Range Changes in British Butterflies: the Roles of Climate, Habitat and Dispersal in Patterns of Spread

KERR, CHANTELLE,LOUISE

How to cite:

KERR, CHANTELLE,LOUISE (2013) *Range Changes in British Butterflies: the Roles of Climate, Habitat and Dispersal in Patterns of Spread*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7353/

Range Changes in British Butterflies: the Roles of Climate, Habitat and Dispersal in Patterns of Spread

Chantelle Louise Kerr B.Sc. (Hons)

Master of Science by Research

Institute of Ecosystem Science,

School of Biological and Biomedical Sciences,

Durham University

2012

Abstract

Habitat associations and demographic parameters of four generalist butterfly species resident to Great Britain, namely *Pararge aegeria* (speckled wood), *Aphantopus hyperantus* (ringlet), *Pyronia tithonus* (gatekeeper) and *Melanargia galathea* (marbled white), were investigated. These species were chosen because they have variable habitat associations and have all expanded their range in recent years. UKBMS transect data was used to generate species specific values for both intrinsic rates of increase, r, and mean density in occupied habitats, ρ, for the four study species. Results indicate that three of the four species studied occur at significantly different densities across two or more of their preferred habitats. High variation in intrinsic rates of increase across all species studies was documented. Results were used to inform the accurate parameterisation of a dynamic model framework used to simulate present-day ranges of the four study species.

Recent spread of species were simulated using spatial dispersal models across a gridded landscape of Great Britain, where cell suitability is modified between 0-1 according to (1) habitat suitability, (2) climate suitability or (3) all cells are given an equal suitability of unity. Spread was simulated with almost equal degrees of success in models run on grids (1) and (2). Model simulations run on grid (3) resulted in poor model outcomes and over-simulation of species current range extent. This suggests that both habitat and climate play a role in observed present day distributions of the four study species. For species whose recent expansion could be simulated well using these models, the best-fit model for each species was run into the future to simulate potential future spread. Future simulations suggest that *Melanargia galathea* and *Pyronia tithonus* will expand their range by 15.3% and 7.8% respectively under present day habitat suitability between 2009 and 2060.

Field data was used to investigate local and regional patterns of temperature at three study sites along a north-south transect in England and relate this to phenology of a chalk grassland specialist butterfly, *M. galathea,* and its preferred nectar source, *Centaurea scabiosa*. Results indicate that mean maximum daily temperature was significantly different the local (variable aspect/topography) and regional scale. Locally, the highest temperatures were observed on south and south west facing slopes and coldest on north facing slopes. Regionally, the highest temperatures observed in the south and coldest in the north. This means insect and plant experience different environmental conditions depending on local or regional situation. There is evidence that heterogeneity in the local environment at each of the three study sites results in an extended flowering period of *C. scabiosa,* increasing the amount of time nectar is available to pollinating insects. Topographically variability could thus act as a buffer to phenological mismatch induced by future climate change and could be used as a reserve selection criterion for conservation organisations. There is also evidence that both timing and duration of the flowering period of *C. scabiosa* varies at both the local and regional scales. The timing of the flight period of *M. galathea* varied among years and sites likely in relation to variable macro and microclimate. This has implications for future translocation studies whereby individuals are moved from one area of the country to another and must be considered if translocations are to be successful.

This thesis has highlighted ecological processes occurring at both fine and broad spatial scales that must be considered if model predictions are to be robust. Future research must continue to recognise the importance of an individualistic approach to forecasting responses of species to environmental change.

Table of Contents

List of Figures

Chapter 2 **Page**

Chapter 3

Chapter 4

List of Tables

Chapter 2 **Page**

Chapter 3

Chapter 4

Abbreviations

ATP/ADP	Ratio of adenosine triphosphate to adenosine diphosphate
AET/PET	Annual ratio of actual to potential evapotranspiration
AIC	Akaike's information criterion
ANOVA	Analysis of variance
BC	Butterfly Conservation
CEH	The Centre for Ecology and Hydrology
CRS	Climate response surface
df	Degrees of freedom
EUNIS	European Nature Information System
FP	Flowering period
FPmg	Flight period of *Melanargia galathea*
GDD5	Growing degree days above 5°C
GLM	General liner model
LCM2000	Land Cover Map 2000
LL	Log likelihood
LLRT	Log likelihood ratio test
MTCO	Mean temperature of the coldest month
PGi	Phosphoglucose isomerase
Spp.	Species
SSSI	Site of Special Scientific Interest
TSS	True skills statistic
UK	United Kingdom
UK BAP	United Kingdom Biodiversity Action Plan
UKBMS	United Kingdom Butterfly Monitoring Scheme

Acknowledgements

Firstly, I would like to thank my primary supervisor Dr. Stephen Willis for his continued support and guidance throughout my studies. Secondly, I would like to say special thank you to my secondary supervisors Dr. Shane Richards, whose statistical know-how, patience and encouragement has been invaluable, and Dr Bob Baxter for his infectious enthusiasm and cheerful nature. I would like to thank all of the members of the Adaptation and Environment Research group for their continued support and inspiration. A special thank you goes to Dr. Yvonne Collingham for her modelling expertise and technical support throughout.

Special thanks to Butterfly Conservation and the Centre for Ecology and Hydrology for providing me with the data necessary for the completion of this project. I would also like to thank the many thousands of volunteers who take part in the UK Butterfly Monitoring Scheme each year to amass this vast and invaluable dataset. I would like to thank the staff and volunteers of Totternhoe Quarry Nature Reserve, Brockadale Nature Reserve and Wingate Quarry Reserve for their help and guidance during my fieldwork. Further thanks go to the Grevillea Trust and Chester Zoo for their contributions towards my funding, without which this thesis would not have been possible.

I would like to thank the land owners and land managers that allowed me access to their sites for field research purposes including the Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire, Natural England, the Yorkshire Wildlife Trust, and Durham City Council.

I would like to say an extra special thank you to my fellow post-graduates and post-docs, Charlie, George, Tom, Phyllida, Naiara, Christine, Amy, Miranda and Robi for never being too busy to answer my questions and making it a pleasure to come into work every day. Georgina Palmer, you deserve two mentions; your expertise, patience and kindness have been truly invaluable to me throughout the completion of this thesis and I appreciate all you have done to help me over the past few years. Finally, I would like to thank my friends and family both in Durham and at home for their continued support throughout my studies.

Chapter 1

Climate change and range shift in British butterflies: the roles of microclimate, phenology, habitat availability and dispersal in patterns of spread

1.1 Introduction

The Earth has experienced two main periods of warming over the past century resulting in mean surface air temperatures increasing by approximately 0.3-0.6°C (IPCC 2007; Working group 1: the scientific basis). The first period of warming occurred between 1910 and 1945, the second from 1976 to the present day. The latter period accounts for approximately 0.2-0.3°C of warming in the last century (Roy *et al.,* 2001) occurring at a rate greater than at any other time in the last millennium. By the end of the 21st century global mean annual temperature is predicted to increase by 1.1-6.4°C, with a best estimate of 1.8-4.0°C (IPCC, 2007; Beaumont and Hughes, 2002). This unprecedented period of warming and predicted increase in global temperatures is of particular concern to global change biologists (Beaumont and Hughes, 2002; Walther *et al.* 2002) many of whom have already documented ecological responses to recent warming (Crozier 2003; Crozier 2004; Hill *et al.,* 2006) the consequences of which, in terms of ecosystem dynamics, are still unclear (Hoegh-Guldberg *et al.,* 2008).

When considering ecological responses of species, populations and communities to climatic warming global averages are often of minimal importance. Ecological responses of species' to climate, across diverse geographical ranges, are governed by regional climates which are highly heterogeneous and spatially variable (Gutierrez and Menendez, 1998; Walther *et al.,* 2002). There is evidence to suggest that this regional climatic heterogeneity will lead to asymmetries in population dynamics even between neighbouring regions (Sparks *et al.,* 2006; Walther *et al.,* 2002). The scale at which these asymmetries occur will depend on the species concerned, their relative habitat size, and the relative effect of microclimates on their respective life cycles. Hughes (2000) summarised the vast ecological effects of human-induced climatic and atmospheric change on species and communities into four broad categories:

1. Physiological effects: metabolic and developmental rates of many animals and plants are directly linked to levels of atmospheric CO_2, temperature and precipitation. Changes to such climatic variables will directly affect processes such as photosynthesis, respiration, growth and tissue composition in plants.

2. Changes in geographic distributions: species are expected to move upwards in elevation and polewards in latitude in response to shifting climatic zones. This expectation corresponds to the predicted shifts of isotherms by 300-400km in latitude (in the temperate zone) and 500m in elevation should a 3°C increase in mean annual temperatures occur.
3. Phenological effects: critical events in the life cycles of many species are triggered by environmental cues such as degree days. If such cues are altered phenological mismatch in relationships between species may occur.
4. Adaptation: phenotypic adaptation may result in true evolutionary change or as a result of phenotypic plasticity (Huntley *et al.,* 2006). Those species most likely to adapt are those with short generation times and rapid population growth rates. Such species might undergo micro-evolutionary change *in situ.*

1.2 Butterflies as indicator species

Butterflies have long been recognised as a model organism with which to study the impacts of climate on ecological and physiological processes and responses (Roy and Sparks, 2000; Stefanescu *et al.,* 2003). They are widely considered an indicator species for monitoring change in ecosystem functioning (Warren *et al.,* 2007; Woods *et al.,* 2008). Their usefulness as a biological indicator can be attributed to their life history strategy and conspicuously charismatic appearance (Woods *et al.,* 2008). Their reliance on plants for completion of their life cycle, both as hosts for egg and larval development and as adult food plants, ultimately links them to climate (Woods *et al.,* 2008). At local scales, physiological processes such as bud burst and leaf fall are governed by climatic variables such as temperature and precipitation (Linderholm, 2006). At regional and global scales climate ultimately influences plant species distribution and community composition (Morison & Morecroft, 2006) which, has a direct bearing on where butterflies are able to persist and subsequent community composition. As poikilothermic organisms, their highly conserved annual life-cycle is highly dependent on and constrained by moisture and temperature (Roy and Sparks, 2000; Hill *et al.,* 2001; Beaumont and Hughes, 2002; Walther *et al.,* 2002). Their activity, fitness, voltinism development, larval emergence, migration, abundance and distribution are all influenced by temperature (Roy *et al.,* 2001; Beaumont and Hughes, 2002; Woods *et al., 2008*). They are also highly fecund, have high rates of dispersal and an annual life-cycle making it easier to detect changes in abundance and distribution across generations and over short time periods (Hill *et al.,* 2001; Walther *et al.,* 2002). In addition, their conspicuous appearance makes them easily identifiable in the field and popular with the public, meaning large and reliable databases containing country-wide annual sightings and flight-period data have been amassed with the help of many highly skilled volunteers (Walther *et al.,* 2002; Fox *et al.,* 2010).

One such database is known as the United Kingdom Butterfly Monitoring Scheme (UKBMS), a national monitoring network that has been running since 1976, co-ordinated by the Centre for Ecology and Hydrology and Joint Nature Conservation Committee (Warren *et al.,* 2007; Fox *et al.,* 2010). UKBMS is a population monitoring scheme and one of the longest running ecological surveys in the world which today comprises some 1000 survey sites (Warren *et al.,* 2007). A second database, 'Butterflies for the New Millennium', has been running since 1995 in collaboration with the charity 'Butterfly Conservation' and is a national distribution recording scheme (Fox *et al.,* 2010). Both datasets have yielded valuable insights into the effect of temperature on butterfly abundances and distributions in the UK (Pollard and Yates, 1993; Roy and Sparks, 2000; Fox *et al.,* 2010). A recent re-evaluation of the Red List of British butterflies has found that the majority of butterfly species are in decline across Britain (Fox *et al.,* 2010). As such, such extensive ecological monitoring is highly valuable to the safeguarding of British butterflies as it will enable the development of informed management and recovery programmes specific to the needs of affected species.

1.3 Variability in Range Shifting Responses of Habitat Generalists and Habitat Specialists

Habitat specialists exhibit a more restricted geographic range, typically making use of fewer host plants (both as nectar sources and larval food plants) and are less mobile. Evidence suggests that such species are declining and becoming increasingly restricted to fragmented habitat owing to habitat loss and anthropogenic degradation and modification (Warren *et al.,* 2001; Hill *et al.,* 2006; Warren *et al.,* 2007; Fox *et al.,* 2010). Habitat generalists on the other hand, also known as wider countryside species, use a much broader range of host plants, have more expansive geographic ranges and exhibit greater mobility (Oliver *et al.,* 2010). Consequently these species are able to respond more readily to environmental change and as such have become more widely abundant across Britain (Asher *et al.,* 2001; Roy *et al.,* 2001; Roy and Asher, 2003; Warren *et al.,* 2007; Gonzalez-Megias, 2008). The overall consequence of such dynamics is a decline in butterfly diversity producing biological communities dominated by habitat generalists (Warren *et al.,* 2001; Menendez *et al.,* 2006; Gonzalez-Megias, 2008).

Warren *et al.* (2001) demonstrated how habitat specialists and more sedentary species tended to lag behind climate to a greater extent than habitat generalists and more mobile species (Wilson *et al.,* 2009) due to difficulties in colonising isolated habitats (Hill *et al.,* 2001; Woods *et al.,* 2008; Willis *et al.,* 2009b). Despite the availability of climatically suitable habitat patches, sedentary species are unable to colonise suitable breeding habitat patches due to their isolation in heavily modified modern landscapes (Hoegh-Guldberg *et al.,* 2008; Woods *et al.,* 2008). Isolation between current range and potentially suitable unoccupied range means that sedentary species are unable to track changing climate to the same degree as more mobile, country-wide species (Hill *et al.,* 1999; Willis *et al.,* 2009b). Wilson *et al.* (2009) found that specialist butterfly *Hesperia comma* (silver-spotted skipper) did not expand northwards to the extent expected by recent climate change or to the extent achieved by many other less specialised British butterflies.

