that dispersal ability may not always be an important driver of species' distribution change. Empirical analyses of the drivers of distribution change (Chapter 3), suggested that dispersal ability may not always be an important driver of species' distribution change, despite some previous research suggesting that it may be (Warren *et al.*, 2001, Anderson *et al.*, 2012) but supporting other studies showing little role for dispersal (Angert *et al.*, 2011). It may be that when studying dispersal ability alongside other potential explanatory variables, dispersal was relatively unimportant. This suggestion is supported by my SPEED modelling results, which showed that greater dispersal ability was only advantageous to range expansion when species' population growth rate, habitat availability and/or climatic suitability were sufficiently high (Chapter 5). Thus if abundance trends and habitat availability are the primary limitations on distribution change, then dispersal ability may only be important when species have both sufficient habitat availability and positive abundance trends; these conditions were certainly not met for the majority of species in the empirical analyses in Chapter 3. Both the empirical analyses and the modelling results emphasise the importance of considering multiple aspects of species' life history simultaneously when trying to understand or to project species' distribution change in response to climate change (Huntley *et al.*, 2010), and imply that the importance of species' traits are likely to vary depending on the environmental conditions experienced.

The research in this thesis has improved our understanding of species distributional responses to climate change by highlighting that species responses are temporally inconsistent and that this inconsistency is related primarily to temporal variation in species' abundance trends. Simulation modelling provided further insight and suggested that the importance of traits, such as habitat availability and dispersal ability, for distribution change are likely to vary depending upon population growth rate, which may help to explain why other studies have found that species' traits had low explanatory power (e.g. Angert *et al.*, 2011).

6.3 CONSERVATION IMPLICATIONS

Conclusions from this research have important implications for species' conservation under climate change. I have shown that species' abundances have generally been in decline since the 1990s, and that negative abundance trends likely limit distribution expansion. This indicates that if abundance trends continue to be largely negative, species will fail to expand their distribution areas in response to climate change when the climate is 'improving' for species. However, I have also shown that distribution expansion is limited by two variables over which we can exert some control; species abundance trends and habitat availability can both be enhanced through conservation efforts.

It has long been understood that positive population growth is required for distribution expansion (Skellam, 1951), yet the relationship between population growth and distribution expansion has received little attention in the context of species' responses to climate change, despite the fact that, where it has been studied, population growth has been shown to be an important determinant of distribution expansion (e.g. Willis *et al.*, 2009b). Moreover, larger population sizes also improve the likelihood of population persistence (Frey *et al.*, 2012), which is a fundamental conservation goal.

There is evidence that targeted conservation efforts can result in species' population recovery (Asher *et al.*, 2011) and that agri-environment schemes can also enhance the abundances of wider countryside species (Brereton *et al.*, 2011). The appropriate management of habitats can increase species' abundances and lead to increased colonisation rates (Lawson *et al.*, 2014), since increased abundances produce a much greater number of dispersing individuals with the potential to colonise new habitat patches (Thomas *et al.*, 2011b). Climatic changes are also predicted to affect species abundances, with an increase in average temperature likely to be beneficial for most species of butterfly (Roy *et al.*, 2001). However, an increase in extreme weather events is likely to have a negative effect (WallisDeVries *et al.*, 2011), and species with a warm-edge margin in Britain are likely to retract under warmer temperatures (Franco *et al.*, 2006). The improvement of habitat quality may however buffer species to some extent from any negative effects of climatic fluctuations, as the variation in abundance due to habitat quality is of a much larger magnitude than variation due to weather (Thomas *et al.*, 2011b). Improving habitat quality is therefore of primary importance for the conservation of species under climate change, and should lead to more stable or increasing species' abundance trends.

For those species with stable or increasing abundances, greater habitat availability can promote more rapid range expansion (Hill *et al.*, 2001), through both the maintenance of larger population sizes with more individuals available for dispersal, and an increased likelihood of dispersers finding and colonising new areas of suitable habitat (Thomas *et al.*, 2011b). The strategy of protecting and/or restoring natural habitat to facilitate distribution expansion has been widely discussed and promoted in conservation research (e.g. Game *et al.*, 2011, Hodgson *et al.*, 2011b, Renton *et al.*, 2012). There is evidence that habitat restoration can facilitate distribution spread (e.g. Davies *et al.*, 2005), but there is ongoing debate over the relative importance of overall habitat amount versus the spatial configuration of habitat in the landscape (Doerr *et al.*, 2011, Hodgson *et al.*, 2011a). There is likely to be a threshold amount of habitat below with species' population struggle to persist or spread (Bergman *et al.*, 2004, Bulman *et al.*, 2007). However some studies suggest that rates of spread can be enhanced for any particular overall amount of habitat, if that habitat is spatially structured to maximise connectivity (Hodgson *et al.*, 2011b). Given the choice it would be ideal to conserve a substantial amount of habitat which was well connected, but this is rarely an option. There is a strong argument for focussing on conserving as much habitat as possible given that we are certain of the benefits of increased habitat area and less certain of what constitutes as connected habitat for a wide range of species (Kindlmann & Burel, 2008, Hodgson *et al.*, 2011a). My results using the SPEED model show that increased habitat availability was advantageous for distribution expansion across the range of dispersal abilities, climatic suitabilities and population growth rates explored. These results therefore provide support for the efficacy of protecting and restoring as much natural habitat as possible for species' conservation under climate change.

The results presented in this thesis very much suggest that a 'back to basics' approach to conservation under climate change is needed; greater focus on improving species' abundance trends through increased habitat quality should increase the proportion of species responding to climate change by shifting their distributions, and greater habitat availability should facilitate more rapid range expansion.

6.4 PROJECT LIMITATIONS

There were, however, limitations to some of the work presented in this thesis due to data availability and quality. The butterfly distribution and abundance dataset (BNM and UKBMS datasets respectively) are an excellent resource and provide some of the longest running records of species' trends available. However distribution data are collected ad-hoc, resulting in large spatial and temporal variation in recording effort. This means that ascertaining when colonisations or extinctions have occurred requires consideration of the recording effort, for which there is frequently limited data. For example, a particular site may have been visited annually, but the recorder may only have noted down the butterflies that they found to be most interesting (e.g. the less common species), or each visit may have lasted a different length of time meaning that the search time, and therefore the number of species recorded, varied. Such information is not available, and generally the approach taken to deal with this variation in recording effort depends upon the particular research aim; in some cases methods to even out the number of records made over space and time may be sufficient (e.g. Fox *et al.*, 2006), while in others a more sophisticated modelling approach may be necessary (e.g. Kéry *et al.*, 2010). Furthermore, there is a spatial bias in data collection, with most recording taking place in the south of Britain (Fox *et al.*, 2006), and in general recorders prefer to visit diverse sites which are not too far from home (Dennis & Thomas, 2000). This spatial bias presents problems for the accurate quantification of species' distribution extents, however the spatial distribution of recording effort is largely maintained over time (Fox *et al.*, 2006), meaning that measures of species' temporal distribution change all contain the same bias, and so the impact on relative rates of distribution change amongst species is minimal.

One is issue that is common to all studies that quantify distribution change, regardless of the data-collection method used, is the problem of resolution. The change in distribution quantified for a species is dependent upon the resolution of the data used, and a coarse resolution is likely to overestimate expansions and underestimate declines (Thomas & Abery, 1995). This is because the colonisation and extinction dynamics of metapopulations occur at relatively fine resolutions (for example at 100m or 1km resolution; Hill *et al.*, 1996), and so many extinctions go unnoticed at a coarser resolution (studies tend to quantify distribution change at 10km resolution or coarser, e.g. Hickling *et al.*, 2006). On the other hand, a single fine-resolution colonisation in a new coarse-resolution grid square will result in an exaggerated increase in species' distribution area. The appropriate resolution for a study will depend upon the extent of the study area and the resolution and quality of the distribution data collected. Studies should bear in mind the effect of scale and how it may impact the conclusions reached – the situation for many species may be worse than the measurements imply.

The abundance data used in this study were collected more rigorously than the distribution data, with volunteers recording butterflies along the same transects on a weekly basis during the flight period (Botham *et al.*, 2010). This provides good temporal consistency, but there is a problem with the spatial locations of transects showing a bias towards protected areas as, given the substantial time commitment, recorders generally prefer to select transects in more natural habitats with a relatively diverse species composition. This dataset therefore provides valuable data on species' abundance trends, but it must be borne in mind that trends may not accurately reflect abundance changes in the wider countryside. Moreover where transects are located in the wider countryside, they are often along field edges and/or hedge rows, which tend to harbour a higher diversity and abundance of species relative to the wider landscape.

The challenges of the butterfly distribution and abundance datasets are such that statistical methods can be employed to reduce potential biases, however the land cover maps used for several analyses in this thesis provide different problems which are less readily tackled. Accurate, high resolution land cover maps are necessary for both quantifying species' habitat availability and projecting species' distribution change. However, while the land cover maps available are undoubtedly a useful resource, they nonetheless provide some problems. Firstly, there are likely to be inaccuracies in the classification of some land cover types (Morton *et al.*, 2011). Inaccuracies result from the difficulty of separating out land cover types, for example calcareous grassland from improved grassland, using satellite imagery. Currently there is no established method for accounting for this uncertainty. Secondly, the land cover categories used are broad, and therefore habitat availability for each species was likely largely over-estimated in the SPEED models applied in Chapters 5 and 6. Finally, and of greatest import for studying temporal changes in species' distributions and abundances, the land cover maps are not comparable between years. Categorisation of land cover has changed with each land cover map produced (Fuller *et al.*, 2002, Morton *et al.*, 2011), making it impossible to quantify changes in habitat availability or structure over time. This places severe limitations on empirical analyses and the parameterisation of species' predictive distribution models, and means that changes in species distributions and abundances over time cannot be related to habitat changes at a national scale. Annual land cover data using consistent categories would allow more in depth analyses to be carried out.

The quantification of species' dispersal ability was also data-limited in analyses in this thesis. A rank mobility score was used to examine the importance of dispersal ability for species' distribution expansion in Chapter 3, which was a relatively crude quantification of dispersal ability, and a range of dispersal abilities were included in models of range changes for each species (Chapter 5) because accurate estimates of dispersal ability are available for very few species. Although dispersal studies have been carried out for a large number of butterfly species in Europe, the collation of these data indicated that, for each species, the estimate of dispersal ability obtained varied depending on the method used to quantify it (Stevens *et al.*, 2010b). Therefore options for accurately quantifying species’ dispersal ability were relatively limited, and more data would prove useful for both understanding the role of dispersal in determining the species’ distribution changes that have been observed, and for projecting species’ distribution changes using integrated models.

The SPEED model itself was a new development, which principally aimed to integrate climate, habitat, dispersal and population growth into a flexible model framework. The model was intended to have the capacity to incorporate further complexity, and given its relatively early stage in development, there are some limitations and potential for improvement. Firstly, the population dynamics component used in the model is relatively simple, and does not include density dependence. Density dependence effects are likely to exist in many species (Schtickzelle *et al.*, 2002) and given the sensitivity of the model to population growth rate, the inclusion of density dependence may affect projected distribution changes. Secondly, there are also likely to be density dependent effects on dispersal rates in many species (Simmons & Thomas, 2004), which the model currently does not consider. The current implementation of dispersal parameters results in a proportion of individuals leaving habitat patches regardless of the population density in the patch. The effect is that small population sizes are further reduced in landscapes which have sparse habitat availability and therefore high dispersal mortality. Density dependent dispersal effects have the potential to alter the colonisation and extinction rates in the model (Altwegg *et al.*, 2013), and therefore affect the projected distribution change. Finally, despite the inclusion of stochasticity in the calculation of realised population growth rate and dispersal distances and directions, there was little variation amongst replicate model runs in the distribution change projected. This suggests that the inclusion of stochasticity in these parameters has little overall effect on projected distribution change. Comparisons of model runs with and without stochastic effects may help to provide clarity on the impact of modelled stochasticity, and it may be worthwhile considering several alternative methods of incorporating realistic stochastic effects into the model (Calder *et al.*, 2003).