Despite this general distinction between specialist and generalist species and their ability to track warming climates, Hill *et al.* (1999) found that *Pararge aegeria* (speckled wood)*,* a moderately mobile species, was unable to track the changing climates of the 20th century. Using assisted colonisation experiments Willis *et al.* (2009b) also found that two generalist species were lagging behind present climatic warming. Populations of both *Melanargia galathea* (marbled white) and *Thymelicus sylvestris* (small skipper) successfully established and expanded their range following artificial introduction into areas of predicted suitable habitat, north of their present day range margin, in Durham and Northumberland respectively. This suggests that climate at the two study sites has been climatically suitable at least since the time of introduction, and as such the introduced species have been lagging behind current climate (Willis *et al.,* 2009b).

1.4 Climate change, habitat fragmentation and range expansion

Global warming is impacting on many aspects of community ecology, in particular the abundance and distribution of organisms (Parmesan *et al.,* 1999; Thomas *et al.,* 2001; Warren *et al.,* 2001; Konvicka *et al.,* 2003; Crozier, 2004; Hickling *et al.,* 2006; Sparks *et al.,* 2007; Fox *et al.,* 2010; Devictor *et al.,* 2012). Insects are likely to be particularly sensitive to changes in global climates due to the effect of climatic variables such as temperature (Hill *et al.,* 2001), relative humidity (Dunlap *et al.,* 2000) and precipitation (Nicholls and Pullin, 2003; Gibbs *et al.,* 2012) on lifecycle completion. Evidence increasingly documents occurrences of poleward shifts in latitudinal ranges and shifts to higher elevations in terrestrial organisms (Hill *et al.,* 1999; Beaumont and Hughes, 2002; Konvika *et al.,* 2003; Crozier, 2004; Hickling *et al.,* 2006; Hill *et al.,* 2006; Thomas *et al.,* 2006; Willis *et al.,* 2009). Konvicka *et al.* (2003) found that between 1950 and 2001, at least 12 species of butterfly native to the Czech Republic ascended in elevation. The shifts affected species associated with a variety of habitats and life histories – specialist and generalist, montane and non-montane, and both endangered and least concern species. Since such a diverse range of species with diverse ecologies were affected, it is unlikely that any causative factor other than climate could explain the range shifts (Konvicka *et* *al.,* 2003). However the magnitude of such range shifts, the direction they take, and the rate at which they occur is likely to be variable across even closely related species (Crozier, 2004). Woods *et al.* (2008) found that species responded to climate individually; such variability in range shifts are a consequence of both non-climatic factors, such as anthropogenic habitat disturbance (Hill *et al.,* 2006) and variable life-history and demographic traits among species (Carroll *et al*., 2009), and climatic factors, such as changing minimum and maximum temperatures (Crozier, 2003). Climate can limit species distributions by interacting with a number of ecological processes. It may directly influence life cycles, impacting on growth and survival, or it may act indirectly via its effects on interacting species such as pathogens, prey and predators (Crozier, 2004). Butterflies in particular are affected by the impact climate has on their larval host plants, adult food plants and their habitat (Woods *et al.,* 2008).

For those species capable of dispersing across landscapes (even highly connected habitats may prove prohibitive for more sedentary species), range shifts and expansion will occur at a greater rate for those species occupying landscapes with greater overall habitat connectivity (Wilson *et al.,* 2009). With this in mind, it is evident that heavily modified human landscapes (Crozier, 2004; Willis *et al.,* 2009a) have resulted in spatially fragmented habitats (Dewenter and Tscharntke, 2000), which have a significant impact on the ability of species' to respond to a warming climate (Hill *et al.,* 2001; Hoegh-Guldberg *et al.,* 2008). Those dispersers unable to overcome anthropogenic barriers and reach new climatically suitable habitat will be unable to track climate change and are likely to be threatened with decline (Hill *et al.,* 1999; Hoegh-Guldberg *et al.,* 2008; Wilson *et al.,* 2009). As such it is important to be able to predict future range shifts in response to climate (McPherson and Jetz, 2007; Zurell *et al.,* 2009), particularly for those most vulnerable species (Warren *et al.,* 2007). Making such predictions is a complex process requiring an understanding of factors affecting species range boundaries which, for the majority of species, are unknown (Lawton, 1995; Crozier, 2004). Uncertainty when making predictions is further amplified by the fact that parameters such as dispersal rate (Thomas *et al.,* 2001; Hughes *et al.,* 2003) and environmental tolerances (Thomas *et al.,* 2001; Oliver *et al.,* 2009) can change during range shifts, a consequence of evolutionary and ecological processes (Crozier, 2004; Dytham, 2009; Hill *et al.,* 2011). For example, increased dispersal ability has been both observed and modelled theoretically at expanding range margins in insects where dispersal is greatest (Hill *et al.,* 2011). Hagg *et al,* (2005) found that colonising individuals from expanding populations of *Araschnia levana* (the map butterfly) have higher levels of the enzyme phosphoglucose isomerase (PGi) which is associated with superior flight metabolic rates and population growth rates when compared to populations from the centre of the range (Hanski and Saccheri, 2006; Hill *et al.,* 2011). Similarly a physiological study into the ratio of ATP/ADP in the flight muscles of the *Melitaea cinxia* (Glanville fritillary butterfly) provides further support that dispersal ability is enhanced at the expanding range margin (Hanski *et al.,* 2004). Populations at the range edge were found to exhibit a higher ratio of ATP to ADP following controlled activity, indicating a greater capacity to renew ATP thus sustain activity.

Thomas *et al.* (1992) detected low colonisation rates within fragmented habitats among butterflies. He concluded that butterflies will be unable to shift their ranges in response to climate if suitable habitat patches are too fragmented or isolated to colonise. Extensive habitat modification and degradation as a consequence of human activities, combined with a changing climate, has resulted in changing animal and plant abundances and distributions across the globe (Hill *et al.,* 1999; Pounds *et al.,* 1999; Hill *et al.,* 2001; Warren *et al.,* 2001; Walther *et al.,* 2002; Root *et al.,* 2003; Crozier, 2004; Hickling *et al.,* 2006; Sparks *et al.,* 2007; Fox *et al.,* 2010; Devictor *et al.,* 2012). Under the hypothesis that climate is limiting, it might be expected that poikilothermic animals in particular would respond positively to climate warming experienced over the past 40 years (Roy and Sparks, 2000; Hill *et al.,* 2001), as it enables range expansion and utilisation of previously climatically unsuitable habitat. To test this theory Warren *et al.* (2001) evaluated range data of 46 species of British butterfly that reach their northern range margin in Britain over a 30 year period of warming. They found that despite climate explanation, three quarters (34/46) of species declined - negative responses to habitat degradation and loss outweighed positive responses to climate warming. This response was amplified amongst habitat specialists, of which 26/28 species declined in distribution size, compared to only 9/18 wider-countryside species (habitat generalists), suggesting these species are limited by factors other than climate such as distribution of suitable habitat (Warren *et al.,* 2001). Beaumont and Hughes (2002) also found, using bioclimatic modelling, that the geographical ranges of a wide range of Australian butterfly species from diverse habitat types would be adversely affected by climate change, despite presently large climatic ranges, with only 2/24 species modelled exhibiting a beneficial response to climate change.

It is generally accepted by ecosystem biologists that animal populations are less stable, experiencing greater fluctuations in numbers, at their range edge compared to the populations found in more central parts of a species range (Thomas *et al.*, 1994). Population instability often impacts genetic diversity of the population. Hill *et al.* (2006) found that genetic diversity was correlated with habitat availability when comparing three species of closely related Satyrinae butterfly. Allozyme variation was significantly reduced toward the expanding range margin in populations of *P. aegeria* a habitat specialist with limited habitat availability. In contrast, *Pyronia tithonus* (gatekeeper), a generalist butterfly that is not limited by habitat availability, and *Maniola jurtina* (meadow brown), a non-expanding control species showed no significant difference in genetic diversity toward their range edge. Furthermore, a comparison of data from populations of *P. aegeria* in Scotland showed that reduced genetic diversity was only evident in populations from England where there is a greater degree of habitat fragmentation (Hill *et al.,* 2006).

This evidence highlights the dramatic effects that habitat fragmentation can have on specialist species at their range edges. Fragmentation of breeding habitat led to founder events during colonisation that resulted in severely reduced genetic diversity in marginal populations (Hill *et al.,* 2006). It is also likely that populations occurring at high latitudes or at the leading range margin are restricted to more particular habitats, such as warm microclimates, compared to those with a more southerly distribution (Oliver *et al.,* 2009) mimicking a fragmented habitat. Reduced diversity at the range edge in such species is likely to have marked effects on the ability of that species to adapt to further environmental change. If habitats continue to be degraded and lost, allowing populations to become increasingly isolated, such effects will only become more severe. As many specialist species are already endangered (Warren *et al.,* 2001; Fox *et al.,* 2010) it is this group that is likely to require substantial conservation intervention if they are to be able to persist in line with present and future climatic change (Hill et al., 2006).

1.5 Climate and range expansion in Lepidoptera

The combination of climatic suitability and habitat availability is crucial when accounting for species distribution in butterflies. Hill *et al.* (1999) found that climate alone did not account for the distribution of *P. aegeria,* at the 10km grid scale. A combination of both woodland availability (the preferred habitat of *P. aegeria*) and climatic suitability was the best predictor of the observed distribution of the species in Britain. Habitat and climate may be able to explain landscape scale population dynamics and species distributions, but short-term, extreme climatic events can also have profound impacts on species dynamics when combined with the pressures associated with fragmented landscapes. For example, the occurrence of an uncharacteristically wet or cold summer during the butterfly flight period can hinder oviposition and depress survival rates, resulting in reduced population levels which may then be vulnerable to extinction by other processes (Roy *et al.,* 2001). Fragmented landscapes reduce the capacity for neighbouring populations to 'rescue' vulnerable populations, ultimately resulting in the collapse of population networks (Hill *et al.,* 1999) despite apparently suitable mean climates.

To predict species ecological and evolutionary responses to changing climates we must identify and understand the mechanisms that link climate and range limits. Those species only limited by climatic suitability will be quick to exhibit range shifting behaviour during periods of warming. Minimum temperature is rising at twice the rate of maximum temperature; in the Northern Hemisphere winter temperatures rose by 2.9˚C, whilst average summer temperatures rose by 1.3˚C between 1951 and 1990 (Karl *et al*., 1993; Crozier, 2003). As such, species limited by minimum temperature (i.e. those with a more northerly distribution) will respond to warming to a greater extent than those limited by maximum temperature (i.e. those with a more southerly distribution) (Crozier, 2003).

Crozier (2003) concluded that *Atalopedes campestris* (Sachem skipper), is limited not by habitat or dispersal ability but solely by minimum temperature. *Atalopedes campestris* is an abundant, generalist and opportunistic skipper butterfly which has undergone marked range expansions during recent periods of warming, expanding northwards from its historical range in the neotropics and southern United States (Crozier, 2003). It lacks hibernal diapause and as such is restricted to areas where the January average temperature is above -4˚C (Crozier, 2003; Crozier 2004). It has recently expanded into eastern Washington, where January minimum temperature has risen by 3°C in the past 50 years (Crozier, 2004). Using cold tolerance experiments, Crozier (2003) deduced that there was a physiological constraint at the current range edge which resulted in a steep mortality gradient from -4°C to -7°C. As such, as temperatures increase at the northern range edge of this species, the probability of over-winter survival will increase allowing range expansion. This effect will be intensified where snow transforms into rain reducing the likelihood of chill injury to caterpillars (Crozier, 2003).

The evolution of cold tolerance at range edges has been observed in species such as *Ostrinia nubilali* (European corn borer), enabling it to colonise habitats markedly different to those of its historical range (McCauley *et al.,* 1995). It could be suggested that such adaptive processes are taking place at the range edges of *A. campestris*, and that it is this process of evolution and not climatic changes at the range edge that are allowing the species to expand its range. However, Crozier (2003) found that there is no evidence to suggest a phenotypic adaptation to cold at the range edge - *A. campestris* failed to survive winter in the Midwest, suggesting a limited capability to adapt to severe cold (Crozier, 2003).

This study provides direct evidence of a link between winter temperature and range shifts, a link which is particularly important when predicting species responses to climate change. Crozier (2004) concludes that *A. campestris* is likely to be typical of southern species limited by the cold, with subtropical/temperate border zone range limits, for example species shifting from north Africa into Europe. The northern range limits of these southern species will be correlated with winter isotherms in contrast to many European species whose distributions are tightly linked to summer temperatures. The northern range margins of most European species are closely correlated with summer isotherms, shifting in response to summer temperatures (Thomas *et al.,* 1994). Hill *et al.* (2001) found that the extent of northward range shifts in *P. aegeria* in England corresponded to shifting climatic isotherms. From the 1940s onwards the range margin of *P. aegeria* has shifted northwards 107km, closely matching the 120km shift of summer isotherms in England over this time (Hill *et al.,* 2001). In addition a North American species, *Euphydryas editha* (Edith's checkerspot butterfly) shifted northwards by 92km during a period of warming when isotherms shifted north by a corresponding 105km (Thomas *et al.,* 2006). This close correlation between climatic isotherms and shifting distributions provides strong evidence that climate is directly affecting butterfly range shifts. As winter temperatures are increasing at a faster rate than summer temperatures, the range shifts of those species tracking winter isotherms will be occurring at a much greater rate than would be predicted by annual mean temperatures alone (Crozier, 2004).

Crozier's study highlights some important ecological responses to climate that are particularly informative for conservation and land managers. Firstly, that lower latitude species have begun shifting their ranges northward with unknown consequences for resident species which may in turn be driven poleward. Secondly, it highlights how the climatic envelope for this species has shifted geographically (Crozier, 2004). If such geographical shifts are occurring for many different species, those less able to track shifting climate envelopes, such as more specialist species (Willis *et al.,* 2009b), will be left in increasingly stressful environments (Woods *et al.,* 2008). Despite this, climatic warming may result in the new climatically suitable territories outside of historical ranges which may be suitable for reintroductions of endangered species. As such habitats that do not seem ecologically important at present may be important future habitats under projected climatic change scenarios, worth protecting for the benefit of endangered species in the future (Crozier, 2003).

1.6 Phenological responses to climate and local adaptation in butterfly populations

Phenology is an area of ecology concerned with time-sensitive, periodic biological phenomena, such as emergence, reproduction, migration, competition and predation (Weiss and Weiss, 1998; Fitter and Fitter, 2002; Stefanescu *et al.,* 2003; Williams and Aberton, 2004; Morecroft *et al.,* 2009; Miller-Rushing *et al.,* 2010; Diamond *et al.,* 2011). Observed phenological changes in response to a warming climate include advanced date of first appearance in butterflies (Gutierrez and Menendez, 1998; Roy and Sparks, 2000; Diamond *et al.,* 2011) earlier peak appearance in temperature regulated insects (Zhou *et al.,* 1995), and earlier migration and egg laying in birds (Crick and Sparks, 1999). Such responses of the various taxonomic groups have been observed throughout all of the climatic biomes (Roy and Asher, 2003).

Sightings data for British butterflies has demonstrated a strong relationship between first appearance and temperature in the last few decades (Roy and Asher, 2003). First appearance of adult British butterflies in 26 of 35 species examined advanced by 2-10 days per 1°C increase in temperature between 1976 and 1999 (Roy and Sparks, 2000; Roy and Asher, 2003). Similar patterns are being observed globally with advanced first appearance dates observed in 16 of 23 species examined in California, USA (Forister and Shapiro, 2003) and all 17 species examined in Spain (Stefanescu *et al.,* 2003). Consistent with global latitudinal temperature gradients from the equator to the pole, Britain exhibits approximately 0.4°C temperature increases per 100km from the south to the north of the country (Roy and Asher, 2003). In line with this, many species of British butterfly, both habitat specialists and generalists, exhibit later first appearance in the cooler north of their range when compared to the warmer south (Warren, 1992; Roy and Asher, 2003). Roy and Asher (2003) found that in over a third of British butterflies analysed first sightings dates were significantly later in the north. Early emergence has varying implications for the species concerned; in univoltine species will result in a lengthened flight period, whilst early emergence in multi-voltine speices will result in the potential for extra generations per year (Roy and Sparks, 2000). Voltinism is not always a fixed life history parameter; some species such as *Polyommatus icarus* (common blue), exhibit flexible voltinism, producing more broods in warmer years (Roy and Sparks, 2000).

There is growing concern that global climate change has led to in shifts in phenology resulting in mismatches between ecological processes with a temporal component (Miller-Rushing *et al.,* 2010). The potential for ecological mismatches between interacting species (Viser and Holleman, 2001), such as predator and prey or plant and pollinator (Miller-Rushing *et al.,* 2010), under altered phenological regimes could have profound impacts on ecosystem composition, dynamics and functioning (Viser and Holleman, 2001; Ibanez *et al.,* 2010).Whilst it is accepted that warming climates will have considerable impacts on ecosystem functioning, it is also well documented that not all species are responding in the same manner to the same climatic changes; there is considerable spatial variation in responses both inter- and intra-specifically (Warren *et al.,* 2001; Walther *et al.,* 2002; Sparks *et al.,* 2006; Thomas *et al.,* 2006; Warren *et al.,* 2007; Gonzalez-Megias, 2008; Ibanez *et al.,* 2010; Diamond *et al.,* 2011; Wilson and Roy, 2011). For example Pollard *et al.* (1991) found no obvious trend between the timing of the first flight of *P. tithonus* and latitude across its British range. Since the latitudinal temperature gradient across Britain is not reflected in the phenology of *P. tithonus*, it could be that local adaptation to temperature has occurred across its range. One way this could have been achieved is through the exploitation of thermal heterogeneity in the form of microclimates within an organism's immediate environment. By doing so, Lepidopteran larvae are able to attain temperatures between 5-20°C above the ambient, simply by altering their orientation and posture relative to thermal microclimates within their habitat (Roy and Asher, 2003). By exploiting warmer microclimates found within their northern ranges, butterflies and in particular their larvae could experience developmental rates more typical of those found in the south. Consequently, emergence of southern and northern butterflies could become synchronised despite difference in their macroclimatic conditions (Roy and Asher, 2003).

Other mechanisms that may lead to synchronisation of emergence and flight periods across a climatically variable range include physiological tradeoffs, such as smaller adult size in northern ranges, for example Ayres and Scriber (1994) reported smaller larvae and adults in Alaskan and Michigan populations of *Papilio Canadensis.* Size clines have been observed in butterflies in Sweden using museum collections of species caught at both their northern and southern ranges (Nylin and Svard, 1991). These observations regarding temperature and size are opposite to those described by the ecogeographic principle Bergmann's rule which states that within a broadly distributed species or population, those of a larger size will be found in colder environments. This is not entirely surprising as the rule most often describes patterns observed among endotherms with its generality among ectotherms still unclear (Kingsolver and Huey, 2008) with Bergmann and converse-Bergmann latitudinal clines observed in arthopods (Mousseau, 1997; Blanckenhorn and Demont, 2004). Local adaptation could also be occurring via physiological mechanisms which allow accelerated development in cooler ranges, a phenomenon which has been documented in some species of fish and other poikilothermic organisms (Roy and Asher, 2003).

Local adaptation may manifest itself in a number of ways including changes in voltinism, dates of emergence and first flight, and timing of maturation of eggs. If such local adaptation to temperature (Beaumont and Hughes, 2002) occurs widely among other species of butterfly, the implications for conservation strategies involving translocation (movement of individuals from one location to another) could be profound. Translocated individuals or populations may emerge too early or too late relative to their new surroundings if they are unable to respond to the temperature at their new site, with possible consequences for survival (Roy and Asher, 2003). Despite this concern, a recent long term study has documented how through assisted colonisation two generalist species of butterfly were able to successfully colonise climatically suitable areas beyond their actual range margins (Willis *et al.,* 2009b). However, such a study is yet to be replicated for more sedentary habitat specialists which are likely to be more prone to local adaptation than the wider ranging, more mobile habitat generalists (Oliver *et al.,* 2010).

Habitat specialists are likely to require more conservation assistance if their populations are to persist in a changing environment, be it climatic change, habitat modification, or both. Therefore it is important to determine which conservation strategies are suitable for these species. Where local adaptation is not occurring within meta-populations, assisted colonisation could become a valuable conservation tool for those species with poor mobility or a patchy habitat distribution (Hoegh-Guldberg *et al.,* 2008; Willis *et al.,* 2009).

Understanding the effect of climate change on phenology is of particular importance to the conservation of biological systems. Forecasting phenological change under future climate scenarios is something that must be addressed using knowledge gained from extensive data sets of actual species responses (such as the UKBMS dataset) and incorporating this knowledge into dynamic biological models. This will enable future predictions of phenological trends for locations and species with limited data to be made (Ibanez *et al.,* 2010). Such an approach however is hindered by variable responses of taxa to temperature (Warren *et al.,* 2001; Walther *et al.,* 2002; Sparks *et al.,* 2006; Thomas *et al.,* 2006; Warren *et al.,* 2007; Gonzalez-Megias, 2008; Wilson and Roy, 2011). Recent analysis has shown that, even within the same species, species' responses to temperature vary greatly between sites (Ibanez *et al.,* 2010; Primack *et al.,* 2009; Menzel *et al.,* 2006) suggesting phenological changes recorded for one population or community may not reflect the dynamic changes and responses occurring within a neighbouring population or community (Ibanez *et al.,* 2010). Thus inferring changes at one site reflect changes occurring at another site may not be a reliable indication of changes in response to temperature. Such spatial variability poses particular problems for forecasting changes occurring within species assemblages at locations with limited or no data available (Ibanez *et al.,* 2010).

1.7 The influence of habitat heterogeneity on population stability

Heterogeneous landscapes are consistently shown to buffer populations from the effects of short-term, extreme, climatic events, such as drought or flood, reducing the risk of localised extinctions (Weiss *et al.,* 1988; Woods *et al.,* 2008; Oliver *et al.,* 2010). Such extreme weather patterns are predicted to increase in frequency under future global climatic change (Easterling *et al.,* 2000a; Easterling *et al.,* 2000b) and as such conservation managers must act to protect populations and communities susceptible to annual fluctuations in climate. Evidence suggests that habitat heterogeneity plays an important role in stabilising populations at both local and landscape levels (Pe'er *et al.,* 2004). The response of organisms to habitat heterogeneity affects the direction of dispersal and movement between patches, ultimately governing the dynamics of spatially structured populations (Pe'er *et al.,* 2004). Population stability is vital if both individual populations and the metapopulation are to persist over time, especially if population stability conveys resilience to environmental change (Oliver *et al.,* 2010).

Heterogeneous landscapes by their definition provide multiple microclimates and resources at a range of spatial and temporal scales. This microclimatic and resource variability contributes to the ability of the habitat to buffer populations against variable climates, promoting greater population stability (Oliver *et al.*, 2010). Whether or not habitat heterogeneity is shown to be critical in the persistence of populations and communities is of particular interest to conservation biologists and policy makers, given that habitat heterogeneity is particularly amenable to anthropogenic manipulation (Oliver *et al.,* 2010). Woods *et al.* (2008) identified the value of environmentally heterogeneous habitat in the long term stability of a diverse butterfly community in Western Ohio, USA. Prioritising highly heterogeneous landscapes (e.g. those with high topographical diversity) for protection is a potentially valuable conservation strategy.

Topographicical heterogeneity is a key source of habitat heterogeneity that influences species' distributions by directing animal movements (Pe'er *et al.,* 2004). Oliver *et al.* (2010) demonstrated that 35 species of British butterfly from 166 sites exhibited more stable population dynamics when associated with more heterogeneous habitats that contained a variety of suitable habitats, in particular when habitats contained a wider variety of topographic aspects. These findings have significant implications for habitat management aiming to conserve biodiversity in the face of climatic change. Areas with high topographic diversity should be prioritised for protection due to their high microclimatic variability, and those with low topographic diversity should be managed in a way which promotes habitat heterogeneity at both fine and coarser scales (Oliver *et al.,* 2010). Topographical variability at both fine and coarser spatial scales is an important component maintaining micro-climatic variability of habitats. Micro-climatic variability is particularly important for the successful development of multiple life stages exhibited in the life-cycles of many arthropods. This is particularly true for those insect species that are subject to seasonality and climatic variability resulting in a timely pressure to complete their life cycles within temporally limited windows of developmental opportunity (Oliver *et al.,* 2010).

Euphydyras editha (Edith's checkerspot butterfly), is a well studied butterfly which has been shown to exhibit marked responses to temperature and changing climate. In an early study, Weiss *et al.* (1988) investigated the effects of microclimate on the developmental stages of the butterfly the subspecies *Euphydyras editha bayensis,* in San Francisco, USA. Weiss *et al.* (1988) found that prediapause larvae exhibit higher survivorship on cooler, north facing slopes where host plant senescence is delayed, resulting in a longer period of food availability. However, these high survivorship prediapause larvae come from eggs laid by early flying females which themselves developed as postdiapause larvae on warmer, south-facing slopes, where pupae develop faster as a result of the higher temperatures, but also where prediapause starvation rates are highest due to the limited window of food availability before host plants senesce. Such a paradoxical relationship has been shown to be important in maintaining populations under climatic extremes such as drought and flood (Weiss *et al.,* 1988). A variety of microclimates can protect populations from decline under most macroclimatic conditions, with at least some of the life stages experiencing favourable conditions for growth and development. Areas with high rates of spatial interfacing between varying slope exposures are of particular value to populations of this butterfly whose larvae are capable of limited dispersal (Weiss *et al.* 1988). It is likely that microclimatic diversity, particularly as a consequence of topographical variability within a habitat, is of significant importance to many small ectothermic animals, particularly those whose development is constrained by temperature.

1.8 Predicting species range shifts in relation to environmental parameters

Biodiversity is dynamic, responding to anthropogenic and natural environmental changes at many spatial and temporal scales. Population and distribution responses of species often lag behind environmental change (Hill *et al.,* 2001; Willis *et al.,* 2009b; Devictor *et al.,* 2012); quantitative predictions of species' responses to changing environments are required if the success of conservation programmes is to be maximised. In order to produce accurate models of habitat connectivity and metapopulation dynamics in a changing environment it is crucial to understand the mechanisms by which species disperse (Pe'er *et al.,* 2004). Fragmented landscapes composed of a patchwork of suitable and unsuitable habitat act as a barrier to dispersal; communities become isolated when organisms are unable to cross areas of unsuitable habitat to colonise new areas of suitable habitat. Understanding the factors which affect dispersal ability and range shifting patterns, particularly when faced with fragmented landscapes, is critical when predicting the actual route taken by a dispersing organism (Pe'er *et al.,* 2004). This information will be highly informative to conservation managers who aim to help facilitate species' responses to climate change (Wilson *et al.*, 2009).

Hesperia comma L., is a rare, specialist butterfly with specific habitat requirements; in England it is restricted to species-rich, calcareous grasslands. The species experienced marked declines following severe habitat loss as a result of agricultural intensification during the 1940s and 50s, which destroyed 80% of calcareous grassland in England. An additional contributing factor was vegetation succession following myxomatosis outbreaks and abandonment of livestock grazing in the same period. By 1982 *H. comma* was restricted to a 2.1km^2 area encompassing eight habitat networks in southern England, hosting 70 populations. Habitat restorations, recovery of rabbit populations, and targeted conservation measures have resulted in recent recovery and expansion of *H. comma* populations. However, despite greatly improved habitat conditions, *H. comma,* has not expanded into ranges where it was not previously present (in the 1982 survey), with more than 90% of recent colonisations within a 10km radius of the 1982 populations (Wilson *et al.,* 2009).

Habitat fragmentation (i.e. the breaking up of continuous habitats into fragmented patches (Zaviezo *et al.,* 2006)) caused by anthropogenic manipulation of the land present barriers to butterfly dispersal (White and Kerr, 2007) Wilson *et al.* (2009). Barriers, such as farmland and urban features including buildings and roads, present little in the way of resources required by species for reproduction and survival meaning individuals and populations are unable to disperse across the landscape to reach and colonise new areas. Wilson *et al.* (2009) used a metapopulation model to help determine what facilitates range expansion in *H.comma*, and whether expansion rates are governed primarily by habitat availability. They demonstrated that poor habitat quality in the form of a highly fragmented landscape hindered species recovery despite general trends for an expanding population and strict, landscape-scale conservation measures implemented to assist in recovery. Such evidence suggests that habitat fragmentation is likely to be an insurmountable barrier to dispersive responses of expanding species at their range margins (Haddad and Baum, 1999; Woods *et al.,* 2008). Hill *et al.* (2001) found that habitat fragmentation reduced rates of range expansion in a specialist woodland butterfly, *P. aegeria,* in England. The high degree of woodland fragmentation in the UK is likely to be a key reason why range expansion in this species is greatly affected by habitat availability. Modelling species' distribution responses to habitat availability is a means of identifying which species and in which landscapes conservation measures are required to facilitate species' recovery and range expansion (Wilson *et al.,* 2009).