6.5 FURTHER RESEARCH

The projections of species' distribution change from SPEED simulations (Chapter 5) were based on climate suitability measures calculated from historical climate data in order that SPEED model outputs could be compared with observed distribution changes over the past three decades. The natural progression from this research therefore is to identify the parameter space that produced the best-fit projections for each species and use these to project distribution changes into the future. Climate change forecasts are available for a range of scenarios, and projecting distribution changes into the future would provide greater insight into expected longer terms trends in distribution expansion. For example, is suitable climate likely to exist across the majority of Britain for most species, or are climatically suitable areas likely to become fragmented and therefore the lack of climate continuity could pose a barrier to species' spread (Early & Sax, 2011, Bennie *et al.*, 2014). Similarly, the SPEED model could be applied using predictions of land use change in order to test how different habitat loss or restoration strategies might affect the rate of species' distribution expansion. An alternative application of the SPEED model would be to ascertain its utility in projecting species' distribution retraction, by applying the model to northerly-distributed butterfly species in Britain. The ability to predict population losses at species' warm range-edges could help inform conservation by identifying the populations that are most likely to persist and therefore should be the focus of conservation efforts.

Further research could also focus on understanding the drivers of species' abundance trends, and on the development of strategies to reverse abundance declines. Given the widespread declines in species' abundances, not only in Britain (Asher *et al.*, 2011) but also across Europe (Maes & Van Dyck, 2001, Van Dyck *et al.*, 2009), there is clearly a general deterioration of habitat quality. In order to prevent species becoming confined to isolated patches of protected habitat, there needs to be an understanding of how species' abundance trends vary both within protected areas and across the wider countryside. The increasing availability of data on species' abundance trends at regularly monitored sites (such as the BMS data used in this thesis) as well as national land cover and protected area maps should facilitate such research, and allow spatial variation in species' abundance trends to be related to habitat type and protection status.

While for some specialist species, which have received particular attention due to their threatened status, there is an understanding of what constitutes high quality habitat and which management strategies result in increased species' abundances (e.g. *Hesperia comma*; Davies *et al.*, 2005), for many species this knowledge is lacking. It has been possible to show that areas entered into agri-environment schemes (Brereton *et al.*, 2011), and areas with more heterogeneous habitat (Oliver *et al.*, 2010), support more stable populations. However the particular management strategy or combination of management strategies that produce this effect is more difficult to deduce. It is important to quantify the efficacy of alternative management strategies in order to ensure not only that money is being well spent, but also that land managers are able to select the strategies that are most likely to be effective when applied to their landscape, and that will provide the greatest benefits for the species already present or likely to colonise the area in the near future. Relating abundance changes to habitat and climatic variables simultaneously should provide further insight, as previously these potential drivers have tended to be studied separately (e.g. climatic effects in Roy *et al.*, 2001; habitat type effects in Collinge *et al.*, 2003; land management effects in Jonason *et al.*, 2011).

Much work has already gone into quantifying how the amount of habitat in the landscape and the spatial configuration of that habitat affects both species persistence and distribution spread, using both empirical and theoretical studies (e.g. Mortelliti *et al.*, 2012, Mokany *et al.*, 2013, Villard & Metzger, 2014). It has been argued that in fact we already know enough to implement conservation strategies that are likely to be effective under climate change (Hannah, 2011). Our theoretical understanding of the effects of habitat amount and connectivity is substantial, and I would suggest that the application of this theory to real landscapes is the necessary next step. A major barrier to effective, informed conservation is the translation of results and conclusions from research into applicable management strategies (Heller & Zavaleta, 2009), therefore closer links between researchers and land managers, and research programs that are more goal-orientated may help to bridge the gap (Guisan *et al.*, 2013).

Finally, while butterflies are an excellent model group for studying species’ responses to climate change, it is necessary to ascertain whether the results and conclusions presented here also apply to other taxa. Butterfly species in Britain cover a wider range of dispersal abilities and habitat associations, but nevertheless it cannot be assumed that conclusions from a single taxonomic group can be applied to all others. Further research should therefore aim to test the drivers of distribution change across a wide range of taxa, in order to determine whether results are similar among taxonomic groups.

6.6 CONCLUSIONS

This work has emphasised the overriding importance of species’ abundance changes and habitat availability for distribution expansion. Species require stable or increasing abundance trends at their core sites in order to be able to expand their distribution areas under climate change, and the more habitat that is available for species with stable abundance trends, the faster they can expand their distribution areas. Thus conservation action should focus on reversing population declines and maintaining stable populations, as well as protecting and restoring natural habitat. A greater understanding of the drivers of abundance declines should help inform conservation strategies; there is already evidence to suggest that population trends can be improved given the appropriate targeted (Brereton *et al.*, 2008, Lawson *et al.*, 2014) or wider countryside (Brereton *et al.*, 2011) management. Much work has been done on quantifying the effect of habitat availability on species' distributions (e.g. Frey *et al.*, 2012, Fernández-Chacón *et al.*, 2014) and range expansions (e.g. Collingham & Huntley, 2000, Hill *et al.*, 2001), and protected areas are considered to be a key strategy for maintaining natural habitat in the landscape. The importance of protected areas for species' distribution expansion has been recognised, with species preferentially colonising protected areas when expanding into newly suitable regions (Thomas *et al.*, 2012, Hiley *et al.*, 2013). This preference for protected areas highlights that the quality of the available habitat is an essential determinant of distribution expansion, and that therefore for species to expand their distributions, there must be a sufficient amount of habitat available and that habitat must be of a sufficiently high quality. Conservation strategies should therefore focus on identifying the causes of species' population decline and reversing these trends, and protecting and restoring natural habitat, in order to facilitate species' distribution expansion under climate change.

Appendix Chapter 2

Table A2. Scientific and vernacular names of species included in analyses. G = habitat generalist (wider-countryside species), S = habitat specialist (classified according to Asher *et al.* 2001). Change in species response variables are given for the first (1970-82 to 1995-99) and second (1995-99 to 2005-09) study periods. Change in polewards (northern) range margin is in km yr^{-1}, change in distribution area is proportional change per year in the number of 10km OS grid squares occupied, and change in abundance is percentage change per year (from regression $\log_{10}$ collated abundance index and year).

			Change in response variable during first study period			Change in response variable during second study period		
Latin name	Common name	Habitat	Range margin	Distribution area	Abundance	Range margin	Distribution area	Abundance
Anthocharis cardamines	Orange Tip	G	1.94	0.007	1.52	-0.62	<0.001	-0.96
Apatura iris	Purple Emperor	S	-2.03	-0.030	-1.15	2.53	0.031	2.98
Aphantopus hyperantus	Ringlet	G	2.22	0.008	6.82	1.97	0.011	2.49
Argynnis adippe	High Brown Fritillary	S	-2.24	-0.043	5.18	-5.05	-0.052	-12.44
Argynnis paphia	Silver-washed Fritillary	S	-0.37	-0.015	0.86	-3.35	0.018	3.45
Boloria euphrosyne	Pearl-bordered Fritillary	S	-1.34	-0.031	-3.28	0.63	-0.051	-6.20
Boloria selene	Small pearl-bordered Fritillary	S	-0.46	-0.017	-2.59	2.13	-0.015	-1.91

Callophrys rubi	Green Hairstreak	S	1.52	-0.015	-0.53	-0.78	0.003	-3.35
Celastrina argiolus	Holly Blue	G	-1.31	0.024	4.81	6.89	-0.006	-3.58
Cupido minimus	Small Blue	S	0.05	-0.021	0.41	-1.25	-0.012	3.50
Erynnis tages	Dingy Skipper	S	-6.38	-0.027	-1.04	2.25	-0.007	-2.28
Euphydryas aurinia	Marsh Fritillary	S	-0.86	-0.024	-2.24	0.18	-0.016	5.64
Gonepteryx rhamni	Brimstone	G	0.67	-0.002	0.26	0.57	<-0.001	-0.01
Hamearis lucina	Duke of Burgundy	S	-5.19	-0.028	0.19	-4.56	-0.033	-6.44
Hesperia comma	Silver-spotted Skipper	S	-0.58	-0.007	13.70	1.00	0.025	-2.07
Hipparchia semele	Grayling	S	-3.18	-0.024	-2.22	1.75	-0.022	-4.09
Lasiommata megera	Wall	G	-5.08	-0.022	-4.07	3.41	-0.020	-4.32
Leptidea sinapis	Wood White	S	-0.08	-0.039	-14.77	-2.01	-0.018	-7.03
Limenitis camilla	White Admiral	S	0.56	-0.016	-2.85	1.91	0.011	-1.16
Lycaena phlaeas	Small Copper	G	-0.26	-0.009	0.49	-4.43	-0.004	-2.86
Melanargia galathea	Marbled White	G	2.78	0.006	3.82	2.90	0.002	-2.54
Melitaea athalia	Heath Fritillary	S	0.85	-0.010	-3.71	1.59	0.012	-5.13
Neozephyrus quercus	Purple Hairstreak	G	-0.42	-0.004	-1.95	0.49	-0.017	-1.62
Pararge aegeria	Speckled Wood	G	2.11	0.014	2.89	3.13	0.024	4.05
Pieris rapae	Small White	G	-2.52	-0.003	0.63	3.42	-0.004	-3.19

Plebeius (Aricia) agestis	Brown Argus	G	2.56	0.011	0.81	5.94	0.015	-5.20
Plebeius argus	Silver-studded Blue	S	0.47	-0.024	1.33	0.50	-0.012	-3.55
Polygonia c-album	Comma	G	9.25	0.016	4.48	11.29	0.010	3.23
Polyommatus bellargus	Adonis Blue	S	-0.92	-0.014	0.53	2.39	0.017	3.31
Polyommatus coridon	Chalkhill Blue	S	-0.39	-0.020	2.41	1.48	-0.008	-3.78
Pyrgus malvae	Grizzled Skipper	S	-3.23	-0.027	-1.24	-1.91	-0.018	-3.59
Pyronia tithonus	Gatekeeper	G	-0.27	0.007	-0.58	0.84	-0.001	-2.85
Ochlodes sylvanus (venata)	Large Skipper	G	1.00	-0.005	1.61	-0.50	-0.005	-4.77
Satyrium w-album	White-letter Hairstreak	G	2.12	-0.030	-3.75	2.45	0.027	-7.61
Thecla betulae	Brown Hairstreak	S	-3.61	-0.027	6.20	1.81	-0.004	-5.22
Thymelicus lineola	Essex Skipper	G	1.49	0.031	2.89	2.89	0.011	-11.26
Thymelicus sylvestris	Small Skipper	G	4.71	0.003	0.70	4.90	-0.001	-10.13

Appendix Chapter 3

A3.1 SUPPLEMENTARY METHODS

A3.1.1 Determinants of change in distribution area

The availability of distribution data was determined by the occurrence of national recording efforts used to produce butterfly distribution atlases (Asher *et al.*, 2001, Fox *et al.*, 2006). Due to the vast spatial extent of data collection, annual data did not achieve sufficient spatial coverage for robust analyses and so data were necessarily grouped into periods of several years. Choice of study periods were this selected as 1970-82 to 1995-99 (first study period) and 1995-99 to 2005-09 (second study period) corresponding to national atlas recording periods. Change in species' distribution area was calculated as the percentage change in the number of 10 km Ordnance Survey grid squares with records. Sub-sampling was carried out on the distribution dataset prior to analysis, to account for the large increase in recording effort over time. For example, there was an increase from 185,649 records in 1970-82 to 1,710,586 records in 1995-99 (Fox *et al.*, 2006). Sub-sampling was carried out per 10 km grid square using an established method (Fox *et al.*, 2006), and aimed to achieve a spatially and temporally consistent recording effort across Britain over time. Thus for each 10 km grid square, sub-samples were taken to produce a consistent number of records of each temporal resolution (records can be collected over a day, month or year) over time. Sub-sampling was carried out 100 times per time period and the mean values of distribution change per species obtained were used in analyses.

A mobility score (Cowley *et al.*, 2001) was used to represent species' dispersal ability. The mobility score was determined by expert opinion from surveys (Cowley *et al.*, 2001). This score was correlated with species' wingspan (linear regression $R^2 = 0.47$, $P<0.001$ taken from publication; Sekar, 2012) and another movement index (Dennis & Shreeve, 1996) created using a composite of mobility variables, including some of the distribution data used in this analysis (linear regression, $F_{1,31}=47.78$, $R^2=0.59$, $P<0.001$). These relationships suggest that the mobility score from expert opinion is relatively robust.