To produce accurate models of range expansion a dynamic and mechanistic approach to understanding species distributional responses to climate change is required (Willis *et al*., 2009b; Zurell *et al.,* 2009). Previous models of range shifting behaviour in butterflies have focussed on climate suitability as a driver of range expansion and range shifts. Since many species have been observed to be lagging behind current climate (Hill *et al.,* 2001; Willis *et al.,* 2009b; Devictor *et al.,* 2012) it is evident that non-climatic factors are driving rates and patterns of range expansion (Willis *et al.,* 2009a). As such it is important to incorporate non-climatic determinants of range expansion into next-generation models of species expansion. Using MIGRATE, a spatially explicit, grid-based mechanistic model Willis *et al.* (2009a) incorporated habitat suitability and demographic parameters into models of spread, accurately predicting recently observed changes in the distribution of three British butterfly species.

1.9 Conclusion

Global climate change is a major contemporary issue and conservation challenge in ecology today (Morecroft *et al.,* 2009); the ecological consequences of global climate change can already be tracked through many biological and physical systems (Parmesan *et al.,* 1999; Thomas *et al.,* 2001; Warren *et al.,* 2001; Hickling *et al.,* 2006; Sparks *et al.,* 2007; Ibanez *et al.,* 2010; Wilson and Roy, 2011). Terrestrial ecosystems are particularly well studied and have yielded a consistent pattern of change in response to warming over time (Menzel *et al.,* 2006). If threatened and rare species are to be managed effectively in light of future climatic change, we must accurately predict how habitat availability and climate will affect species' abundance and distribution in the future (Wilson *et al.,* 2009). In order to achieve such a goal, an in depth understanding of phenological processes that shape the distribution and demography of populations and communities is vital (Chuine, 2010). Parameters affecting population dynamics, in particular those factors affecting species distribution and abundance must be identified, and worked in to predictions for species' responses if populations and communities are to be conserved and protected in light of recent and predicted future climatic change (Woods *et al.,* 2008).

In order to detect changes and attribute causes as to the effects of environmental change on biodiversity it is crucial to develop scientifically robust means of monitoring change in the natural environment (Morecroft *et al.,* 2009). As one of the most intensively studied invertebrate fauna in the World, British butterflies (Warren *et al.,* 2007; Fox *et al.,* 2010) offer a unique opportunity to make qualitative assessments on the affects of climatic change on ecological communities over time. Many biological agents of decline have already been identified; degraded habitat, habitat loss, introduced competitors, loss of native larval and food plants, and agricultural intensification and pesticide use (Woods *et al.,* 2008). It is how such biological agents will interact with a changing physical environment that is of particular concern to ecologists when predicting species responses to future climate change.

From a conservation perspective, if management is to be targeted and effective, it is crucial to distinguish between factors contributing to observed species' responses to environmental change (Morecroft *et al.,* 2009). Along with continued monitoring to produce long-term datasets, biological models can aid in identifying key parameters in an organisms life-history that affect species responses to environmental change. In addition they can help to determine the spatial distribution of species and suitable habitat in a fragmented landscape (Luoto *et al.,* 2002), presently and in the future under various predicted climate regimes. Such information will be invaluable for developing conservation initiatives for species that are currently threatened by both anthropogenic pressures and global climate change.

1.10 Thesis Plan

In this thesis I will consider how environmental factors operating at both fine and broad spatial scales impact the current range extent of a subset of generalist butterflies in Great Britain. By its conclusion, this thesis will have made important steps in improving the predictive power of models designed to inform our understanding of the effects of environmental change on British butterfly species, and by extension many other insect taxa from across the globe. By considering both fine and broad scale environmental factors I hope to highlight the importance of utilising ecological field data, collected in natural systems, to improve our ability to generate and accurately inform robust ecological models and subsequently conservation initiatives. To achieve these aims I will progress through the data chapters outlined below.

Chapter 2

The primary aim of this chapter is to utilise UKBMS transect data to inform the parameterisation of a dynamic species distribution model utilised in Chapter 3. Values for both intrinsic rates of increase and mean density in occupied habitats will be generated for four generalist butterfly species, resident to Great Britain, using data collected from populations throughout each species range and in multiple occupied habitats. In order to increase the ecological validity of the modelling framework that will be utilised in Chapter 3, this chapter will discern whether it is appropriate to allocate variable carrying capacity values to different suitable and occupied habitats. To my knowledge, this is the first time variable density in different, occupied habitats has been investigated for the primary purpose of directly increasing the predictive power of a dynamic modelling approach.

Chapter 3

Following from Chapter 2, this chapter will utilise species specific demographic parameters, habitat and climate suitability grids to inform a spatially explicit, grid -based, mechanistic dynamic species distribution model. I aim to accurately simulate the recorded spread of the four butterfly species examined in Chapter 2, between the years 1970 and 2009. In doing so, I aim to assess the relative ability of habitat and climate to explain observed patterns of spread during this time. Further to this, I will discuss whether habitat, climate or both may be limiting the current range extent of the study species. If models prove to be successful I will run models into the future to predict future range extent of a subset of the studied species.

Chapter 4

In this chapter I aim to investigate fine-scale environmental characteristics on local and regional patterns of phenology of a butterfly species, *M. galathea* and its favoured nectar plant, *Centaurea scabiosa*. To achieve this I will utilise annual UKBMS transect data and flowering phenological data collected in previous years by researchers and volunteers, and compliment this with field data collected along a south-north transect across England during the 2011 flight and flowering season. I aim to demonstrate how heterogeneous environments (with regards to aspect and topography) have the potential to extend the overall flowering period observed at a given site, increasing the time over which insects can utilise nectar resources.

Chapter 5

I will make final conclusions and discuss recommendations and challenges for the future.

Chapter 2

Estimating carrying capacities and intrinsic rates of increase for four generalist butterfly species

Abstract

Background: Almost all species occupy habitats that are inherently heterogeneous in both space and time. Generalist butterfly species occupy multiple habitats of varying suitability often at different population densities. As the subjects of one of the longest running ecological surveys in the world, British butterflies represent a unique opportunity to study population dynamics and demographic stochasticity across multiple occupied habitats. This study aims to improve the accuracy of dynamic species distribution models by capturing and incorporating demographic stochasticity across the multiple occupied habitats of four generalist butterfly species - *Parage aegeria, Aphantopus hyperantus, Pyronia tithonus* and *Melanargia galathea*.

Methods: UKBMS transect data was used to generate species specific values for both intrinsic rates of increase, r, and mean density in occupied habitats, ρ, for the four study species. A single best estimate of r was calculated for each species; a univariate general liner model was performed on annual density ratios from which a y-intercept parameter estimate for r was obtained. Mean density of each the four study species was calculated for each occupied habitat. Densities among habitats were compared using one-way ANOVA. Post-hoc Tukey's tests were performed to determine which habitats differed significantly in their mean density of butterflies.

Results: Best estimates of r for each of the four study species demonstrated a high degree of uncertainty. All four species had a lower 95% confidence bound below 0 indicating some sites demonstrate negative growth between years. Three species showed significant differences in adult butterfly densities across two or more analysed habitats: *P. aegeria* (ANOVA; $F_{6, 72} = 5.06$, $P < 0.001$), *M. galathea* (ANOVA; $F_{4, 66} = 25.79$, $P < 0.001$) and *A. hyperantus* (ANOVA; $F_{2, 32} = 6.320$, $P = 0.005$).

Conclusions: High variation in intrinsic rates of increase across all species studies was documented. This is in accordance with past research and solidifies the need further investigate demographic stochasticity within populations to improve the robustness of models of range expansion. Three out of the four species studied occur at significantly different densities in their occupied habitats highlighting a need to incorporate habitat specific population estimates into spatially explicit, dynamic population demographic models if predictions are to be robust.

2.1 Introduction

Almost all organisms inhabit environments that are inherently heterogeneous in both space and time (Morris *et al.,* 2004; Oliver *et al.,* 2010). Dispersal among habitat patches by populations is thus essential for population persistence (Morris *et al.,* 2004). Species distribution modelling is an expanding field of research, which relates current species distributions to selected environmental variables, often in an effort to predict the impacts of environmental change on species distributions (Pagel and Schurr, 2011). However, as purely correlative, phenomenological models, statistical species distribution models (SDMs) do not represent the spatial population dynamic processes that underlie the formation of species ranges (Zurell, 2009), resulting in mismatches between species niches and distributions (Holt, 2009; Pagel and Schurr, 2011). In nature, species ranges are shaped not only by environmental limitations, but also by demographic stochasticity and dispersal ability (Holt *et al.,* 2005; Pagel and Schurr, 2011).

If community and population dynamics are to be modelled accurately, those parameters relating to population growth and dispersal must be accurately informed and quantified. Due to difficulties in quantifying such parameters (Morin and Thuiller, 2009), dynamic, process-based models of species ranges that combine demographic response functions with populations dynamics and dispersal are rare (Thuiller *et al.,* 2008). As the subjects of one of the longest running ecological surveys in the world (Fox *et al.,* 2010), British butterflies represent a unique opportunity to accurately parameterise and test dynamic species range models. The UK Butterfly Monitoring Scheme (www.ukbms.org) is a population monitoring scheme that has run since 1976 and has resulted in the collation of a comprehensive dataset of the abundance and distribution of British species across a broad range of British habitats (Asher *et al.,* 2001; Warren *et al.,* 2007; Fox *et al.,* 2010). British butterfly species thus represent an ideal opportunity to accurately inform and produce models of spatial population dynamics.

Early models concerned with spatial population dynamics (e.g. the Ricker [Ricker, 1954] and the logistic [Hutchinson, 1978] models) assume individuals within populations are subject to the same, uniform environment (Underwood, 2007). However, in nature, this assumption is unrealistic, particularly for species with high mobility and inhabiting large ranges containing heterogeneous landscapes (Oliver *et al.,* 2010). Butterfly species are traditionally subdivided into two broad categories on the basis of habitat specialisation, diet breadth and mobility (Stefanescu *et al.,* 2011). Specialist species exhibit limited mobility and restricted habitat and host plant associations, whilst generalist species are characterised by higher levels of mobility and are able to make use of a wider range of host plants thus, occupy a broader range of habitats (Warren *et al.,* 2001; Hill *et al.,* 2006; Stefanescu *et al.,* 2011) This study is concerned with generalist species; the majority of generalist species in temperate countries occupy open areas, such as, grasslands, woodland glades and wetlands (Thomas, 1984; Warren, 1992; Thomas, 1995; Bergman, 2001). Within the 'generalist' subdivision of butterflies, different species exhibit differences in habitat association, preference and specialisation, resulting in differences in the relative size of populations across a species occupied range (Thomas, 1984). If population dynamic models are to accurately predict species spread, it is important to incorporate differences in population demographics across their occupied range into predictive models of spread.

Underwood and Rausher (2000) showed that populations of herbivorous insects moved through a network of host plants (environmental patches) varying in quality. Since generalist butterflies are known to occupy a range of habitats, migrating individuals and populations are also likely to move through a network of habitats, of varying quality. Recent empirical studies have demonstrated that such spatial variation in habitat quality (patchy environments) results in spatial variation of two demographic parameters fundamental in the population dynamics of a species (Underwood, 2007). The first, intrinsic rate of increase, is defined as the maximum rate of increase that a population can achieve in the absence of density dependence and in an unlimited environment (Birch, 1948; Root, 1960; Caughley and Birch, 1971). Such growth is exponential and controls the rate of population growth at low densities (Helms *et al.,* 2004; Underwood, 2007). The second, carrying capacity, controls density dependence and is often termed the equilibrium population size (Hutchinson, 1978; McLeod, 1997).

If population dynamics are to be accurately predicted and model outputs produced that are relevant to conservation of species in their natural environments (McPherson and Jetz, 2007), ecological models concerned with regulated population dynamics must carefully consider the quantification of both intrinsic growth rates and density dependence (McLeod, 1997). With this in mind, the primary aim of this chapter is to use species specific, time series data from UKBMS survey sites, to accurately inform the parameterisation of population dynamic models, in order to simulate range changes of four generalist butterfly species, resident to Britain. To achieve this I develop techniques to derive values of intrinsic rates of increase, r, for each of the four study species. Secondly, I test the hypothesis that species persist at different mean densities in different occupied habitats by deriving separate values of density in suitable habitat (ρ) in occupied habitats, for each of the four study species.

2.2 Methods

2.2.1 Species abundance data - The UK Butterfly Monitoring Scheme

The UK butterfly monitoring scheme (UKBMS) has been operating as a national scheme since 1976 and involves weekly butterfly counts along designated transect routes at sites between April and September each year, when weather conditions are suitable for butterfly activity: dry conditions, wind speed less than Beaufort scale 5, temperature greater than 13°C or greater if there is at least 60% sunshine, or more than 17°C if overcast (www.UKBMS.org/Methods; Pollard and Yates, 1993; Pollard and Yates, 1996). Transects are typically 5 m wide, between 1.5 and 3 km in length, and walked once a week, for up to 26 weeks of the year, encompassing the main flight periods of UK butterflies (Oliver *et al.,* 2010). UKBMS classifies trends at monitored sites as increasing, decreasing and stable for each species observed at each site. Trends are calculated using a site index (an annual estimate of butterfly abundance from transect counts) where the regression slope of log index on years is used as the measure of trend. The significance of the trend is assessed to classify trends as; increasing where the regression slope is positive and $p<0.05$, decreasing where the regression slope is negative and $p<0.05$, stable where $p>=0.05$, e.g. not significant (www.ukbms.org). In order to calculate intrinsic rates of increase and density in suitable habitat annual abundance data (the total number of butterflies recorded at a given site on a given year) was utilised from sites classified as stable and increasing respectively. Full details of UKBMS recording methods can be found in Pollard and Yates (1993).

2.2.2 Study species

Four butterfly species resident in Britain were chosen for analysis: *Pararge aegeria* (speckled wood)*, Aphantopus hyperantus* (ringlet), *Pyronia tithonus* (gatekeeper) and *Melanargia galathea* (marbled white). They are classified as wider-countryside species (generalists) and are widespread and locally common within their UK range (Asher *et al.,* 2001; Fox *et al.,* 2008). All four species are members of the family Nymphalidae, subfamily Satyridae. These species were chosen because they have been the subjects of a substantial body of research (Hill *et al.,* 1999; Baguette *et al.,* 2000; Hill *et al.,* 2001; Schweiger *et al.,* 2006; Merckx and Dyck, 2007; Willis *et al.,* 2009a; Willis *et al.,* 2009b) meaning life-history trait information is readily available. They also have variable habitat requirements (Asher *et al.,* 2001) and have all expanded their range in recent decades (Table 2.1), with *P. aegeria* showing the largest proportional increase (Fox *et al.,* 2008).

Table 2.1: Study species habitat requirements, larval host plants and distribution trend since the 1970s.

Species	Habitat	Larval host plants	Distribution trend since 1970s
Pararge aegeria	Favours damp woodland rides and glades with partial shade. Also found in gardens, parks and hedgerows.	*Coarse grasses including Brachypodium sylvaticum* (False Brome); *Dactylis glomerata* (Cock's-foot); *Holcus lanatus* (Yorkshire-fog); *Elytrigia repens* (Common Couch).	+31%
Aphantopus hyperantus	Woodland rides and glades. Tall damp, partially shaded grassland. Also occurs on commons, verges and riverbanks, especially on clay soils. In northern areas found in more open and less shady habitats.	Coarser grasses including *Dactylis glomerata*, *Brachypodium sylvaticum*, *Deschampsia cespitosa* (Tufted Hair-grass), *Elytrigia repens*, *Poa* spp. (meadow grasses).	+16%
Pyronia tithonus	Tall grass close to hedges, trees or scrub. Typically along hedgerows and woodland rides. Also occur under cliffs, heathland and on downland where there are patches of scrub.	Various grasses; preference for fine grasses such *Agrostis* spp. (bents), *Festuca* spp. (fescues), and *Poa* spp. (meadow grasses). *Elytrigia repens* is also used.	+12%
Melanargia galathea	Unimproved grassland with tall sward. Strongest populations found on chalk or limestone grasslands. Habitats such as; woodland rides and clearings, coastal grassland, road verges and railway embankments are also used.	*Festuca rubra* (Red Fescue) is thought to be essential in the diet of larvae but *F. ovina* (Sheep's Fescue), *Holcus lanatus*, and *Brachypodium pinnatum* (Tor grass) are also eaten.	+11%

2.2.3 Intrinsic rates of natural increase

Due to the limited number of sites classified by UKBMS as holding ‘increasing’ populations for each of the four study species it was not possible to calculate a value of *r* for each habitat class as with density values. Instead a single, best estimate of r was calculated for each species using the annual abundance data from UKBMS sites. To estimate *r*, data from sites where populations of a species were classified as 'increasing' were extracted from the UKBMS database (Appendix Table A1). Upon further inspection of these data it became clear that, despite this classification, some site populations were displaying signs of a stabilising or, in a few cases, declining. To ensure that estimates of *r* were derived from sites with populations that were increasing, the natural log of site specific annual butterfly densities (per m^2) against time was plotted and linear regression slopes fitted. Only sites with an r^2 value ≥ 0.5, signifying positive growth, were used in the final derivation of *r*.

Birch (1948) defines the intrinsic rate of increase as a basic parameter which describes the per capita rate of increase, under specified physical conditions, in an unlimited environment, where the effects of increasing density do not need to be considered. The growth of such a population is, by definition, exponential and can be described by the differential equation for population increase in an unlimited environment (Equation 2.2).

$$\frac{dN}{dt} = rN \qquad \text{(Equation 2.2)}$$

where, $\frac{dN}{dt}$ = change in population size, *r* = intrinsic rate of increase (equals birth rate minus death rate), N = population size (Birch, 1948). However, in nature, populations persist in a limited environment and are subject to laws of density dependence, and thus it is likely that rates of increase will decline as population size increases and resources are spent. As such, when considering natural butterfly populations it is more accurate to describe population growth in the integrated form of the equation (Equation 2.3).

$$N_t = N_0 \, e^{r\,t} \qquad \text{(Equation 2.3)}$$

where, N_0 = number of animals at time zero, N_t = number of animals at time *t*, *r* = intrinsic rate of increase. In order to gain an estimate of *r* which depends on population size with time, this integrated equation can be solved by the ratio expressed in Equation 2.4.

$$r = \ln \frac{N(t+1)}{N(t)} \qquad \text{(Equation 2.4)}$$

To obtain a value of *r* for each species that, on average, represents what is occurring in their natural populations, data from 10 sites across each species range were selected (on the basis of the aforementioned criteria). A univariate, general linear model (GLM) was performed using IBM SPSS version 20.0 statistical software on annual density ratios (Equation 2.4), accounting for site as a random effect. A y-intercept parameter estimate was obtained for each species and this value was used as a final best estimate of *r*. 95% confidence intervals were obtained to demonstrate uncertainty in estimating *r*.

2.2.4 Density in suitable habitat

An estimate of density (ρ) was calculated for those broad habitat classifications occupied by each of the four study species with appropriate amounts of data for statistical analysis (Appendix Tables A2-A5).

Each UKBMS site is allocated a single broad habitat description, following the European Nature Information System (EUNIS) of habitat classification (Davis *et al.,* 2004). Table 2.2 outlines those habitat types selected for comparative analysis; each habitat classification chosen for comparative analysis has at least 5 representative sites hosting a stable population of the butterfly under analysis. For those habitat classifications with more than 20 representative sites classified as stable only 20 sites were randomly selected for analysis due to time constraints in extracting data. In order for butterfly densities to be calculated it was important to know the length and width of survey transects; only those sites with transects of known lengths were included in the analysis. Since discounting sites with unknown transect widths would have resulted in the loss of a large proportion of data, UKBMS sites with no information regarding transect widths on the UKBMS explanatory web-pages were assumed to have a width of 5m (standard transect size as defined by UKBMS transect survey guidelines).

Table 2.2: Habitat types used for comparative analysis; UKBMS transect habitat classifications and corresponding shortened classification adopted for ease of reading throughout the remainder of this research chapter.

UKMBS Habitat Classification	Shortened Classification
Dry semi/unimproved flower-rich chalk/limestone grassland	Chalk/limestone grassland
Dry semi/unimproved flower-rich neutral grassland	Neutral grassland
Seasonally wet and wet marshy grasslands	Marshy grasslands
Mature broadleaved woodland	Broadleaved woodland
Mature mixed broadleaved and coniferous woodland	Mixed woodland
Wet and dry heathland/dry heather moorland	Heathland/heather moorland
'Bare ground/weed communities of post-industrial sites e.g. quarries/pits/road/rail/landfill sites'	Post-industrial sites

Butterfly densities at stable sites (per hectare per year) were calculated by first summing the total number of butterflies counted during weekly counts throughout the flight periods of the four study species, and dividing this value by the relevant transect proportions to gain a value for density per m^2. This value was then multiplied by 10,000 to gain a density value for individuals per hectare per year (individuals per ha). A mean density value was then calculated for each site across years by summing the densities per ha and dividing this value by the number of years of counts. A minimum of 5 years of counts was stipulated for inclusion of a site in density calculations. Mean site densities were used for statistical analysis in order to allow for inter-site variation. Densities among habitats were compared for each species using one-way ANOVA performed using IBM SPSS version 20.0 statistical software. Post-hoc Tukey's tests were performed to determine which habitats differed in their carrying capacity of butterflies.

2.3 Results

2.3.1 Intrinsic rates of increase

Both mean estimates of *r* at individual sites (Figure 2.1) and y-intercept best estimates of *r* for each of the four study species demonstrated a high degree of uncertainty (Figure 2.2). All sites used in the estimation of *r* had negative growth in some years (Figure 2.1).

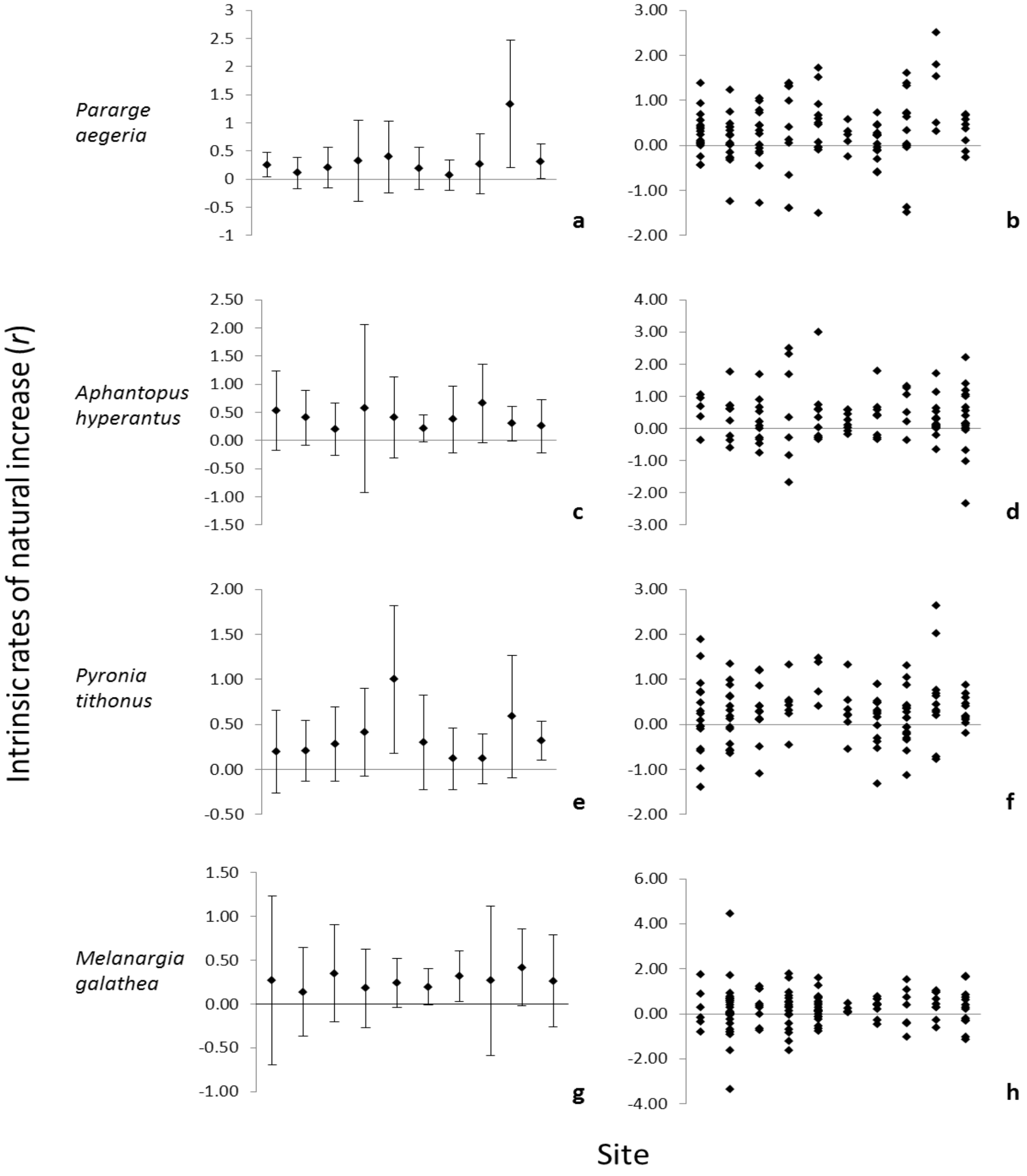


Figure 2.1: Mean intrinsic rates of natural increase (*r*) (a, c, e, g) and actual estimates of *r* between years (b, d, f, h) for natural populations of the four study species at 10 monitored sites. Sites are different for each species and do not correspond to one another. Bars indicate 95% confidence intervals for the mean.

Best estimates of *r* for individual species ranged from the lowest of 0.26 (*M. galathea*) to the highest 0.32 (*P. tithonus*). All four species had a lower 95% confidence bound below 0, indicating that, despite the rigorous data selection process, some sites demonstrate negative growth between years. All four species had 95% confidence bounds between 0.79 and -0.23 (Figure 2.2).

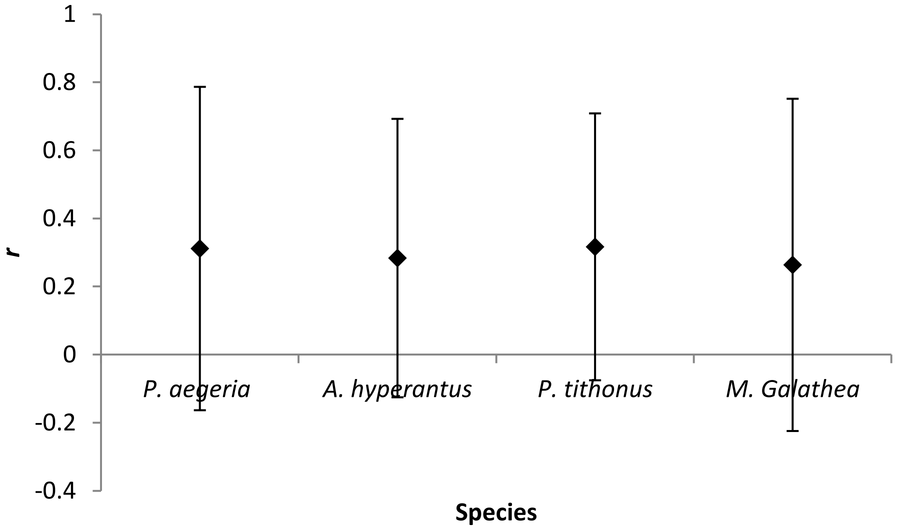


Figure 2.2: Mean estimates of intrinsic rate of natural increase (*r*) in natural populations of four generalist species of butterfly at monitored sites. Bars indicate 95% confidence intervals from univariate, general linear model when N was 119 – *P. aegeria;* 97 – *A, hyperantus;* 115 – *P. tithonus;* 124 – *M. galathea*.