Habitat availability for each species was quantified as the proportion of each species' breeding habitat in the landscape using LCM2000 (Fuller *et al.*, 2002) (for the first study period; 1970-82 to 1995-99) and LCM2007 (Morton *et al.*, 2011) (for the second study period; 1995-99 to 2005-09) 25m resolution raster data. Land cover categories considered to be species' breeding habitat were identified using expert opinion (Asher *et al.*, 2001), and their importance was weighted based on the frequency with which species' distribution records were from grid squares containing that land cover type. Weighting was based by computing the total number of 100 m grid square records containing both the species of interest and its breeding land cover type; this value was then divided by the total number of 100 m grid records of any butterfly species containing the focal species' habitat land cover type. This gives a metric for the frequency of a given butterfly species in a particular land cover category, relative to records of all butterfly species. Only grid cells within the Ordnance Survey 100 km grid squares of the focal species' distribution were included to control for other factors limiting species' ranges such as dispersal and climate. This provided a method for weighting each land cover type in relation to the focal species' use of the habitat (Table A3.3.2). The proportion of habitat available at the species' distribution leading edge (defined as the 10 km grid squares which were unoccupied at the start of the study period, but colonised by the end of the study period) was estimated from land cover datasets and multiplied by the species' habitat weighting, to give an index of habitat availability for each species. For species breeding in more than one habitat type, values were summed across all breeding habitats to produce the index. The habitat availability index was then transformed ($\log_{10}$) to give a normalised distribution.

Change in abundance was calculated using only continuously-occupied transect sites in order to exclude population increases that occur following colonisation. Thus for 1995-99 to 2005-09, sites had to be continuously occupied by a species since 1990 to be included (1-31 transects per species, median = 7.6). For 1970-82 to 1995-99, the lack of early data (UKBMS started in 1976; Pollard *et al.*, 1995) meant that sites had to be continuously occupied from 1982 to be included (1-25 transects per species, median = 5). For each species, abundance trends were computed from fitting mixed models by regressing $\log_{10}$ abundance index against year, with transect site as a random variable.

We employed an information-theoretic approach to identify the best models for explaining distribution changes in relation to abundance trends, habitat availability and dispersal ability. For each of the two study periods (1970-82 to 1995-99 and 1995-99 to 2005-09), we constructed general linear models to assess distribution change against all three explanatory variables (habitat availability, dispersal ability and abundance change) and their interactions (the literature provided evidence for linear relationships between distribution change and change in abundance (Warren *et al.*, 2001), dispersal ability (Mattila *et al.*, 2011) and habitat availability (Hill *et al.*, 2001), as did initial data exploration). Interactions between habitat availability and dispersal might be expected if the effect of habitat availability on expansion depended on the dispersal rate. Also, we might expect that if abundance trends were related to change in distribution area, then positive effects of habitat availability and dispersal ability might be contingent on stable or increasing abundance trends. Thus all interactions between variables were explored in our analyses. Explanatory variables were standardized using the function *standardize* in the package *arm* (in the statistical program R; R Core Team, 2012) and the function *dredge* in the package *MuMIn* was used to rank models based on AICc values and Akaikes weights. Where Δ AICc < 2, model averaging was used (only models with Δ AICc < 2 relative to the top-ranked model were included in model averaging), otherwise the model with the lowest AICc value was considered the best fit. Change in abundance was calculated from a different number of transect sites for each species, and therefore our confidence in the estimates of this variable differed among species, so we weighted species abundance trend data by the inverse of the standard error of change in abundance. These analyses with weighting were then evaluated against models which did not include weights, and weighting was found to be the better model for distribution change in the second study period (both when species' change in abundance was computed from continuously-occupied transect sites and when it was computed across all transect sites, Table A3.3.4b&d).

A3.1.2 Colonisation distance distributions

Distributions of colonisation distances were extracted from the BNM dataset for the second study period (1995-99 to 2005-09; data from the earlier period 1970-82 were of too low spatial resolution and coverage for this analysis). Analyses were carried out at 1km grid resolution and only colonisations occurring at species' distribution leading edges were included (defined as 10 km grid squares which were unoccupied in 1995-99 but colonised by 2005-09; N = 11 species, total colonisations = 12234 colonisations at 1km grid resolution, 14-1722 per species); colonisations occurring in 10 km grid squares where the species was already present were considered to be distribution infilling and were not included in these analyses.

Colonisation distances were extracted in R. The function *ndist2* in the package *splancs* was implemented to calculate the straight line distance from each new colony (grid square centre point) in 2005-09 to the nearest existing colony (grid square centre point) present in 1995-99. Records were included regardless of whether one individual or multiple individuals of species were recorded. There are, however, likely to be effects of spatial and temporal variation in recording effort, thus we explored different definitions of 'existing' and 'new' colonies (see Fig. A3.2.1). Existing colonies can be considered to be (i) any 1 km grid square where the species was recorded in 1995-99, or they can be considered to be (ii) only the 1 km grid squares where the species was recorded in both 1995-99 and 2005-09. New colonies can be considered to be (i) any new 1 km grid square where a species was first recorded in 2005-09, or (ii) only 1 km grid squares where the species was known to be absent in 1995-99 (i.e. the grid square was visited but the species was not recorded), and colonised in 2005-09.

We elected to present results using the most rigorous definitions, thus existing colonies were those recorded in both 1995-99 and 2005-09, and new colonies were those which were visited in 1995-99 but the species was not recorded present until 2005-09. Colonisation distance distributions for each species were binned at 2 km intervals and fitted with an inverse power function, which is a better fit than the negative exponential distribution for fat-tailed distributions (Chapman *et al.*, 2007). Since colonisation kernels describe a curve rather than a single value, the median distance (i.e. the distance at which the cumulative proportion of frequencies of colonisation distances was 0.5) was used as a summary value of the fitted distributions (Fig 3.2, Table A3.3.5). A multi-model inference framework was applied following the same methods as outlined above for analysing distribution changes, to determine relationships between median colonisation distance and habitat availability, dispersal ability and change in abundance (Table A3.3.6).

In order to determine how our results varied according to the different definitions of existing and new colonies, we extracted colonisation distance distributions using all alternative combinations and applied all alternative median colonisation distances to our analyses. In each case, habitat availability was found to be the most important explanatory variable, with some less important positive associations shown for dispersal ability and change in abundance (Table A3.3.7). This suggests that recording effort has a quantitative impact on our results, but that this effect is not sufficient to change our qualitative conclusions, which maintain that habitat availability is the most important variable for determining colonisation distance once the expansion is taking place.

A3.1.3 Phylogenetic analyses

In order to assess the importance of species' phylogenetic relationships in our analyses, we used AICc values and Akaike weights to compare global models incorporating phylogenetic structure against global models without phylogenetic structure. A phylogenetic tree for European butterflies was obtained from the literature (Cizek & Konvicka, 2005) and branch lengths were calculated based on Grafen's methods using the function *compute.brln* in the package *ape* in R (R Core Team, 2012). The phylogenetic tree was then trimmed to include only the study species. We built generalized least squares (GLS) models containing all three explanatory variables and their interactions (GLS models produce the same results as linear models but are directly comparable with models including phylogeny), and used AICc values and Akaike weights to compare these GLS models against phylogenetic generalized least squares (PGLS) models incorporating phylogeny as the within-group correlation structure. We found that models incorporating phylogeny had consistently higher AICc scores and lower Akaike weights than models without phylogeny (Table A3.3.3), and therefore were a poorer fit to the data.

Phylogenetic analyses make the assumption that a phylogenetic signal is present in the data (Hernández *et al.*, 2013), therefore if no signal is detected it may not be appropriate to carry out phylogenetic analyses (Ashton, 2004). We tested whether a phylogenetic signal was present in our dataset in order to determine whether the poorer fit of the PGLS models was due to a lack of phylogenetic signal. We used the *pgls* function in the R package *caper* to estimate the value of λ (a branch length scaling parameter) using maximum likelihood. Where $\lambda = 0$ there is no evidence of a phylogenetic signal, and where $\lambda = 1$ there is strong support for a Brownian model of evolution (Pagel, 1999, Hernández *et al.*, 2013). We found that in all cases there was no evidence for a phylogenetic signal in our data (Table A3.3.3). Detection of a phylogenetic signal is reliant on sample size as well as the accuracy of the phylogenetic tree and the data (Blomberg *et al.*, 2003) therefore a lack of signal may be due to the relatively small sample size of our dataset (Freckleton *et al.*, 2002) or uncertainties in Lepidoptera phylogeny. Nevertheless we found no evidence that phylogenetic analyses would be appropriate or that inclusion of phylogenetic correlations would produce models with a better fit to our data. Thus we present data for non-phylogenetically-controlled analyses in the main text.

A3.2 SUPPLEMENTARY FIGURES

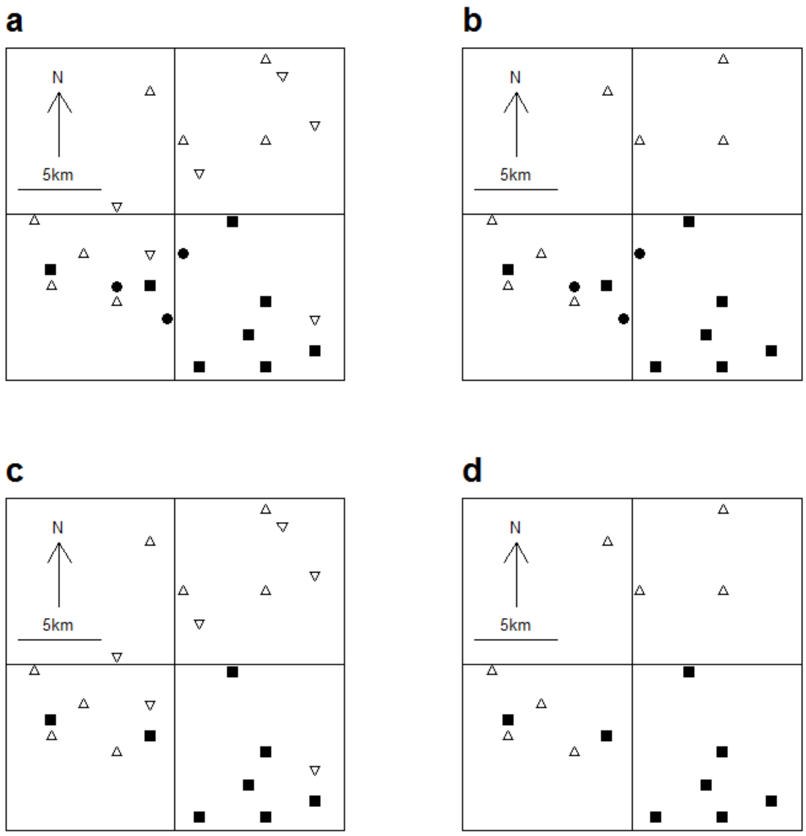


Figure A3.2.1. Schematic of different definitions of ‘existing’ and ‘new’ colonies, illustrating an example of a 20 km x 20 km square area containing butterfly records at a 1km grid square resolution. Existing colonies are 1 km grid squares with a species record in 1995-99 (solid symbols), however these consist of those colonies which were recorded only in 1995-99 (solid circles), or colonies which were recorded in both 1995-99 and 2005-09 (solid squares). New colonies are 1 km grid squares with a new species record in 2005-09 (open symbols), and these consist of grid squares which were visited in 1995-99 and the species was not recorded (upward open triangles), and grid squares which were not visited in 1995-99 so previous absence of the species is not confirmed (downward open triangles). Thus the available combinations of definitions are: **a** any existing colony (solid symbols) and any new colony (open symbols), **b** any existing colony (solid symbols) and previously visited new colonies (upward open triangles) **c** continuously occupied existing colonies (solid squares) and any new colonies (open symbols), and **d** continuously occupied existing colonies (solid squares) and previously visited new colonies (upward open triangles). The results of using different definitions are shown in Table A3.3.7.

A3.3 SUPPLEMENTARY TABLES

Table A3.3.1. Species' change in distribution area, change in abundance, dispersal ability and habitat availability in the first and second study period.