2.3.2 Carrying capacity

Herein UKBMS habitat classifications are shortened for ease of reading. Table 2.2 outlines original and shortened classification titles. Three species showed significant differences in adult butterfly densities across two or more analysed habitats (Figure 2.3): *P. aegeria* (ANOVA; $F_{6,\ 72}$ = 5.06, *P* <0.001), *M. galathea* (ANOVA; $F_{4,\ 66}$ = 25.79, *P* <0.001) and *A. hyperantus* (ANOVA; $F_{2,\ 32}$ = 6.320, *P* = 0.005). Chalk/limestone grassland, broadleaved woodland and mixed woodland habitats were utilised by all four species. With the exception of *M. galathea,* the two woodland habitat classes (broadleaved woodland and mixed woodland) host high mean densities of adult butterflies. Reliance on specific habitat classes is variable among the four species; *M. galathea* persists at significantly higher densities at chalk/limestone grassland habitats than it does in other occupied habitats (Figure 2.30), an observation which is consistent with literature regarding habitat preference of this species (Asher *et al.,* 2001; Willis *et al.,* 2009a). *P. tithonus* also persists at high populations densities in chalk/limestone grassland sites but is less reliant on this habitat class, occurring also at similar population densities in broadleaved woodland and mixed woodland (ANOVA; $F_{2,35}$ = 1.751, *P* = 0.189). *P. aegeria* occurs at significantly higher population densities in mixed woodland sites, consistent with the fact that it is primarily a woodland butterfly (Hill *et al.,* 1999; Hill *et al.,* 2001). Of the four species, *A. hyperantus* occurred at the highest mean population densities, in mixed woodland.

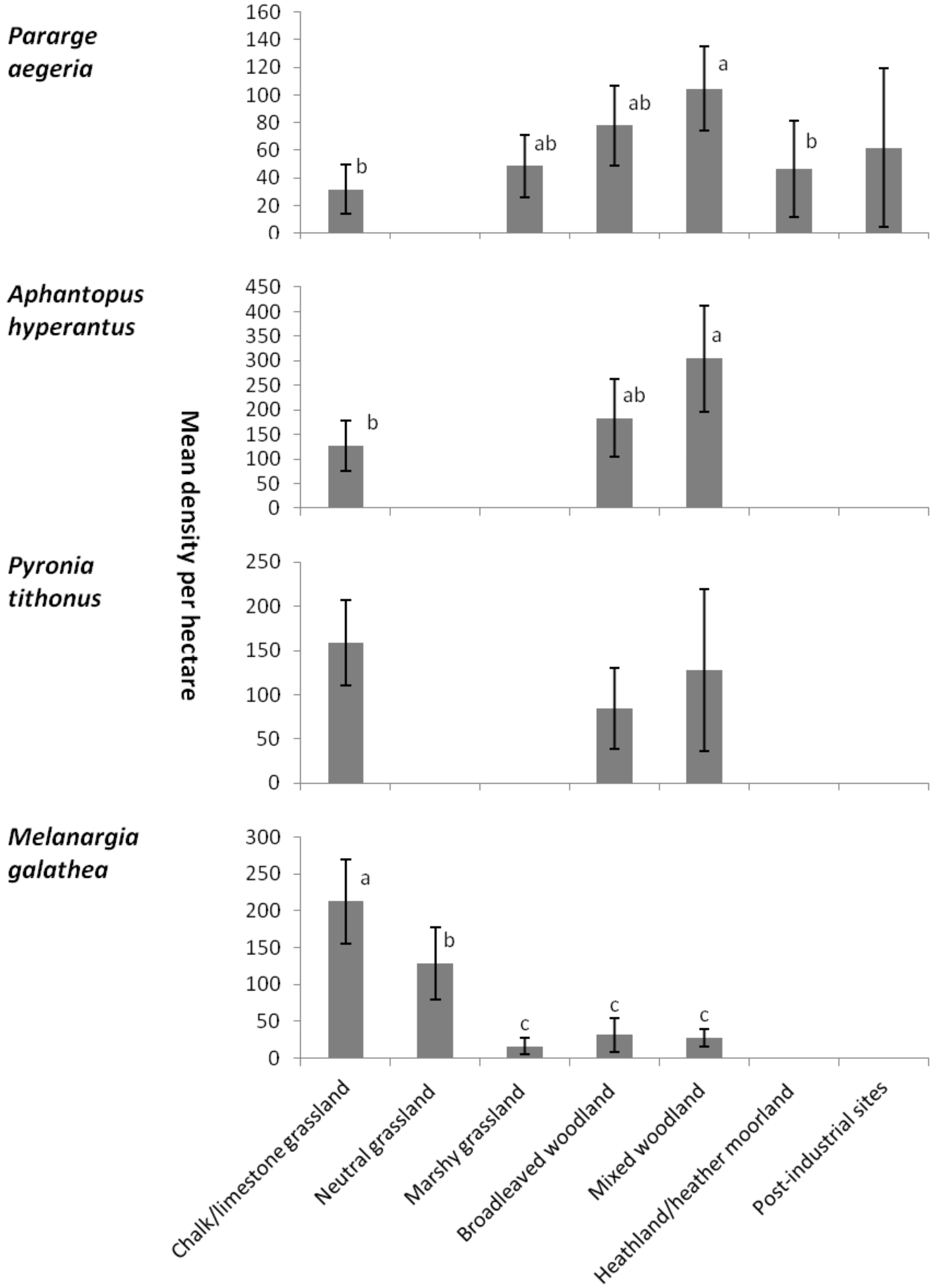


Figure 2.3: Mean density of four generalist butterflies per hectare, in different habitat types. Bars indicate 95% confidence intervals for the mean. Symbols indicate which means are significantly different α = 0.05. Refer to Table 2.2 for full habitat classifications.

Table 2.3: Mean density (ρ, individuals per hectare) in occupied habitats and species specific intrinsic rates of increase, r, for four generalist butterfly species calculated from UKBMS transect data.

Species	UKBMS Habitat Classification	Density (ind. per hectare)	*r*
Pararge aegeria	Dry semi/unimproved flower-rich chalk/limestone grassland	32	0.31
	Seasonally wet and wet marshy grasslands	48	
	Mature broadleaved woodland	78	
	Mature mixed broadleaved and coniferous woodland	105	
	Wet and dry heathland/dry heather moorland	46	
	Bare ground/weed communities of post-industrial sites	62	
Aphantopus hyperantus	Dry semi/unimproved flower-rich chalk/limestone grassland	127	0.28
	Mature broadleaved woodland	183	
	Mature mixed broadleaved and coniferous woodland	305	
Pryronia tithonus	Dry semi/unimproved flower-rich chalk/limestone grassland	159	0.32
	Mature broadleaved woodland	84	
	Mature mixed broadleaved and coniferous woodland	127	
Melanargia galathea	Dry semi/unimproved flower-rich chalk/limestone grassland	213	0.26
	Dry semi/unimproved flower-rich neutral grassland	129	
	Seasonally wet and wet marshy grasslands	16	
	Mature broadleaved woodland	32	
	Mature mixed broadleaved and coniferous woodland	28	

2.4 Discussion

Three out of the four study species occurred at significantly different densities across their occupied habitats. Thomas (1984) demonstrated that UK butterflies occur at population densities 25-200 times greater in optimal habitat compared to sub-optimal (yet suitable) habitat. Whilst these data do not show such extremes, of those three species which occurred at significantly different population densities across occupied habitats, the habitats with the highest densities accorded with other literature regarding species' preferred habitats (Asher *et al.,* 2001). Density analysis for *P. aegeria was* consistent with the view that this species is essentially a woodland butterfly (Hill *et al.,* 1999; Hill *et al.,* 2001). Likewise, the more specialised habitat requirements of *M. galathea* (Baguette, 2000; Willis *et al.,* 2009b) were apparent in this analysis; results were consistent with literature which describes *M. galathea* as reliant on chalk grassland due to the presence of preferred larval food plants (Baguette *et al.,* 2000). Thomas *et al.* (2001) found that butterfly density was positively correlated with habitat quality. On this basis, it could be assumed that those sites which host the highest population densities of adult butterflies in this analysis are those that offer the best quality habitat.

Despite being broadly classified as a generalist species (Asher *et al.,* 2001; Pullin, 1995) *P. aegeria* is often documented as reliant on woodland and commonly described as a woodland butterfly (Hill *et al.,* 1999; Asher *et al.,* 2001; Hill *et al.,* 2001). This reliance, however, is not uniform throughout its range; in the south and west of its range it is much less restricted to woodland compared to populations in the north and east of its range (Hill *et al.,* 1999). Using data from populations classified as stable by UKBMS (see methods) this analysis highlighted how *P. aegeria* is able to maintain stable populations in sites that are primarily composed of habitat types other than woodland. Previous species distribution models concerned with the spread of *P. aegeria* have ignored this more varied distribution among habitats in the south and west, and opted to define habitat suitability solely by the existence of woodland (Hill *et al.,* 2001). Since these models are concerned with spread at the range edge (and reliance on woodland habitat is greater at the range edge), this is a reasonable approach to take. However, restricting habitat suitability to woodland in this way will undoubted impact on the ability of individuals and populations to disperse. In nature, it is reasonable to assume that as a wider-countryside species *P. aegeria* utilises sub-optimal (non-woodland) habitats as a means of dispersal to more optimal, woodland habitats. Ignoring these 'dispersal corridors' could potentially result in a simulation which is too restrictive and not representative of the actual potential for species dispersal. In order to accurately simulate changes in species ranges it would be beneficial to distinguish between parameter values for different occupied habitats.

A. hyperantus is a generalist species which favours grassy places including meadows, hedgerows, verges and woodland clearings (Asher *et al.,* 2001). This analysis suggests woodland habitats host a higher density of adult butterflies than other occupied habitats; this species sustains significantly higher population densities in habitats broadly classified as mixed woodland and broadleaved woodland, than in chalk/limestone grassland sites. Conversely, population densities of *P. tithonus* did not differ among the same three broad habitat types. This supports the notion that *P. tithonus* is a generalist butterfly typically found in habitats such as meadows, grassy hedgerows and woodland margins (Asher *et al.,* 2001). It could be implied that those species that do not differ in population density among habitats are truly generalist, doing equally well in all occupied habitats.

The broad habitat classification of post-industrial sites has proven to support high density, populations of *P. aegeria* (Figure 2.3). This was also the habitat for which the greatest variation of observed densities for this species was observed, suggesting varying suitability among sites. Given the relatively high densities observed at these sites, it would be of conservation value to investigate whether they also host high density populations of specialist butterfly species that are of greater conservation concern. Post-industrial sites are known to be particularly important sources of suitable habitat for the nationally rare *Pyrgus malvae* , grizzled skipper butterfly*,* (Ellis, 2006) which thrives in sparsely vegetated habitats (Worcestershire Biodiversity Action Plan, 2008). Eyre *et al.* (2003) assessed the importance of brown-field (post-industrial and urban) sites to beetles in a conservation context, and concluded that these sites help maintain populations of rare species in an urban landscape. They found that site drainage and vegetation cover were the most important habitat characteristics dictating the distribution of ground and rove beetle assemblages. In an increasingly urbanised environment post-industrial sites are an important conservation resource (Box, 1999; Eyre *et al.,* 2003; Warren *et al.,* 2007), the true value of which is not yet appreciated. This perspective is in conflict with the government's current position statement on concentrating development on brownfield sites in order to reduce pressure on greenfield land (www.environment-agency.gov.uk). It would be advisable to assess planning proposals on brownfield sites on a case by case basis in order to protect species and habitats within them.

P. aegeria and A. hyperantus persist at significantly higher mean population densities in mixed woodland sites than broadleaved woodland sites (Figure 2.3). This suggests that heterogeneity in a woodland environment is favourable for persistence of high density butterfly populations, and is consistent with findings by Thomas *et al.* (2001) who found that habitat heterogeneity resulted in greater population stability in 35 species of British butterfly. The occurrence of stable populations of the four study species in a wide range of broad habitat types, outside of those traditionally described as ideal, is encouraging from a conservation perspective. It suggests that a reasonable level of habitat heterogeneity is being maintained within broad habitat types enabling the persistence of populations of butterfly species traditionally associated with other habitat types. The relative importance of these populations to the persistence of the species at the meta-population scale is an area of potential further study. A study into the inter-annual stability of populations across a range of habitat types, and the factors that affect stability of populations, would also benefit our understanding of population dynamics at local and regional scales.

Due to the limited number of sites classified by UKBMS as holding 'increasing' populations that met study criteria (5 sites with known transect lengths, known habitat classifications and with at least 4 consecutive years of data with an r^2 value of >0.5) it was not possible to calculate a value of r for each habitat class as with density values. Instead, a general estimate of *r* was calculated for each of the study species. Best estimates of *r* demonstrated a high degree of uncertainty. This is not surprising, since estimates of *r* were derived with data from natural populations which, are inherently subject to a variable environment (Pollard, 1988). It is well documented that butterflies, in particular, are vulnerable to environmental change and stress, with populations fluctuating in accordance with yearly environmental conditions (Pollard, 1991). This sensitivity is, in part, what makes butterflies such valuable indicators of environmental change (Hill *et al.,* 2001; Woods *et al.,* 2008). A more certain estimate of *r* may have been attained had data from optimal habitats alone been selected. However, since this analysis will be used to parameterise habitat suitability grids representing a broad range of occupied habitats, differing in their relative optimality, it is more ecologically accurate to obtain a best estimate of *r* which was representative of population growth throughout the entire range of the species under study.