	First study period (1970-82 to 1995-99)					Second study period (1995-99 to 2005-09)			
Species	Dispersal ability*	Change in distribution area (% yr^{-1})‡	Change in abundance at continuously occupied sites (% yr^{-1})§	Change in abundance across all sites (% yr^{-1}) §	Habitat availability†	Change in distribution area (% yr^{-1})‡	Change in abundance at continuously occupied sites (% yr^{-1}) §	Change in abundance across all sites (% yr^{-1}) §	Habitat availability†
Aglais io	39	0.55	1.06	3.30	0.039	1.71	-6.09	-2.99	0.015
Anthocharis cardamines	32	0.65	3.80	1.52	0.080	-0.02	-4.28	-0.96	0.021
Aphantopus hyperantus	16	0.75	1.57	6.82	0.005	0.77	-2.37	2.49	0.007
Argynnis paphia	31	-1.54	0.38	0.86	0.006	1.06	6.84	3.45	0.008
Aricia agestis	12	1.06	1.27	0.82	0.007	0.61	-9.23	-5.20	0.003
Boloria euphrosyne	18	-3.09	5.56	-3.28	0.005	-	-	-	-
Boloria selene	19	-1.68	4.28	-2.59	0.012	-1.33	29.38	-1.91	0.014
Callophrys rubi	14	-1.53	-23.65	-0.53	0.006	0.39	-21.17	-3.35	0.014
Celastrina argiolus	34	-	-	-	-	-0.87	-19.15	-3.58	0.017
Cupido minimus	1	-2.10	-12.62	0.41	0.001	-	-	-	-

Erynnis tages	10	-2.67	2.02	-1.04	0.003	-0.72	-53.32	-2.28	0.001
Gonepteryx rhamni	36	-0.15	-7.23	0.26	0.035	-0.10	-2.22	-0.01	0.029
Hesperia comma	15	-0.71	10.09	13.70	0.001	3.55	-11.75	-2.07	0.001
Hipparchia semele	22	-2.41	-0.57	-2.21	0.004	-2.06	4.45	-4.09	0.002
Lasiommata megera	30	-2.24	-17.58	-4.07	0.008	-2.18	-17.59	-4.32	0.008
Limenitis camilla	27	-	-	-	-	1.37	-4.53	-1.16	0.006
Lycaena phlaeas	26	-0.88	-3.41	0.49	0.011	-0.65	-11.54	-2.86	0.010
Melanargia galathea	24	0.61	5.50	3.81	0.008	0.03	-2.22	-2.54	0.004
Melitaea athalia	5	-1.05	4.88	-3.71	0.002	-	-	-	-
Pararge aegeria	23	1.43	3.98	2.89	0.037	2.13	5.78	4.05	0.022
Pieris rapae	40	-0.31	-2.31	0.63	0.032	-0.53	-7.14	-3.19	0.016
Plebejus argus	2	-	-	-	-	-0.65	-10.11	-3.55	0.002
Polygonia c-album	33	1.62	-4.21	4.48	0.029	0.68	6.51	3.23	0.019
Polyommatus bellargus	8	-1.42	7.44	0.53	0.003	0.27	11.93	3.31	0.002
Polyommatus coridon	11	-2.04	19.30	2.41	0.004	-0.05	-5.30	-3.78	0.001
Pyronia tithonus	21	0.66	-3.50	-0.58	0.031	-0.35	-7.93	-2.85	0.020
Ochlodes sylvanus	20	-0.49	-2.65	1.61	0.028	-0.87	-19.15	-4.77	0.014
Thymelicus sylvestris	19	0.30	-6.15	0.70	0.012	-0.32	-20.37	-10.13	0.012

* Dispersal ability is a ranked index from expert opinion (Cowley *et al.*, 2001)

‡ Change in distribution area is the percentage change in the number of 10km grid squares occupied per year (from BNM data; Asher *et al.*, 2001, see Appendix 3.1)

§ Change in abundance was calculated using BMS data (Botham *et al.*, 2010) at continuously occupied transect sites (where the focal species was present every year during the study period) and across all transect sites (see Appendix 3.1)

†Habitat availability from LCM 2000 (Fuller *et al.*, 2002) and LCM2007 (Morton *et al.*, 2011) (see Appendix 3.1 and Table A3.3.2)

Missing values indicate insufficient species' data for the species to be included in analyses for that study period.

Table A3.3.2. Habitat availability data for each species, giving species' scientific names and the land cover category(s) which they are considered to use as breeding habitat.

a 1970-82 to 1995-99

Species	Land cover category*		Proportion in landscape†	Weight‡	Available§	Total habitat availability¶
Aglais io	1.1	Broadleaved woodland	0.0687	0.2849	0.0195	0.0393
	17.1	Suburban	0.0508	0.2810	0.0142	
	17.2	Urban	0.0216	0.2531	0.0054	
Anthocharis cardamines	1.1	Broadleaved woodland	0.0708	0.2173	0.0153	0.0798
	5.1	Improved grassland	0.2345	0.1914	0.0448	
	6.1	Neutral grass	0.0510	0.1655	0.0084	
	17.1	Suburban	0.0523	0.2125	0.0111	
Aphantopus hyperantus	5.2	Setaside grass	0.0083	0.1644	0.0013	0.0050
	6.1	Neutral grass	0.0486	0.0746	0.0036	
Argynnis paphia	1.1	Broadleaved woodland	0.1144	0.0514	0.0058	0.0058
Aricia agestis	5.2	Setaside grass	0.0235	0.0835	0.0019	0.0067
	6.1	Neutral grass	0.0178	0.0313	0.0005	
	7.1	Calcareous grass	0.0567	0.0689	0.0039	
	8.1	Acid grass	0.0064	0.0176	0.0001	
	19.1	Supra-littoral sediment	0.0015	0.1273	0.0002	
Boloria euphrosyne	1.1	Broadleaved woodland	0.0918	0.0204	0.0018	0.0052
	9.1	Bracken	0.0091	0.0260	0.0002	
	10.2	Open dwarf shrub heath	0.1276	0.0247	0.0031	
Boloria selene	1.1	Broadleaved woodland	0.0641	0.0198	0.0012	0.0123
	5.2	Setaside grass	0.0013	0.0058	0.0000	
	9.1	Bracken	0.0151	0.0662	0.0010	
	10.2	Open dwarf shrub heath	0.1222	0.0820	0.0100	
Callophrys rubi	5.2	Setaside grass	0.0092	0.0334	0.0003	0.0056
	7.1	Calcareous grass	0.0552	0.0315	0.0017	
	10.2	Open dwarf shrub heath	0.0545	0.0526	0.0028	
	12.1	Bogs	0.0121	0.0597	0.0007	
Cupido minimus	7.1	Calcareous grass	0.0632	0.0208	0.0013	0.0014
	19.1	Supra-littoral sediment	0.0018	0.0601	0.0001	
Erynnis tages	7.1	Calcareous grass	0.0673	0.0411	0.0027	0.0028
	19.1	Supra-littoral sediment	0.0014	0.0607	0.0001	

Gonepteryx rhamni	1.1	Broadleaved woodland	0.0812	0.1805	0.0146	0.0349
	5.2	Setaside grass	0.0129	0.1697	0.0021	
	6.1	Neutral grass	0.0326	0.0719	0.0023	
	17.1	Suburban	0.0725	0.1651	0.0119	
	17.2	Urban	0.0330	0.1141	0.0037	
Hesperia comma	7.1	Calcareous grass	0.0665	0.0210	0.0013	0.0013
Hipparchia semele	7.1	Calcareous grass	0.0460	0.0175	0.0008	0.0039
	10.2	Open dwarf shrub heath	0.0523	0.0511	0.0026	
	18.1	Supra-littoral rock	0.0003	0.3636	0.0001	
	19.1	Supra-littoral sediment	0.0024	0.1532	0.0003	
Lasiommata megera	5.2	Setaside grass	0.0101	0.0446	0.0004	0.0081
	7.1	Calcareous grass	0.0603	0.0807	0.0048	
	8.1	Acid grass	0.0356	0.0751	0.0026	
	19.1	Supra-littoral sediment	0.0010	0.1746	0.0001	
Lycaena phlaeas	5.2	Setaside grass	0.0088	0.1356	0.0012	0.0111
	7.1	Calcareous grass	0.0554	0.1299	0.0072	
	10.2	Open dwarf shrub heath	0.0313	0.0790	0.0024	
	19.1	Supra-littoral sediment	0.0010	0.3013	0.0003	
Melanargia galathea	5.2	Setaside grass	0.0186	0.1200	0.0022	0.0084
	6.1	Neutral grass	0.0213	0.0415	0.0008	
	7.1	Calcareous grass	0.0587	0.0899	0.0052	
Melitaea athalia	1.1	Broadleaved woodland	0.1216	0.0110	0.0013	0.0020
	10.2	Open dwarf shrub heath	0.0177	0.0412	0.0007	
Pararge aegeria	1.1	Broadleaved woodland	0.0745	0.2999	0.0223	0.0370
	17.1	Suburban	0.0647	0.2266	0.0146	
Pieris rapae	5.2	Setaside grass	0.0076	0.3126	0.0023	0.0324
	6.1	Neutral grass	0.0554	0.2488	0.0137	
	17.1	Suburban	0.0470	0.3457	0.0162	
Polygonia c-album	1.1	Broadleaved woodland	0.0798	0.1727	0.0137	0.0288
	17.1	Suburban	0.0669	0.1630	0.0109	
	17.2	Urban	0.0292	0.1410	0.0041	
Polyommatus bellargus	7.1	Calcareous grass	0.0685	0.0526	0.0036	0.0036
Polyommatus coridon	7.1	Calcareous grass	0.0713	0.0503	0.0035	0.0035
Pyronia tithonus	5.2	Setaside grass	0.0113	0.3064	0.0034	0.0307
	6.1	Neutral grass	0.0357	0.1613	0.0057	
	7.1	Calcareous grass	0.0623	0.2452	0.0152	

	17.2	Urban	0.0344	0.1814	0.0062	
Ochlodes sylvanus	1.1	Broadleaved woodland	0.0779	0.1621	0.0126	0.0275
	5.2	Setaside grass	0.0109	0.1725	0.0018	
	6.1	Neutral grass	0.0413	0.1213	0.0050	
	7.1	Calcareous grass	0.0597	0.1344	0.0080	
Thymelicus sylvestris	5.2	Setaside grass	0.0113	0.1963	0.0022	0.0120
	6.1	Neutral grass	0.0395	0.1448	0.0057	
	8.1	Acid grass	0.0387	0.1058	0.0040	

b 1995-99 to 2005-09

Species	Land cover category		Proportion in landscape	Weight	Available	Total habitat availability
Aglias io	1	Broadleaved woodland	0.0349	0.2868	0.0100	0.0146
	22	Urban	0.0040	0.2331	0.0009	
	23	Suburban	0.0127	0.2888	0.0036	
Anthocharis cardamines	1	Broadleaved woodland	0.0418	0.1986	0.0083	0.0211
	5	Rough grassland	0.0493	0.1572	0.0077	
	6	Neutral grassland	0.0034	0.2158	0.0007	
	23	Suburban	0.0226	0.1927	0.0043	
Aphantopus hyperantus	5	Rough grassland	0.0458	0.1437	0.0065	0.0072
	6	Neutral grassland	0.0041	0.1484	0.0006	
Argynnis paphia	1	Broadleaved woodland	0.0816	0.0969	0.0079	0.0079
Aricia agestis	5	Rough grassland	0.0285	0.0693	0.0019	0.0025
	6	Neutral grassland	0.0089	0.0440	0.0003	
	7	Calcareous grassland	0.0000	0.2272	0.0001	
	8	Acid grassland	0.0022	0.0239	0.0001	
	18	Supra-littoral sediment	0.0018	0.0597	0.0001	
Boloria selene	1	Broadleaved woodland	0.0412	0.0358	0.0014	0.0139
	5	Rough grassland	0.0576	0.0504	0.0029	
	11	Heather grassland	0.0964	0.0990	0.0095	
Callophrys rubi	5	Rough grassland	0.0508	0.0459	0.0023	0.0140
	7	Calcareous grassland	0.0017	0.1151	0.0002	
	10	Heather	0.0398	0.0833	0.0033	
	11	Heather grassland	0.0629	0.0761	0.0047	
	12	Bog	0.0348	0.0984	0.0034	
Celastrina	1	Broadleaved woodland	0.0534	0.1026	0.0054	0.0170

argiolus	5	Rough grassland	0.0438	0.0724	0.0031	
	23	Suburban	0.0425	0.1978	0.0084	
Erynnis tages	7	Calcareous grassland	0.0005	0.2146	0.0001	0.0010
	10	Heather	0.0194	0.0246	0.0004	
	11	Heather grassland	0.0140	0.0179	0.0002	
	18	Supra-littoral sediment	0.0019	0.0957	0.0001	
Gonepteryx rhamni	1	Broadleaved woodland	0.0513	0.1965	0.0100	0.0285
	5	Rough grassland	0.0388	0.136	0.0052	
	6	Neutral grassland	0.0067	0.1613	0.0010	
	22	Urban	0.0189	0.1058	0.0020	
	23	Suburban	0.0556	0.1815	0.0100	
Hesperia comma	7	Calcareous grassland	0.0075	0.0906	0.0006	0.0006
Hipparchia semele	7	Calcareous grassland	0.0001	0.0377	0.0001	0.0024
	10	Heather	0.0160	0.0494	0.0007	
	11	Heather grassland	0.0365	0.0349	0.0012	
	17	Supra-littoral rock	0.0001	0.0606	0.0001	
	18	Supra-littoral sediment	0.0032	0.0830	0.0002	
	21	Saltmarsh	0.0026	0.0208	0.0001	
Lasiommata megera	5	Rough grassland	0.0520	0.0752	0.0039	0.0080
	7	Calcareous grassland	0.0009	0.1434	0.0001	
	8	Acid grassland	0.0522	0.0731	0.0038	
	18	Supra-littoral sediment	0.0013	0.1279	0.0001	
Limenitis camilla	1	Broadleaved woodland	0.0843	0.0677	0.0057	0.0057
Lycaena phlaeas	5	Rough grassland	0.0486	0.1182	0.0057	0.0095
	7	Calcareous grassland	0.0012	0.1321	0.0001	
	11	Heather grassland	0.0424	0.0816	0.0034	
	18	Supra-littoral sediment	0.0008	0.1591	0.0001	
Melanargia galathea	5	Rough grassland	0.0361	0.0953	0.0034	0.0040
	6	Neutral grassland	0.0070	0.085	0.0005	
	7	Calcareous grassland	0.0001	0.2317	0.0001	
Pararge aegeria	1	Broadleaved woodland	0.0401	0.3293	0.0132	0.0215
	23	Suburban	0.0303	0.2762	0.0083	
Pieris rapae	5	Rough grassland	0.0540	0.1837	0.0099	0.0161
	6	Neutral grassland	0.0028	0.2674	0.0007	
	23	Suburban	0.0174	0.3109	0.0054	
Plebejus argus	10	Heather	0.0038	0.1832	0.0007	0.0016
	11	Heather grassland	0.0049	0.1858	0.0009	

Polygonia c-album	1	Broadleaved woodland	0.0504	0.2019	0.0101	0.0190
	22	Urban	0.0111	0.1470	0.0016	
	23	Suburban	0.0346	0.2091	0.0072	
Polyommatus bellargus	7	Calcareous grassland	0.0086	0.2050	0.0017	0.0017
Polyommatus coridon	7	Calcareous grassland	0.0082	0.1573	0.0013	0.0013
Pyronia tithonus	5	Rough grassland	0.0523	0.1938	0.0101	0.0202
	6	Neutral grassland	0.0056	0.2131	0.0011	
	7	Calcareous grassland	0.0022	0.1985	0.0004	
	23	Suburban	0.0467	0.1821	0.0085	
Ochlodes sylvanus	1	Broadleaved woodland	0.0515	0.1384	0.0071	0.0138
	5	Rough grassland	0.0479	0.1216	0.0058	
	6	Neutral grassland	0.0062	0.1222	0.0007	
	7	Calcareous grassland	0.0005	0.1292	0.0001	
Thymelicus sylvestris	5	Rough grassland	0.0482	0.1286	0.0062	0.0120
	6	Neutral grassland	0.0064	0.1434	0.0009	
	8	Acid grassland	0.0520	0.0938	0.0048	

a the earlier study period (1970-82 to 1995-99, LCM2000; Fuller *et al.*, 2002)

b the later study period (1995-99 to 2005-09, LCM2007; Morton *et al.*, 2011)

* land cover category numbers given refer to the class number associated with each land cover category in the respective datasets

† the proportional area that the specific land cover type covers at the species' distribution leading edges

‡ calculated by dividing the number of 100m BNM records which contained both the species record and their preferred land cover type, by the number of 100m BNM records (of any species) that contained the land cover type

§ proportion of land cover type at the distribution leading edge multiplied by the weight

¶ the sum of 'available' for each species

Note that these land cover types are relatively coarse and hence habitat availability is a relative metric and does not represent the absolute proportion of landscape that is actually suitable habitat.

Table A3.3.3. Comparison of global models with and without phylogenetic structure using AICc and Akaike weights, and maximum likelihood estimation of the parameter λ.

	Global model without phylogenetic correlations*		Global model including phylogenetic correlations†		Maximum likelihood estimates for λ ‡
Response variable	AICc	Weight	AICc	Weight	λ estimate (95% CI)
1970-82 to 1995-99					
Distribution change (abundance at continuously occupied sites)	87.59	0.9999	107.62	<0.0001	0 (NA, 0.482)
Distribution change (abundance at all sites)	73.78	0.9999	95.06	<0.0001	0 (NA, 0.502)
1995-99 to 2005-09					
Distribution change (abundance at continuously occupied sites)	97.09	0.9893	106.13	0.0107	0 (NA, 0.338)
Distribution change (abundance at all sites)	91.21	0.9978	103.44	0.0022	0 (NA, 0.351)
Median colonisation distance	103.56	0.7231	105.47	0.2769	0 (NA, 0.598)

* Generalized least squares global model with all three explanatory variables (change in abundance, habitat availability and dispersal ability) and their interactions but no phylogenetic structure.

† Phylogenetic generalized least squares global model with all three explanatory variables and their interactions, and species' phylogenetic relationships incorporated as the within-group correlation structure.

‡ Maximum likelihood estimates for λ. A global model was built including phylogenetic correlations with a Brownian model of evolution assumed and maximum likelihood was used to estimate the value of λ (a branch length scaling parameter). Where λ = 0 there is no evidence of phylogenetic signal, and where λ = 1 there is strong support that the trait matches a Brownian model of evolution

Table A3.3.4. Alternative general linear models assessed using an information-theoretic approach.

a Change in distribution area (1970-82 to 1995-99, species' change in abundance from continuously-occupied transect sites only)

Intercept	Abundance	Habitat	Dispersal	Abundance x Habitat	Abundance x dispersal	Habitat x dispersal	df	logLik	AICc	ΔAICc	Weight	Adj R^2
-0.67		1.69					3	-36.9	81.0	0.00	0.480	0.35
-0.67		2.20	-0.66				4	-36.5	82.9	1.91	0.185	0.35
-0.67	0.35	1.74					4	-36.6	83.2	2.22	0.158	0.34
-0.67	0.31	2.21	-0.62				5	-36.2	85.5	4.53	0.050	0.33
-0.71		2.20	-0.65			0.25	5	-36.4	86.0	4.99	0.040	0.32
-0.67	0.33	1.74		-0.06			5	-36.6	86.4	5.37	0.033	0.31
-0.64	0.50	2.11	-0.46		0.75		6	-35.9	88.5	7.54	0.011	0.31
-0.68	0.18	2.30	-0.70	-0.49			6	-36.1	88.9	7.90	0.009	0.30
-0.71	0.31	2.21	-0.61			0.25	6	-36.1	89.0	7.96	0.009	0.30
-0.67			1.05				3	-40.9	89.0	8.02	0.009	0.11
-0.67							2	-42.9	90.3	9.34	0.004	0.00
-0.66	0.17	2.38	-0.59	-2.79	2.47		7	-34.9	90.4	9.42	0.004	0.33
-0.67	0.29		1.09				4	-40.8	91.6	10.55	0.002	0.08
-0.66	0.49	2.12	-0.46		0.72	0.11	7	-35.9	92.4	11.45	0.002	0.28
-0.75	0.14	2.31	-0.72	-0.62		0.36	7	-36.0	92.7	11.67	0.001	0.27
-0.67	0.12						3	-42.9	92.9	11.89	0.001	-0.04
-0.61	0.65		1.25		1.43		5	-40.1	93.4	12.38	0.001	0.09
-0.71	0.14	2.39	-0.61	-2.85	2.44	0.24	8	-34.9	94.8	13.75	0.000	0.30

b Change in distribution area (1995-99 to 2005-09, species' change in abundance from continuously-occupied transect sites)

Intercept	Abundance	Habitat	Dispersal	Abundance x Habitat	Abundance x dispersal	Habitat x dispersal	df	logLik	AICc	ΔAICc	Weight	Adj R^2
0.23	1.43						3	-39.0	85.1	0.00	0.411	0.15
0.29	1.52	-0.36					4	-38.7	87.5	2.35	0.127	0.13
0.26	1.49		-0.30				4	-38.8	87.6	2.42	0.123	0.12
0.31							2	-41.5	87.6	2.42	0.123	0.00
0.24	1.56	-0.35		1.28			5	-38.0	89.2	4.08	0.053	0.13
0.33			-0.12				3	-41.5	90.1	4.96	0.034	-0.04
0.33		-0.10					3	-41.5	90.1	4.98	0.034	-0.04
0.22	1.65		-0.33		1.09		5	-38.5	90.2	5.03	0.033	0.10
0.29	1.53	-0.25	-0.17				5	-38.7	90.6	5.43	0.027	0.09
0.24	1.57	-0.25	-0.16	1.28			6	-38.0	92.6	7.51	0.010	0.09
0.33		-0.04	-0.10				4	-41.5	93.0	7.82	0.008	-0.09
0.25	1.68	-0.23	-0.21		1.07		6	-38.4	93.5	8.41	0.006	0.06
0.24	1.54	-0.17	-0.24			0.30	6	-38.7	94.0	8.87	0.005	0.04
0.32		-0.01	-0.12			0.09	5	-41.5	96.1	10.97	0.002	-0.14
0.25	1.50	-0.26	-0.14	1.59	-0.57		7	-38.0	96.5	11.37	0.001	0.05
0.25	1.56	-0.27	-0.14	1.30		-0.10	7	-38.0	96.6	11.43	0.001	0.05
0.22	1.68	-0.19	-0.24		1.04	0.15	7	-38.4	97.5	12.32	0.001	0.01
0.26	1.49	-0.29	-0.11	1.62	-0.58	-0.11	8	-38.0	100.9	15.77	0.000	0.00

c Change in distribution area (1970-82 to 1995-99, species' abundances from all transect sites)

Intercept	Abundance	Habitat	Dispersal	Abundance x Habitat	Abundance x dispersal	Habitat x dispersal	df	logLik	AICc	ΔAICc	Weight	Adj R^2
-0.65	2.23	1.50		1.78			5	-27.7	68.6	0.00	0.241	0.66
-0.65	2.21	2.20	-0.86	1.56			6	-26.0	68.7	0.14	0.224	0.69
-0.70	1.77	2.28	-0.76		1.86		6	-26.4	69.4	0.80	0.161	0.68
-0.67	1.49	2.56	-1.03				5	-28.3	69.7	1.14	0.136	0.65
-0.67	1.39	1.76					4	-30.3	70.6	2.04	0.087	0.60
-0.57	2.28	2.18	-0.86	1.68		-0.40	7	-25.8	72.2	3.63	0.039	0.68
-0.57	1.87	2.24	-0.72		2.30	-0.69	7	-25.8	72.2	3.63	0.039	0.68
-0.67	2.11	2.19	-0.79	1.08	0.81		7	-25.8	72.3	3.71	0.038	0.68
-0.66	1.49	2.56	-1.03			-0.04	6	-28.3	73.2	4.65	0.024	0.63
-0.56	2.16	2.16	-0.75	0.96	1.32	-0.62	8	-25.4	75.8	7.21	0.007	0.67
-0.67		1.69					3	-36.9	81.0	12.42	0.000	0.35
-0.71	1.76		1.06		3.10		5	-34.6	82.4	13.79	0.000	0.41
-0.67		2.20	-0.66				4	-36.5	82.9	14.33	0.000	0.35
-0.67	1.25		0.97				4	-37.5	85.0	16.43	0.000	0.29
-0.71		2.20	-0.65			0.25	5	-36.4	86.0	17.41	0.000	0.32
-0.67	1.31						3	-39.7	86.5	17.93	0.000	0.19
-0.67			1.05				3	-40.9	89.0	20.44	0.000	0.11
-0.67							2	-42.9	90.3	21.76	0.000	0.00

d Change in distribution area (1995-99 to 2005-09, species' abundances from all transect sites)