Of course, *r* is not only dependent on habitat type, but is influenced by many interacting biotic and abiotic factors associated with a butterfly's environment. These may include climate, distribution of habitat patches, habitat connectivity, heterogeneity in landscape, isolation of habitat patch, and land use practices including the use of agrochemicals (herbicides and pesticides) within and neighbouring a habitat patch. Rundolf and Smith (2006) found that organic farming (characterised by the prohibition of insecticides and inorganic fertilisers [agrochemicals] - ECC regulation 2092/91) and habitat heterogeneity significantly increased butterfly abundance. But that the benefits of organic farming on butterfly abundance were only apparent in homogeneous landscapes as a pose to heterogeneous landscapes. This suggests that habitat heterogeneity within an inorganic farming landscape is enough to buffer against the negative effects of agrochemical use on butterfly numbers. The use of insecticides directly effects the survival of larval and adult butterflies (Davis *et al.,* 1991), whilst the use of herbicides indirectly effects survival and fecundity via its impact on the availability of larval host and adult nectar plants (Rundolf and Smith, 2006). Such factors may have been in play at or neighbouring UKBMS sites and so may have had a bearing on butterfly numbers observed. If the study were to be repeated, it would be useful to investigate management practices at individual UKBMS sites and test for effects of management practices on relative butterfly abundance.

Results from this study are in accordance with past empirical studies that have documented variation in intrinsic rates of increase. Baguette and Schtickzelle (2003) found that growth rate differed across a network of habitat patches; six estimates of growth rate for *Boloria aquilionaris*, the cranberry fritillary butterfly, showed large variations between sites indicating demographic asynchrony. This high degree of uncertainty in estimates of growth rate is also likely to be caused, in some part, by declining growth rates with time. Pollard *et al.* (1996) found that annual growth rates of newly colonised populations of *P. aegeria* declined significantly over time after a period of strong growth following initial establishment. It is highly probable that declining growth rates with time are the consequence of density dependent effects as populations approach a carrying capacity set by the availability of necessary resources (Pollard *et al.,* 1996). Alternatively, rates of mortality may be increasing in response to greater pressure from predators and parasitoids that have located the populations some years after the initial colonisation event, an alternative explanation which may be density-dependent or independent.

The UKBMS dataset is a valuable asset documenting butterfly abundance and distribution across the UK. Whilst recording methodologies are standardised, and butterfly counts only undertaken when conditions are suitable for butterflies (see methods section 2.2.1), there is likely to be individual recorder bias as a result of variation in expertise and survey effort. In addition, some species are inherently more conspicuous than others, for example the marbled white versus the ringlet butterfly, and thus more or less likely to be observed by a recorder. The same is true of open and closed habitats such as grassland versus woodland; individuals occupying more closed habitats like woodland are less likely to be observed and may exhibit a more patchy distribution within an occupied habitat. This may have led to under-estimation of populations persisting in closed habitat types. This bias is always going to be an issue when comparing relative abundance of animals, varying in their degree of conspicuousness, in different habitat types but could be addressed in some part by increasing survey effort (e.g. time spent surveying, number of surveyors) for those species less likely to be observed and in closed habitats.

If responses of different species to climate and habitat change are to be predicted accurately we must first ensure that parameterisation of predictive models is accurate and representative of natural populations. Past research concerned with spatially explicit, dynamic population demographic models using butterfly species (Hill *et al.,* 2001; Willis *et al.,* 2009a), have assumed that species occupy all suitable habitat at the same density. This analysis has demonstrated that for three out of the four species studied this is not true. To improve the predictive power of dynamic population models and better assess the potential of habitats for population persistence, it is thus necessary to incorporate different maximum densities for each of the habitat types occupied by any given species. Density analysis performed here will be used to inform the formation of habitat suitability grids consisting of multiple, broad habitat types, exhibiting a range of carrying capacities (mean density in suitable habitat), for each of the four study species. Estimates of growth rate in natural populations are scarce (Baguette and Schtickzelle, 2003) and this study, along with others who have tackled this subject (Underwood, 2007), have found a high degree of variation both within and between habitat patches and populations. It would be beneficial to the field of dynamic species distribution modelling and population dynamics to investigate both variation in intrinsic growth rates and other associated demographic parameters in butterfly populations further, particularly in the face of the ever changing landscapes in which species find themselves (Ockinger and Smith, 2006; McPherson and Jetz, 2007; Turner *et al.,* 2009). This will enable more accurate predictive models to be produced which will allow us to better understand the resilience of populations under environmental change. These predictions can then be used to target conservation of the most vulnerable species and habitats and inform management plans of the future.

Chapter 3

Modelling range shifts in British butterflies incorporating climate, habitat suitability and demographic parameters

Abstract

Background: Species distributions are highly sensitive to changing climate and habitat suitability, with range shifting behaviour affected by a combination of the two. The ability of a species to respond to changes in its environment relate to life-history traits, habitat requirements and original distribution extent. The ability of climatic and habitat factors predict the current distributions of four study species was investigated. Following on from Chapter 2, I used species specific demographic parameters, habitat and climate suitability grids to inform a spatially explicit, grid-based, and mechanistic dynamic species distribution model.

Methods: Recent spread was simulated using spatial dispersal models across a gridded landscape of Great Britain according to (1) habitat (2) climate and (3) no environmental limits to spread. Models were seeded with historical (1940-1970) distribution data from the Centre for Ecology and Hydrology (CEH) and Butterfly Conservation (BC). Habitat suitability grids were generated using the CEH Landcover Map 2000 dataset and climate suitability grids were generated using the CRU TS 3.1 dataset. The benefit of including sub-optimal habitats in habitat suitability grids for *Melanargia galathea* and *Pararge aegeria* was tested. Models were run between 1970 and 2009 and outputs compared with present day distribution data (2005-2010) compiled by CEH and BC using the true-skills statistic (TSS). Potential future spread was simulated using best fitting models for *Pyronia tithonus and M. galathea*.

Results: Present day distributions were accurately predicted for habitat models (maximum TSS>0.64) and climate models (maximum TSS>0.59). Model simulations run on grid (3) resulted in poor model outcomes and over-simulation of species current range extent. Alternative habitat grid simulations for *M. galathea* and *P. aegeria* showed that best model fit was achieved when simulating spread using habitat grids including sub-optimal habitats. Future simulations suggest that *M. galathea* and *P. tithonus* will expand their range by 15.3% and 7.8% respectively under present day habitat suitability between 2009 and 2060.

Conclusions: Both habitat and climate play a role in observed present day distributions of the four study species. In contrast to habitat only models, model fit was reduced for climate only models as a result of over-simulation, suggesting species currently lag behind suitable climate space. Results suggest inclusion of sub-optimal habitats as a means of dispersal between optimal habitats improves model predictions.

3.1 Introduction

Species distributions are highly sensitive, and inextricably linked, to changing climate (Huntley *et al.,* 1995; Dell *et al.,* 2005; Brook *et al.,* 2009; Zurell, 2009) and habitat suitability (Willis *et al.,* 2009b), with range shifting behaviour affected by a combination of the two (Warren *et al.,* 2001; Fox *et al.,* 2008). Shifts in species distributions are becoming apparent across a range of taxa (Parmesan and Yohe, 2003; Walther *et al.,* 2002; Parmesan, 2006; Sparks *et al.,* 2007). In some butterflies, a distributional shift polewards and to higher elevations has been observed to have occurred as a result of recent climatic warming (Hughes, 2000; Hill *et al.,* 2002; Hickling *et al.,* 2006). Despite this, there is growing concern that these observed shifts are still lagging behind climate with species unable to track suitable climates (Warren *et al.,* 2001; Braschler and Hill, 2007; Willis *et al.,* 2009b; Wilson *et al.,* 2010; Devictor *et al.,*2012).This lag is likely to be in part a consequence of the expected natural lag between climate and habitat suitability; as climates change habitats also adjust and change, developing new climax communities, under new climatic regimes (Hill *et al.,* 2001; Willis *et al.,* 2009b; Wilson *et al.,* 2010). But this natural lag is likely to have been exacerbated by anthropogenic barriers to colonisation, including destruction of habitats, agricultural intensification (Milsom *et al.,* 2000) and construction of large urban settlements (Willis *et al.,* 2009b) leading to fragmentation of suitable habitat. The ability of species to track climate through an increasingly urbanised landscape is of concern to conservation policy makers (Wilson *et al.,* 2010). Disentangling the effects of climate and habitat on species movements is central to understanding this aspect of species ecology.

The ability of any given species to respond to environmental change is largely governed by their life-history traits, habitat requirements and original distribution extent (Gonzalez-Megias *et al.,* 2008). Mathematical modelling aims to capture these factors numerically with the aim of generating predictive simulations. Today, modelling is used as an increasingly important tool in ecological research, particularly in the context of global change biology (Guisan and Thuiller, 2005; Keith *et al.,* 2008; Zurell, 2009). The distributions of numerous organisms have been modelled in the context of climate (Hill *et al.,* 2001; Peterson *et al.,* 2002; Pearson and Dawson, 2003; Keith *et al.,* 2008) and habitat suitability (Schwartz *et al.,* 2001; Milson, *et al.,* 2000; Willis *et al.,* 2009a). Researchers are increasingly recognising the importance of integrating models simulating species responses to climate change and habitat availability with species specific population dynamics and demographics (Keith *et al.,* 2008; Brook *et al.,* 2009; Willis *et al.,* 2009a; Midgeley *et al.,* 2010). Such model approaches have highlighted the importance of recognising complex, dynamic interactions between a species and their environment when modelling species responses to global change (Keith *et al.,* 2008).

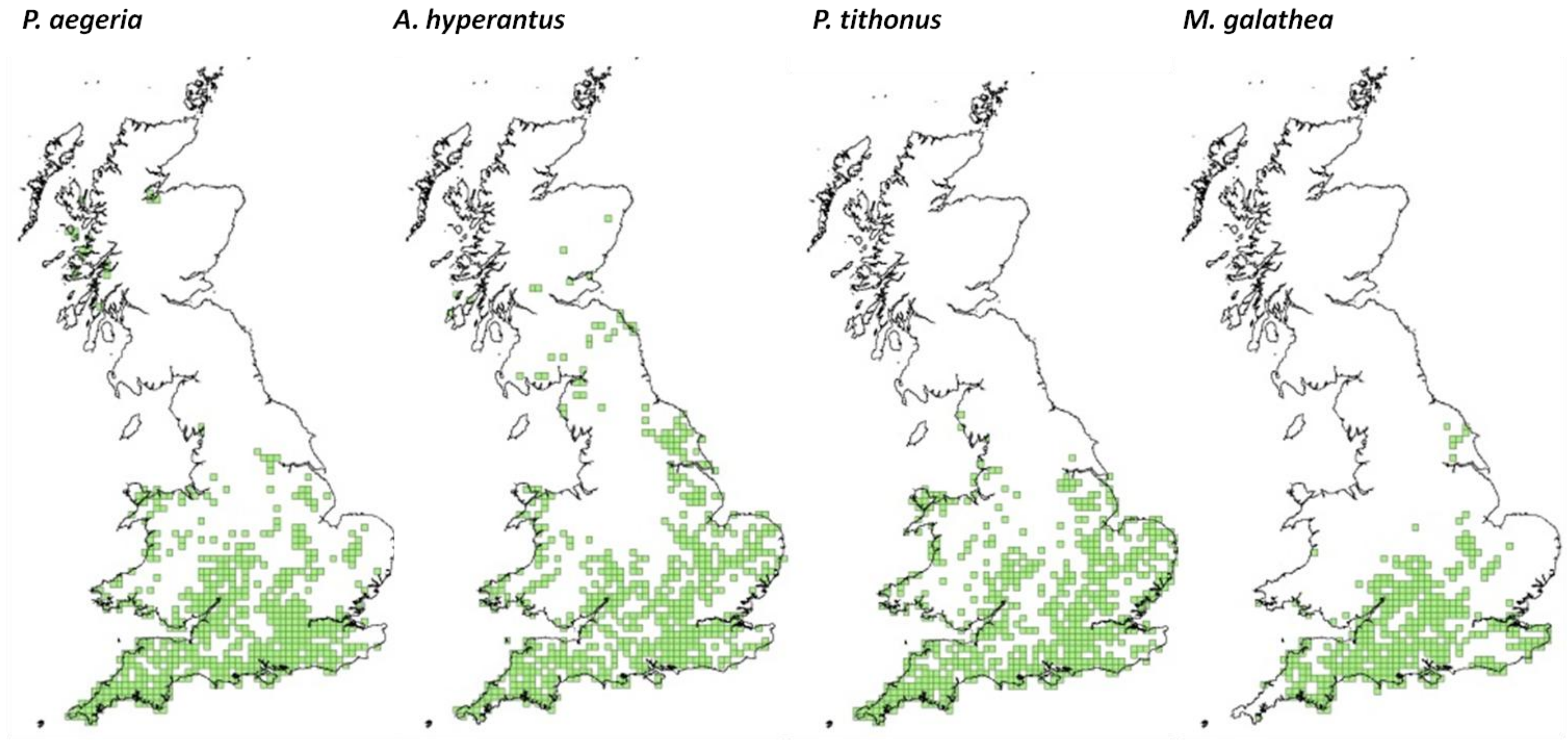
Range shifting behaviour of generalist butterflies in Britain is well documented (Parmesan *et al.,* 1999; Hill *et al.,* 2002; Braschler and Hill, 2007), and studies have been undertaken to model such changes in relation to habitat (Willis *et al.,* 2009a) and climate (Hill *et al.,* 2001). Few studies however, have examined the relative effects of both climate and habitat on species distributions (Pearson *et al.,* 2004). In this chapter I aim to systematically assess the relative importance of both climate and habitat on accurately predicting the extent of present-day ranges of four generalist butterfly species native to Britain. Building on research conducted in Chapter 2, this chapter aims to enhance the ecological validity of previous modelling approaches by more accurately representing population dynamics within the model framework. To achieve this, habitat specific maximum densities for those species known to occupy multiple suitable habitats will be incorporated into the model framework. When modelling range shifting behaviour previous modelling approaches have assumed equal carrying capacity across all suitable habitats within a species range (Hill *et al.,* 2001; Willis *et al.,* 2009a). This is often not truly representative of natural populations of generalist butterflies which are known to occupy, and persist in, multiple habitats of variable quality (Thomas, 1984; Asher *et al.,* 2001; Thomas *et al.,* 2001; Oliver *et al.,* 2010) at different population densities (Thomas, 1984). Assuming equal population density across a species' range will most likely result in erroneous predictions with regards to rate and extent of spread. So, to attempt to improve the predictive power of dynamic species population models and gain better understanding of species responses to climate and habitat change it is important to accurately represent natural population dynamics.