Intercept	Abundance	Habitat	Dispersal	Abundance x Habitat	Abundance x dispersal	Habitat x dispersal	df	logLik	AICc	ΔAICc	Weight	Adj R^2
0.09	1.26						3	-37.6	82.4	0.00	0.518	0.35
0.10	1.30	-0.28					4	-37.4	84.8	2.46	0.151	0.36
0.09	1.29		-0.18				4	-37.5	85.1	2.71	0.134	0.33
0.15	1.54	-0.29		-1.11			5	-37.1	87.3	4.92	0.044	0.33
0.10							2	-41.4	87.3	4.95	0.044	0.00
0.11	1.30	-0.29	0.02				5	-37.4	88.0	5.62	0.031	0.33
0.10	1.27		-0.17		-0.31		5	-37.5	88.2	5.81	0.028	0.31
0.10			0.06				3	-41.4	89.9	7.53	0.012	-0.04
0.10		-0.05					3	-41.4	89.9	7.54	0.012	-0.04
0.15	1.54	-0.33	0.07	-1.13			6	-37.1	90.8	8.42	0.008	0.30
0.11	1.29	-0.28	0.02		-0.24		6	-37.4	91.5	9.09	0.005	0.30
0.09	1.30	-0.26	0.00			0.10	6	-37.4	91.5	9.12	0.005	0.30
0.11		-0.15	0.17				4	-41.4	92.7	10.34	0.003	-0.09
0.15	1.65	-0.38	0.09	-1.55	0.65		7	-37.0	94.6	12.17	0.001	0.27
0.11	1.53	-0.25	0.02	-1.18		0.26	7	-37.0	94.7	12.29	0.001	0.26
0.09	1.28	-0.23	-0.01		-0.27	0.16	7	-37.4	95.4	13.00	0.001	0.27
-0.01		0.06	0.03			0.72	5	-41.2	95.6	13.20	0.001	-0.14
0.12	1.64	-0.32	0.06	-1.56	0.61	0.19	8	-37.0	98.9	16.55	0.000	0.23

a distribution change in the first study period (1970-82 to 1995-99, using species' change in abundance at continuously-occupied transect sites)

b distribution change in the second study period (1995-99 to 2005-09, using species' change in abundance at continuously-occupied sites only)

c distribution change in the first study period (using species' change in abundance across all transect sites)

d distribution change in the second study period (using species' change in abundance across all transect sites)

Variable estimates are given, along with the log likelihood, AICc value, difference in AICc between the top model and all other models (ΔAICc), Akaike weights and the adjusted R-squared value for each model. Models are ordered starting with the best fit.

Table A3.3.5. Summary data for colonisation distance distributions for each species for the second study period (1995-99 to 2005-09).

		Inverse power function‡		
Species	Sample size†	Fitted equation	R^2	Median distance (km)
Aglais io	1285	$I = 2.52\ (\pm 0.48)\ D^{1.39\ (\pm 0.13)}$	0.71	10.06
Anthocharis cardamines	384	$I = 2.00\ (\pm 0.38)\ D^{1.56\ (\pm 0.11)}$	0.86	5.61
Aphantopus hyperantus	1018	$I = 3.38\ (\pm 0.48)\ D^{2.13\ (\pm 0.13)}$	0.85	6.78
Argynnis paphia	444	$I = 3.19\ (\pm 0.40)\ D^{1.72\ (\pm 0.10)}$	0.81	9.57
Aricia agestis	569	$I = 1.68\ (\pm 0.62)\ D^{1.30\ (\pm 0.22)}$	0.65	6.24
Boloria selene	258	$I = 1.93\ (\pm 0.66)\ D^{1.49\ (\pm 0.23)}$	0.68	5.75
Callophrys rubi	408	$I = 2.20\ (\pm 0.65)\ D^{1.57\ (\pm 0.21)}$	0.69	6.33
Celastrina argiolus	597	$I = 3.42\ (\pm 0.46)\ D^{1.96\ (\pm 0.12)}$	0.82	8.18
Erynnis tages	153	$I = 2.17\ (\pm 0.47)\ D^{1.63\ (\pm 0.15)}$	0.82	4.70
Gonepteryx rhamni	556	$I = 2.78\ (\pm 0.29)\ D^{1.91\ (\pm 0.07)}$	0.90	6.19
Hesperia comma	48	$I = 1.70\ (\pm 0.60)\ D^{1.49\ (\pm 0.22)}$	0.73	4.97
Hipparchia semele	190	$I = 1.33\ (\pm 0.19)\ D^{0.90\ (\pm 0.05)}$	0.86	9.55
Lasiommata megera	514	$I = 1.99\ (\pm 0.75)\ D^{1.64\ (\pm 0.27)}$	0.67	5.15
Limenitis camilla	241	$I = 2.39\ (\pm 0.37)\ D^{1.70\ (\pm 0.11)}$	0.87	6.13
Lycaena phlaeas	764	$I = 3.01\ (\pm 0.47)\ D^{2.25\ (\pm 0.14)}$	0.88	5.18
Melanargia galathea	246	$I = 2.13\ (\pm 0.23)\ D^{1.35\ (\pm 0.05)}$	0.89	8.03
Pararge aegeria	1722	$I = 4.37\ (\pm 0.48)\ D^{2.05\ (\pm 0.11)}$	0.79	12.69
Pieris rapae	538	$I = 2.39\ (\pm 0.21)\ D^{1.61\ (\pm 0.05)}$	0.93	6.76
Plebejus argus	14	$I = 0.82\ (\pm 0.40)\ D^{0.77\ (\pm 0.16)}$	0.63	7.12
Polygonia c-album	750	$I = 3.28\ (\pm 0.33)\ D^{1.74\ (\pm 0.08)}$	0.86	9.74
Polyommatus bellargus	52	$I = 1.23\ (\pm 0.43)\ D^{1.21\ (\pm 0.16)}$	0.78	4.91
Polyommatus coridon	71	$I = 1.04\ (\pm 0.31)\ D^{0.97\ (\pm 0.11)}$	0.80	5.94
Pyronia tithonus	258	$I = 1.38\ (\pm 0.24)\ D^{1.36\ (\pm 0.07)}$	0.92	4.61
Ochlodes sylvanus	614	$I = 2.36\ (\pm 0.94)\ D^{1.99\ (\pm 0.34)}$	0.67	4.62
Thymelicus sylvestris	540	$I = 1.76\ (\pm 0.27)\ D^{1.46\ (\pm 0.08)}$	0.90	5.37

† sample size is number of new 1 km colonies included in analysis

‡ the fitted inverse power function equation with the R-squared value indicating the fit of the function to the raw data and the median colonisation distance from the fitted equation

Total sample size = 12234 colonisations at the 1 km resolution.

Table A3.3.6. Alternative general linear models assessed using an information-theoretic approach for species' median colonisation distance in the later study period (1995-99 to 2005-09).

Intercept	Abundance	Habitat	Dispersal	Abundance x Habitat	Abundance x dispersal	Habitat x dispersal	df	logLik	AICc	ΔAICc	Weight	Adj R^2
7.77		3.80					3	-20.0	49.5	0.00	0.476	0.55
7.77	1.46	3.62					4	-18.7	52.1	2.61	0.129	0.60
7.77		2.77	1.73				4	-18.8	52.3	2.83	0.116	0.59
7.77			3.38				3	-21.5	52.4	2.93	0.110	0.41
7.67	1.35	3.93		3.66			5	-15.2	52.5	2.99	0.107	0.76
7.77							2	-25.0	55.5	6.02	0.023	0.00
7.77	1.24		3.12				4	-20.8	56.3	6.82	0.016	0.42
7.77	1.25	2.77	1.47				5	-17.7	57.3	7.85	0.009	0.62
7.77	1.90						3	-24.1	57.7	8.18	0.008	0.05
7.53		3.23	1.41			1.74	5	-18.6	59.2	9.72	0.004	0.55
7.63	2.07		2.77		2.90		5	-20.1	62.2	12.75	0.001	0.41
7.68	1.28	3.58	0.56	3.31			6	-15.0	63.0	13.55	0.001	0.73
7.70	1.67	2.57	1.41		1.48		6	-17.4	67.7	18.27	0.000	0.58
7.73	1.21	2.86	1.42			0.32	6	-17.7	68.3	18.83	0.000	0.56
7.73	0.82	4.02	0.39	4.15	-1.66		7	-14.7	80.6	31.15	0.000	0.70
7.64	1.25	3.65	0.51	3.30		0.27	7	-15.0	81.4	31.87	0.000	0.67
7.57	1.61	2.77	1.27		1.65	0.86	7	-17.3	86.0	36.49	0.000	0.51
7.78	0.83	3.96	0.43	4.21	-1.77	-0.32	8	-14.6	117.3	67.80	0.000	0.62

Variable estimated are given, along with the log likelihood, AICc value, difference in AICc between the top model and all other models (ΔAICc), Akaike weights and the adjusted r-squared value for each model. Models are ordered starting with the best fit.

Table A3.3.7. Average model parameter estimates, standard errors and relative variable importance for median colonisation distance using different definitions of existing and new colonies.

Best-fit model variables	Estimate	Unconditional S.E.	Relative variable importance*
(a) Using any existing and any new			
Habitat availability	3.441	0.857	1
Change in abundance	1.372	0.668	0.62
Habitat x abundance	4.414	1.272	0.62
(b) Any existing and previously visited new			
Habitat availability	3.319	1.023	0.79
Change in abundance	1.445	0.783	0.43
Habitat x abundance	5.074	1.492	0.43
Dispersal ability	2.975	1.291	0.21
(c) Continuously occupied existing and any new			
Habitat availability	3.776	1.143	1
Dispersal ability	2.039	1.018	0.4

a any existing and any new colonies (Fig A3.2.1a)

b any existing and previously visited new colonies (Fig A3.2.1b)

c continuously occupied existing colonies and any new colonies (Fig. A3.2.1c)

* Relative importance of variables of 1 indicates that the variable was present in all top models, or was the only variable when model averaging was not necessary because the difference in AICc between the first and second highest ranking models was > 2.

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Appendix Chapter 4

Table A4.1. Number of 10 km grid squares predicted to be occupied by *Pararge aegeria* in 2004 when a range of detection thresholds are applied. The threshold densities applied were 0.1%, 0.5%, 1%, 5% and 10% of the maximum density (1,200,000 individuals per 10 km grid square).

Model run	Density threshold in 10km grid square (% of maximum density)				
	1200 (0.1%)	6000 (0.5%)	12000 (1%)	60000 (5%)	1200000 (10%)
Starting run	1927	1786	1693	1215	688
+25% reproduction	2087	1962	1875	1459	949
-25% reproduction	1537	1336	1230	715	349
+25% dispersal	1955	1809	1723	1232	692
-25% dispersal	1848	1715	1628	1175	669
+25% carrying capacity	1929	1798	1717	1348	873
-25% carrying capacity	1895	1742	1649	1042	435

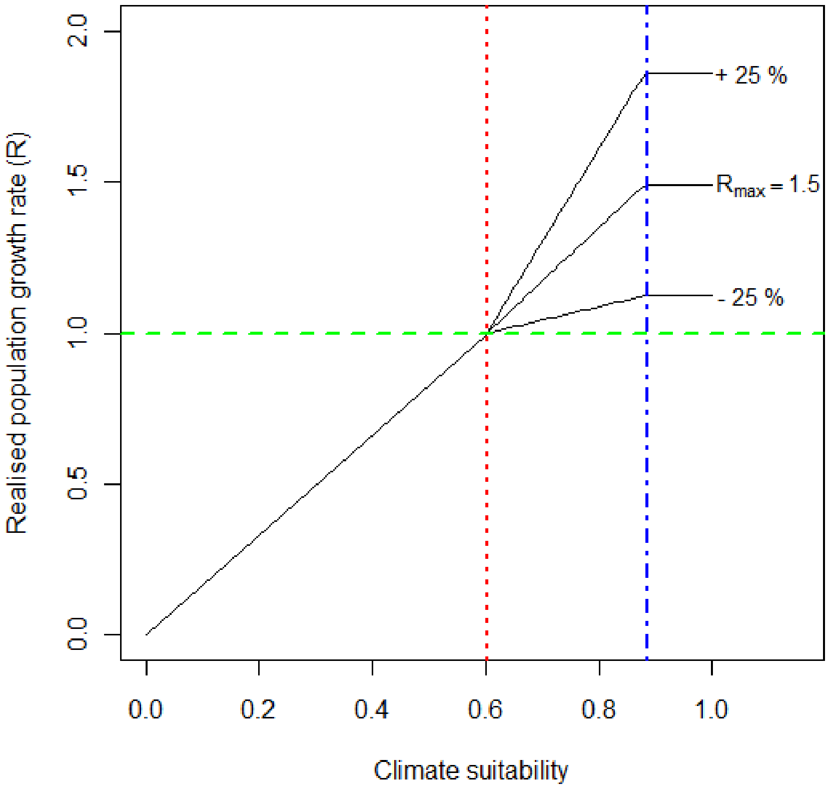

Figure A4.1. The relationship between realised population growth rate (R) and climatic suitability for *P. aegeria*. Population growth rate increases linearly from zero at climate suitability = 0, to one (reproductive replacement; dashed green line) at the minimum climate suitability for reproductive replacement (the 'break-even' point; dotted red line, see methods). Population growth rate then increases linearly between the 'break-even' point and the climate suitability at which the maximum population growth rate (R_{max}) is reached (dot-dash blue line; beyond this the species does not show any further increase in R). For our example species, we first ran the model with R_{max} =1.5 (Willis *et al.*, 2009), and then re-ran the model varying R_{max} by ±25% (see Table 4.1).

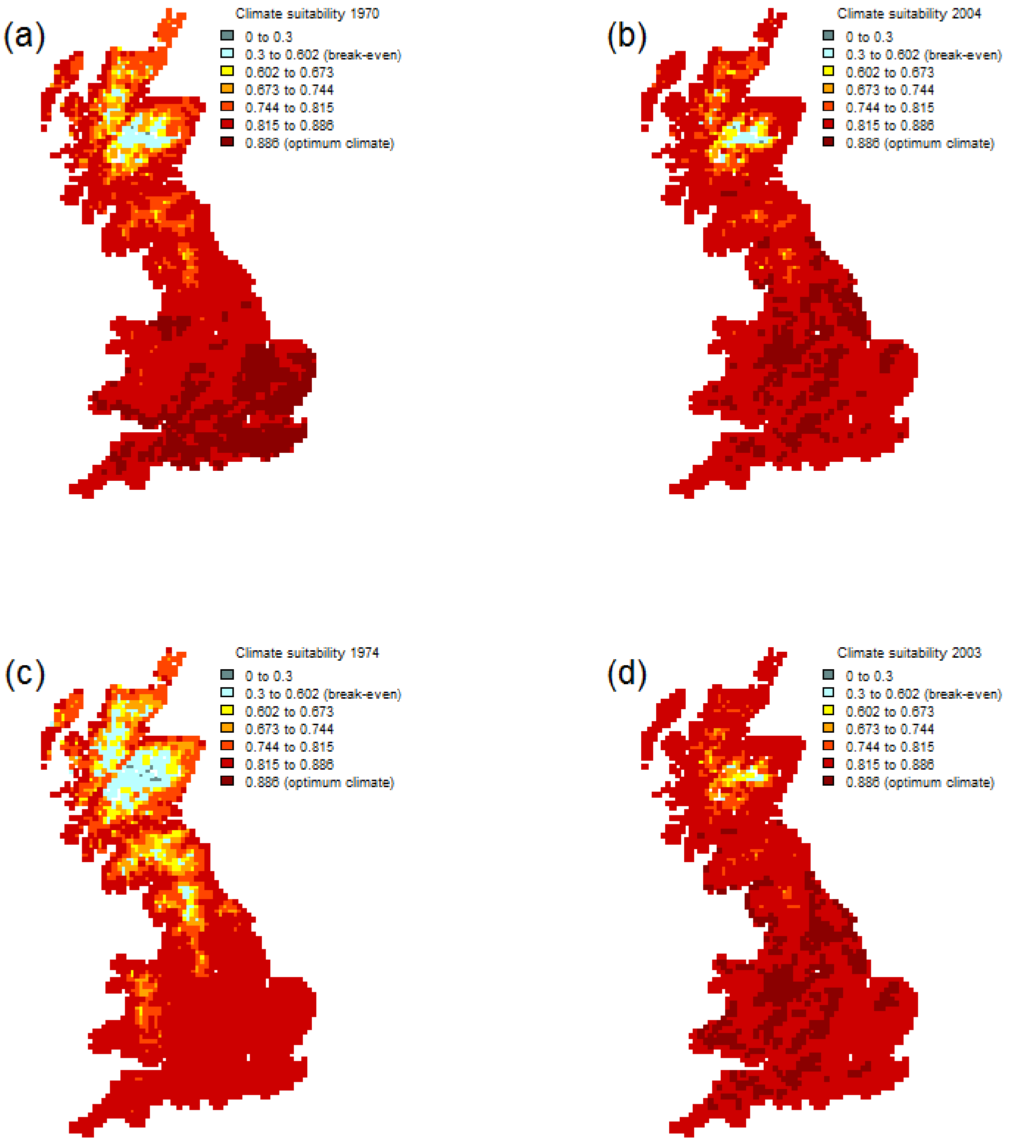

Figure A4.2. Climate suitability for *Pararge aegeria* in **(a)** 1970 (start of the model run), **(b)** 2004 (end of the model run), **(c)** 1974 (the worst year), and **(d)** 2003 (the best year). Climate suitability is graded from 0 = unsuitable, to 1 = suitable. The 'break-even' point is the value at which the species achieves reproductive replacement (i.e. R = 1; calculated from the AUC threshold, see methods), and the 'optimum climate' is the value at which maximum population growth rate (R_{max}) is achieved and above which population growth rate no longer increases with improving climate (see methods).

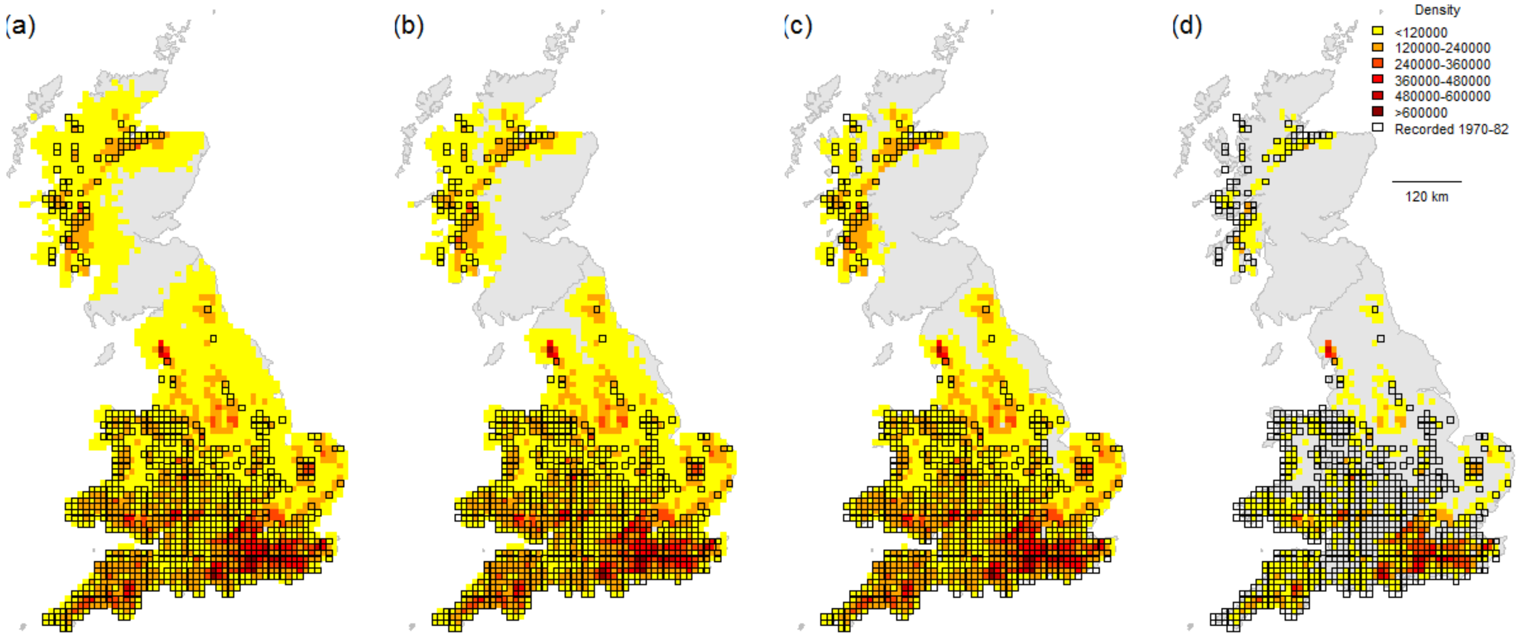

Figure A4.3. The effect on predicted distribution extent of *P. aegeria* in 2004 at a 10 km grid square resolution of varying the detection threshold through **(a)** all densities, **(b)** ≥0.1% maximum density (1,200 individuals per 10 km grid square), **(c)** ≥1% maximum density (12,000 individuals per 10 km grid square; as used in the data presented in the main text), and **(d)** ≥10% maximum density (120,000 individuals per 10 km grid square).

Appendix Chapter 5

5.1 SUPPLEMENTARY TABLES

Table A5.1.1. Study species (N = 28), observed distribution area in 1970-82 and 2000-04 (quantified as the number of 10 km grid squares occupied; observed species’ distributions in 1970-82 were used to seed the model), sensitivity of the climate envelope (the proportion of the observed species’ distribution which was projected to be at or above the climate threshold), mean climate suitability (quantified by firstly calculating for each year the proportion of 10 km grid squares in the landscape which were at or above the species’ climate threshold (the climatic suitability at which the species achieves reproductive replacement), and then taking the mean proportion over all years of the model run), and habitat availability (the proportion of species-specific suitable habitat (25 m resolution) within the 100 km grid squares of the species’ seeded distribution area).

Species	Distribution area 1970-82	Distribution area 2000-04	Climate envelope sensitivity	Mean climate suitability	Habitat availability
Aglais io	1457	2162	0.999	0.953	0.119
Apatura iris	76	79	1.000	0.726	0.111
Aphantopus hyperantus	1087	1718	0.998	0.927	0.040
Argynnis paphia	393	404	1.000	0.917	0.064
Boloria euphrosyne	344	154	1.000	1.000	0.124
Boloria selene	637	533	1.000	0.996	0.126
Celastrina argiolus	756	1312	0.999	0.967	0.159
Cupido minimus	197	218	1.000	1.000	0.006
Erynnis tages	595	495	1.000	0.948	0.023
Euphydryas aurinia	261	185	1.000	0.978	0.046
Gonepteryx rhamni	900	1192	1.000	0.935	0.183
Hamearis lucina	120	74	0.983	0.614	0.008
Hesperia comma	23	40	1.000	0.939	0.013

Lasiommata megera	1327	1224	0.997	0.863	0.062
Leptidea sinapis	118	61	0.992	0.821	0.067
Melitaea athalia	13	11	0.846	0.544	0.042
Neozephyrus quercus	561	818	0.998	0.949	0.066
Ochledes sylvanus	1188	1428	0.997	0.877	0.102
Pararge aegeria	928	1578	0.999	0.970	0.115
Plebejus argus	102	79	1.000	0.857	0.012
Polygonia c-album	840	1541	0.992	0.886	0.127
Pyronia tithonus	1050	1392	1.000	0.895	0.097
Satyrium pruni	25	24	1.000	0.808	0.059
Satyrium w-album	448	505	1.000	0.910	0.069
Thecla betulae	163	113	1.000	0.820	0.067
Thymelicus acteon	11	13	1.000	0.475	0.000
Thymelicus lineola	280	645	1.000	0.733	0.033
Thymelicus sylvestris	1055	1420	0.978	0.755	0.058

Table A5.1.2. Linear models estimates, standard errors, t values and *P* values for **(a)** the minimum value of R_{max} required by each species for distribution expansion against species' starting distribution area, habitat availability and climate suitability (model $R^2=0.60$, $F_{3,23}=11.67$, $P<0.001$), and **(b)** the minimum value of R_{max} required by each species for overall population increase against species' starting distribution area, habitat availability and climate suitability (model $R^2=0.69$, $F_{3,23}=17.07$, $P<0.001$).

(a)

	Estimate	S.E.	t value	*P*
Intercept	0.605	0.106	5.724	<0.001
Starting distribution area	<0.001	<0.0001	0.542	0.593
Log habitat availability	-0.893	0.410	-2.176	0.040
Climate suitability	-0.554	0.129	-4.295	<0.001

(b)

	Estimate	S.E.	t value	*P*
Intercept	0.278	0.026	10.869	<0.001
Starting distribution area	< -0.001	<0.001	-1.791	0.087
Log habitat availability	0.188	0.099	1.896	0.071
Climate suitability	-0.197	0.031	-6.316	<0.001

Table A5.1.3. The best fit (ΔAICc > 2) or averaged models (where ΔAICc < 2) for each value of R_{max} separately, for linear mixed effects models of change in distribution area against dispersal ability, climate suitability, habitat availability and starting distribution area and all two-way interactions. Estimates and relative importance are given for each parameter. When relative importance = 1, the variable appears in all the top models (or in the case of a single best-fit model, the variable appears in the top model).

R_{max}		Dispersal ability	Climate suitability	Habitat availability	Starting distribution area	Dispersal x climate	Dispersal x habitat	Dispersal x start	Climate x habitat	Climate x start	Habitat x start
1	Estimate	-0.78	139.43	1076.37	-	-2.67	36.73	-	-550.07	-	-
	Relative importance	1	1	1	-	1	1	-	1	-	-
1.11	Estimate	-2.72	285.27	888.38	-0.01	8.91	64.47	-0.01	620.41	-	-1.20
	Relative importance	1	1	1	1	1	1	1	1	-	1
1.22	Estimate	-12.23	455.14	1457.52	-0.04	23.34	59.66	-0.01	94.26	-	-1.36
	Relative importance	1	1	1	1	1	1	1	1	-	1
1.35	Estimate	-5.97	588.25	2375.67	-0.17	31.98	59.62	-0.02	-850.32	-	-1.43
	Relative importance	1	1	1	1	1	1	1	1	-	1
1.49	Estimate	7.61	451.65	3658.97	-0.15	14.07	134.21	-0.03	-974.37	-	-2.26
	Relative importance	1	1	1	1	1	1	1	1	-	-
1.65	Estimate	-1.60	542.90	3634.60	-0.23	37.48	99.24	-0.03	-1191.92	-	-2.14
	Relative importance	1	1	1	1	1	1	1	1	-	1
1.82	Estimate	41.11	166.19	4195.05	-0.29	-10.24	174.46	-0.04	-782.89	0.05	-2.68
	Relative importance	1	1	1	1	1	1	1	1	0.27	1
2.01	Estimate	4.84	552.91	5705.20	-0.39	37.88	178.21	-0.05	-2564.10	0.05	-2.45
	Relative importance	1	1	1	1	1	1	1	1	0.30	1

2.23	Estimate	61.44	170.04	7517.60	-0.57	-19.91	217.51	-0.05	-4156.00	0.19	-2.49
	Relative importance	1	1	1	1	1	1	1	1	0.38	1
2.46	Estimate	37.03	366.55	6691.57	-0.72	25.22	196.04	-0.07	-3878.01	0.16	-1.74
	Relative importance	1	1	1	1	1	1	1	1	0.33	0.82
2.72	Estimate	61.58	-33.99	9435.22	-0.88	-17.90	362.64	-0.07	-4858.47	0.42	-2.86
	Relative importance	1	1	1	1	1	1	1	1	0.50	1
3.00	Estimate	88.35	-42.36	12467.42	-0.96	-43.44	342.60	-0.07	-8167.56	0.49	-2.87
	Relative importance	1	1	1	1	1	1	1	1	0.52	1
3.32	Estimate	96.48	-81.47	13310.64	-1.07	-43.90	347.15	-0.08	-8979.79	0.56	-2.91
	Relative importance	1	1	1	1	1	1	1	1	0.54	1
3.67	Estimate	125.46	-185.40	14875.81	-1.14	-75.29	370.89	-0.08	-10653.14	0.56	-2.63
	Relative importance	1	1	1	1	1	1	1	1	0.55	1
4.06	Estimate	183.29	-853.59	15910.53	-1.59	-134.34	454.00	-0.09	-10994.77	1.00	-2.92
	Relative importance	1	1	1	1	1	1	1	1	0.65	1
4.48	Estimate	208.61	-955.87	17282.07	-1.69	-159.36	447.22	-0.09	-12726.82	1.07	-2.66
	Relative importance	1	1	1	1	1	1	1	1	0.66	1

5.2 SUPPLEMENTARY FIGURES

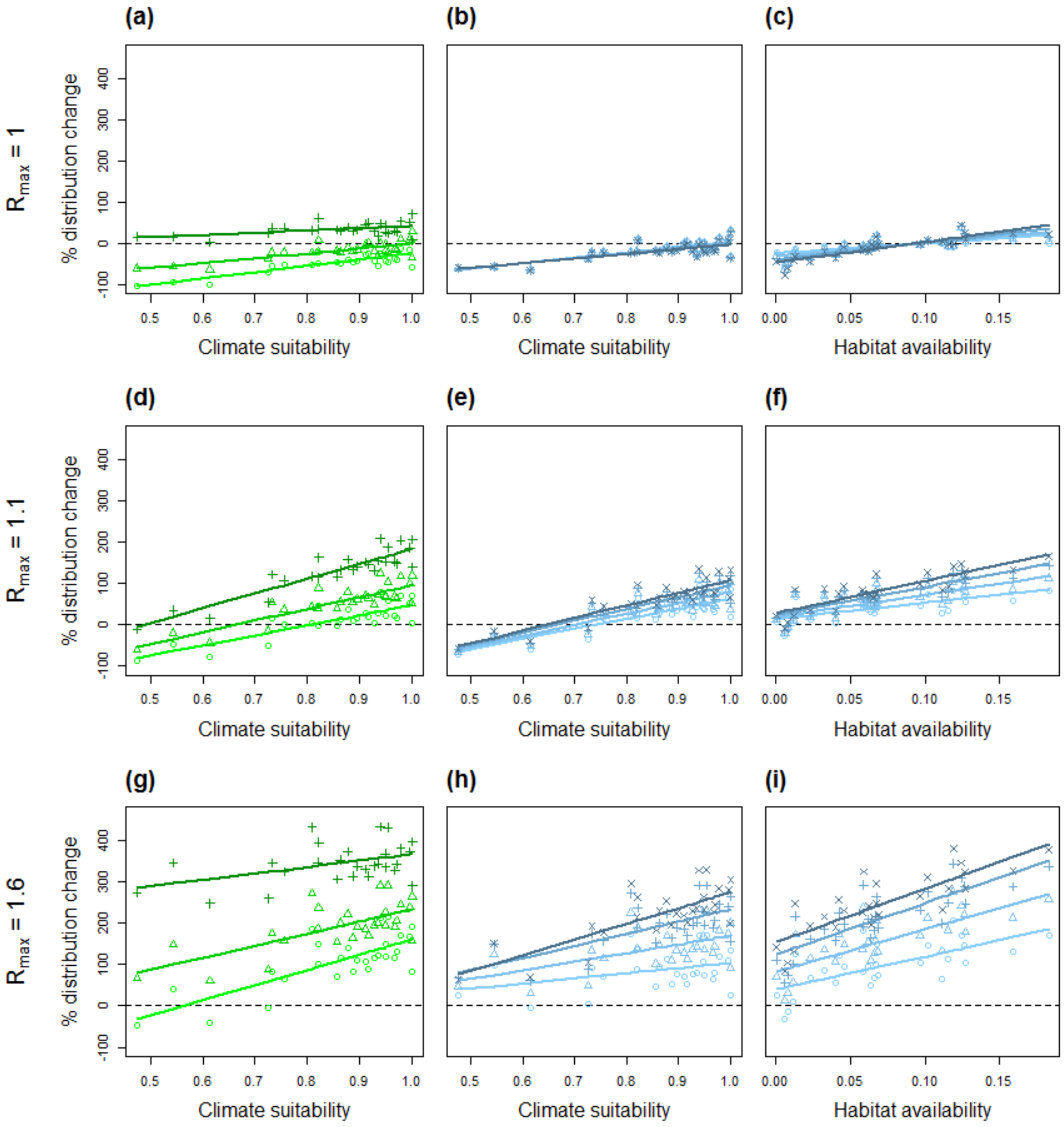

Figure A5.2.1. The interactions between dispersal, habitat and climate at **(a-c)** R_{max} = 1, **(d-f)** R_{max} = 1.1, and **(g-i)** R_{max} = 1.6. Distribution change was predicted for **(a,d,g)** maximum habitat (dark green), median habitat (green) and minimum habitat (light green) availability as climate varies, **(b,e,h)** each of the four dispersal abilities (proportion following long distance dispersal = 0.0001, 0.001, 0.01 and 0.1, graded from light to dark blue respectively) as climate varies, and **(c,f,i)** each of the four dispersal abilities as habitat availability varies. Regression lines were applied to highlight the direction of the interactions.

5.3 SUPPLEMENTARY INFORMATION FOR FIGURE A5.2.1

In order to ascertain the importance and direction of any interactive effects between explanatory variables (e.g. do species with greater habitat availability benefit more from increased dispersal than species with low habitat availability), I applied a multi-model inference approach to each value of R_{max} separately. The global model included change in distribution area as the response variable, species was included as a random variable, and dispersal ability, habitat availability, climate suitability and starting distribution area were potential explanatory variables, with all two-way interactions included. The best-fit and averaged models for each value of R_{max} are presented in full in Table A5.1.3.

Starting distribution area did not appear in the top models for all values of R_{max}, however when it was an important variable, it consistently showed a negative interaction with dispersal ability and habitat availability, and a positive interaction with climate suitability (Table A5.1.3). Thus, species with small starting distribution areas showed a greater increase in rate of distribution expansion given higher dispersal ability and habitat availability than did species with large starting distribution areas. In contrast, the species with large starting distribution areas benefited relatively more from increased climatic suitability than did species with small starting distribution areas.

Other interactions were less consistent as R_{max} was varied, therefore I have selected three examples (R_{max} = 1, 1.1 and 1.6) to present the interactions between dispersal, habitat and climate as R_{max} is varied (Fig A5.2.1). To illustrate interactions, I used the best-fitting model to predict distribution change for (i) variation in climate suitability at minimum, median and maximum habitat availability (from across species, min = 0.0004, median = 0.0648, max = 0.1824; starting distribution area and dispersal ability were kept constant by using the median starting distribution area and proportion following long distance dispersal = 0.01 respectively) (Fig A5.2.1a,d,g); (ii) variation in climatic suitability at each of the four dispersal abilities (keeping starting distribution area and habitat availability constant by using the median values of each) (Fig A5.2.1b,e,h); and (iii) variation in habitat availability at each of the four dispersal abilities (keeping starting distribution area and climate suitability constant by using the median values of each) (Fig A5.2.1c,f,i). I then fitted regression lines to the predicted values to highlight the direction of each interaction.

At R_{max}=1 (reproductive replacement), all of the interactions were relatively weak, given that all species were either contracting slightly or expanding slightly (Fig A5.2.1a-c). At low habitat availability, increased dispersal ability actually resulted in greater distribution retraction (through high dispersal-related mortality), whereas at high habitat availability, increased dispersal ability resulted in greater distribution expansion (Fig A5.2.1c).

At R_{max}=1.1, the effects were much larger, as some species continued to decline, whereas species with favourable combinations of habitat, dispersal and climate could expand (Fig A5.2.1d-f). Species with high climate suitability showed relatively greater increases in distribution expansion given greater habitat availability (Fig A5.2.1d) or greater dispersal ability (Fig A5.2.1e), compared to species with low climate suitability. Similarly, species with high habitat availability benefited more from increased dispersal ability than did species with low habitat availability (Fig A5.2.1f).

At R_{max}=1.6, effects were larger still (Fig A5.2.1g-i). As before, species with high climate suitability or high habitat availability benefited relatively more from increased dispersal ability compared to species with low climate suitability (Fig A5.2.1h) or habitat availability (Fig A5.2.1i).

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