I will simulate range shifting behaviour of four generalist species using a spatially explicit, population-dynamic, species distribution model, taking into account variable population densities across all occupied habitats. Models will be seeded with historical distribution data and range changes simulated between 1970 and 2009. Model outputs will then be compared with present day (2010) distributions and the ability of the model to simulate recent distributional shifts of the study species assessed. Models will be parameterised with species specific demographic parameters (see Chapter 2 section 2.3) derived from observed field data obtained through collaboration with the UK Butterfly Monitoring Scheme (UKBMS). These parameters will include demographic traits specific to the modelled species, including intrinsic rate of increase and carrying capacity in occupied habitats, habitat suitability grids incorporating knowledge of variable population density in different occupied habitats and species specific climate suitability grids. I will evaluate, in turn, how well both climatic and habitat factors predict the current distributions of four study species resident to Britain; *Pararge aegeria (*speckled wood)*, Aphantopus hyperantus* (ringlet), *Pyronia tithonus* (gatekeeper) and *Melanargia galathea* (marbled white). I will also run models using an entirely suitable grid of Great Britain (i.e. no limits to spread) to evaluate the relative impacts of climate and habitat on restricting current species ranges. It is expected that the utilisation of all of these parameters in one model will enable more realistic and individualistic models of spread to be generated. This increase in the ecological validity of dynamic, species population modelling will enable us to identify how well species will fare under projected climate and habitat changes in the coming decades enabling specific and targeted conservation efforts that will be effective both at present and in the future.

3.2 Methods

3.2.1 Study species and distribution data

The four study species have been described previously in Chapter 2 (section 2.2). The models were initiated based on known distributions of each of the four butterfly species across Great Britain from 1940-1970. Historical and present day distribution data for each of the species was in the form of presence/absence data and obtained at the 10 km grid resolution from the Centre for Ecology and Hydrology (CEH) Biological Records Centre and Butterfly Conservation. To allow for incomplete recording in the historical dataset all records from 1940-1970 were assumed to represent the extent of the initial distribution in 1970 (following Willis et al., 2009a). Models were seeded using the historical distribution presence records at a 10km scale (Figure 3.1); three 1km grid cells within the 10km presence grid cell were chosen at random and seeded with 10 butterflies for model initiation.



P. aegeria *A. hyperantus* *P. tithonus* *M. galathea*

Figure 3.1: $10km^2$ 1970 seed cells for the four study species complied CEH Records Centre and Butterfly Conservation.

3.2.2 Colonisation model

This study utilised a spatially explicit, grid-based, population dynamic colonisation model coded in C (Georgina Palmer, unpublished). It incorporates a range of species specific biological parameters, along with habitat suitability grids (generated using Centre for Ecology and Hydrology landcover map 2000 data - see section 3.2.2) to produce simulations of species range expansion at a landscape scale. The environment is represented by a grid of 1km cells covering the area of Great Britain. Each cell has an associated maximum density, expressed as the number of individuals a cell can support. This is computed using the percentage of a cell covered by suitable area along with the maximum density of the study species in suitable habitats as computed using UKBMS data in Chapter 2. Final estimates of maximum density, ρ (Equation 3.1), for each species in each of their occupied habitats were calculated using Equation 3.1.

$$\rho = \sum_h p_h \rho_h \qquad \text{(Equation 3.1)}$$

where = ρ is the density of adult butterflies, h = habitat type, P_h = proportion of cell that is habitat type h, and ρ_h density in a cell of habitat type *h.*

One time step of the colonisation model represents one year (a full breeding cycle). Each time step the number of individuals in a cell is calculated as a function of current number of individuals in a cell, the probability that those individuals will breed, the number of eggs per breeding female and the probability of offspring survival. Each year surviving offspring disperse in accordance with cell specific carrying capacities and a dispersal function concerned with the probability an individual will disperse and the maximum dispersal distance of any given individual (see section 3.2.3 for further details). Dispersers will move into the adjacent cell with the highest proportion of suitable area, or chose randomly between cells of equal suitability. This directional movement is justified by research by Conradt *et al.* (2000) who found that when the Satyrid butterfly, *Maniola jurtina,* was released in non-suitable habitat a short distance from suitable habitat, they orientated their movement towards suitable habitat. When released a long distance from suitable habitat in non-suitable habitat they used a systematic search strategy to locate suitable habitat. If no suitable habitat is available in neighbouring cells, dispersers will move again into adjacent cells in line with the dispersal kernel up to a maximum number of dispersal steps (Figure 3.4; section 3.2.3).

3.2.3 Parameterisation of the colonisation model

Habitat Data

Suitable habitat, for each individual species, was determined following analysis of UKBMS transect data detailing occurrence of butterflies in classified habitats (based on EUNIS codes – European Nature Information System; Davies *et al.,* 2004) across Great Britain (refer to Chapter 2 section 2.2 for further details). Habitat types input into the model were compiled using data obtained from the Centre for Ecology and Hydrology (CEH) Land Cover Map 2000 (LCM2000) dataset. LCM2000 is a thematic classification of spectral data recorded by satellite images (Fuller *et al.,* 2002a). This dataset classifies land under fewer habitat descriptions than the EUNIS code used to describe the UKBMS transect survey sites. As such, some level of discretion was used when choosing suitable habitat classes for the formation of habitat suitability grids from the LCM2000 dataset. Habitat subclasses, rather than aggregate classes, were used in this study as they best represent the habitat types used to classify UKBMS transects. Those subclasses which best represent suitable habitat for each of the four study species were combined using ArcGRID to form habitat suitability grids for Great Britain, at a 1km grid scale, for input into the colonisation model. The subclasses used in the formation of habitat suitability grids for each of the four study species are outlined in Table 3.1. Each 1km grid cell has an associated value between 0-1 representing the proportion of suitability of that cell. A cell with a suitability value of 0 indicates that a cell is entirely unsuitable, whilst a value of 1 indicates that a cell is entirely suitable.

Following on from Chapter 2, each suitable habitat type used in the formation of species specific habitat suitability grids had an associated habitat specific carrying capacity (Table 3.1). In this way habitats that are not traditionally described as suitable or are of poor suitability for a given species, but that were occupied by a small number of butterflies, are included but allocated lower carrying capacity values. This allows species to move along corridors of poor habitat to reach more suitable habitat and makes for a much more realistic ecological model. Habitat suitability grids, taking into account variable carrying capacity in different occupied habitats for each of the four study species are shown in Figure 3.2.

Table 3.1: UKBMS habitat classifications and equivalent CEH LCM2000 landcover types (Fuller *et al.,* 2002a) used in the formation of habitat suitability grids for the four species. Estimates of density of adult butterflies (individuals per hectare) in each habitat classification are shown along with species specific values of intrinsic rate of increase as calculated in the Chapter 2 analysis.

Species	**UKBMS Habitat Classification**	**LCM2000 Subclass**	**Density (ind. per km^2)**	**r**
Pararge aegeria	Dry semi/unimproved flower-rich chalk/limestone grassland	Calcareous grassland	42	0.31
	Seasonally wet and wet marshy grasslands	Fen swamp marsh	42	
	Mature broadleaved woodland	Broad-leaved / mixed woodland	92	
	Mature mixed broadleaved and coniferous woodland	Broad-leaved / mixed woodland	92	
	Wet and dry heathland/dry heather moorland	Open/dense dwarf shrub heath	42	
Aphantopus hyperantus	Dry semi/unimproved flower-rich chalk/limestone grassland	Calcareous grassland	127	0.28
	Mature broadleaved woodland	Broad-leaved / mixed woodland	244	
	Mature mixed broadleaved and coniferous woodland	Broad-leaved / mixed woodland	244	
Pryronia tithonus	Dry semi/unimproved flower-rich chalk/limestone grassland	Calcareous grassland	123	0.32
	Mature broadleaved woodland	Broad-leaved / mixed woodland	123	
	Mature mixed broadleaved and coniferous woodland	Broad-leaved / mixed woodland	123	
Melanargia galathea	Dry semi/unimproved flower-rich chalk/limestone grassland	Calcareous grassland	213	0.26
	Dry semi/unimproved flower-rich neutral grassland	Neutral grassland	129	
	Seasonally wet and wet marshy grasslands	Fen swamp marsh	25	
	Mature broadleaved woodland	Broad-leaved / mixed woodland	25	
	Mature mixed broadleaved and coniferous woodland	Broad-leaved / mixed woodland	25	

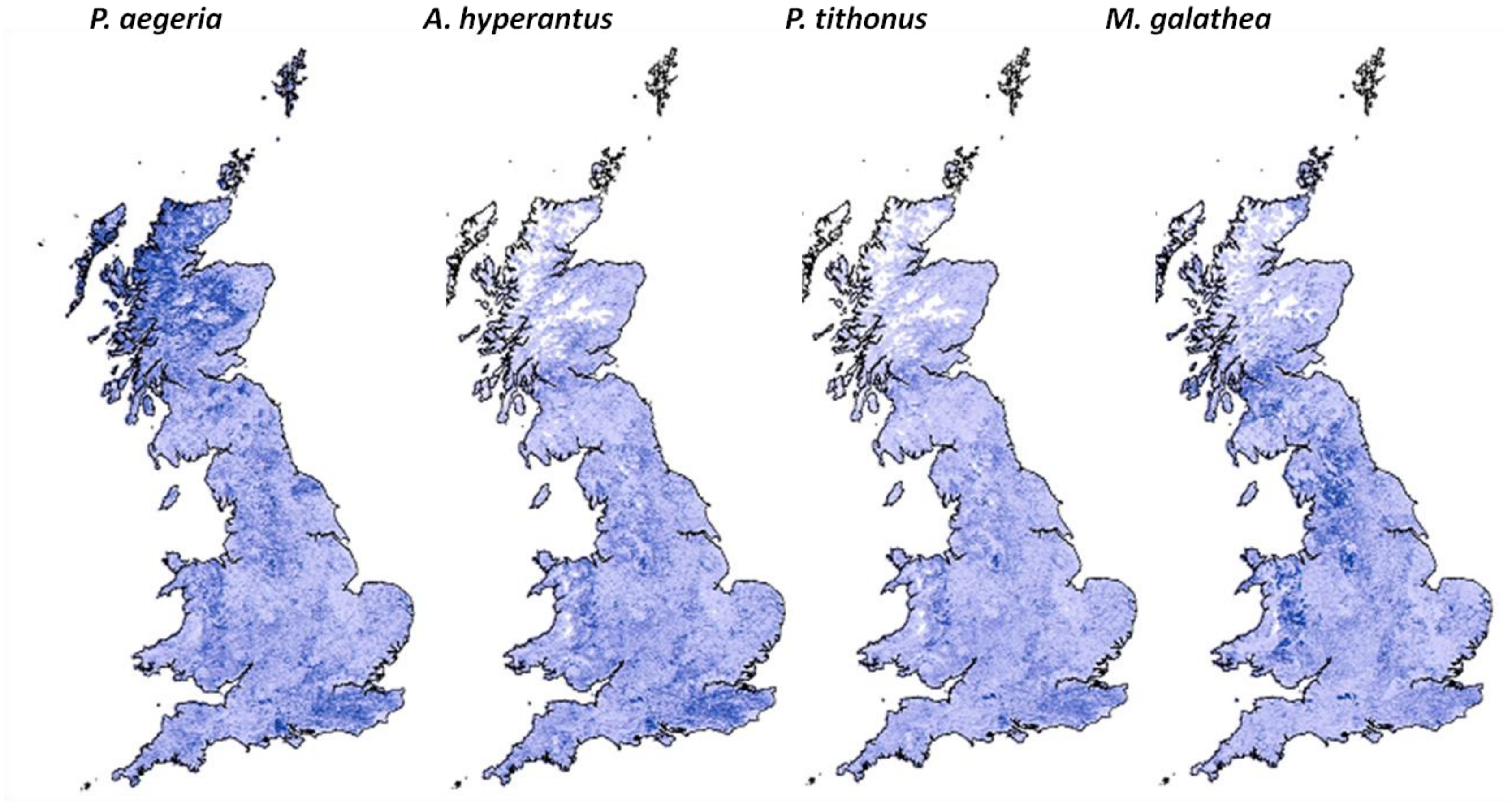


Figure 3.2: Species specific habitat suitability grids for each of the four study species used for input into the dynamic distribution model. Darker areas indicate areas of higher suitability.

Bioclimatic Data

Climate suitability, for each of the four study species, was mapped for Great Britain at the 10km grid square resolution between years 1970-2009. Climate response surface (CRS) models were used to generate climate suitability grids. Climate response surfaces represent the relationship between observed species distributions and the climatic variables you are interested in. They utilise gridded presence/absence data (describing the distribution of any given species) along with gridded data pertaining to a chosen set of climatic variables, in order to generate a probability response surface. The resultant response surface, fitted by locally-weighted regression (Cleveland and Devlin, 1988; Huntley *et al.,* 1995), details where in climate space (as defined by your chosen climatic variables) you would predict a species to occur with associated probabilities (Huntley *et al.,* 1995).

Climate response surface models were fit at a 10km grid square resolution to British distributions for the four study species. Response surfaces were fit with respect to three biologically appropriate climatic response variables; the temperature sum above a 5°C threshold, GDD5, mean temperature in the coldest month, MTCO, and an estimate of the ratio between actual to potential evapotranspiration, AET/PET (Huntley *et al.,* 1995), data for which was extracted from the CRU TS 3.1 dataset.

Each cell of the resultant climate suitability grids was assigned a value between 0-1. These values reflect the suitability of the climate in a given cell for a given species and the probability a given species would be observed in that cell given the three climatic variables used to generate the CRS. Figure 3.3 gives an example of the resultant species specific climate suitability grids that were input into the climate model runs. They demonstrate how climate suitability can vary both between species and years (1976 and 1977). 1976 was a drought year for Great Britain and climate suitability for species preferring cooler, damp conditions, such as *A. hyperantus*, was reduced in southern areas, but increased in northern areas relative to 1977, a year more typical of Great Britain's annual climate.

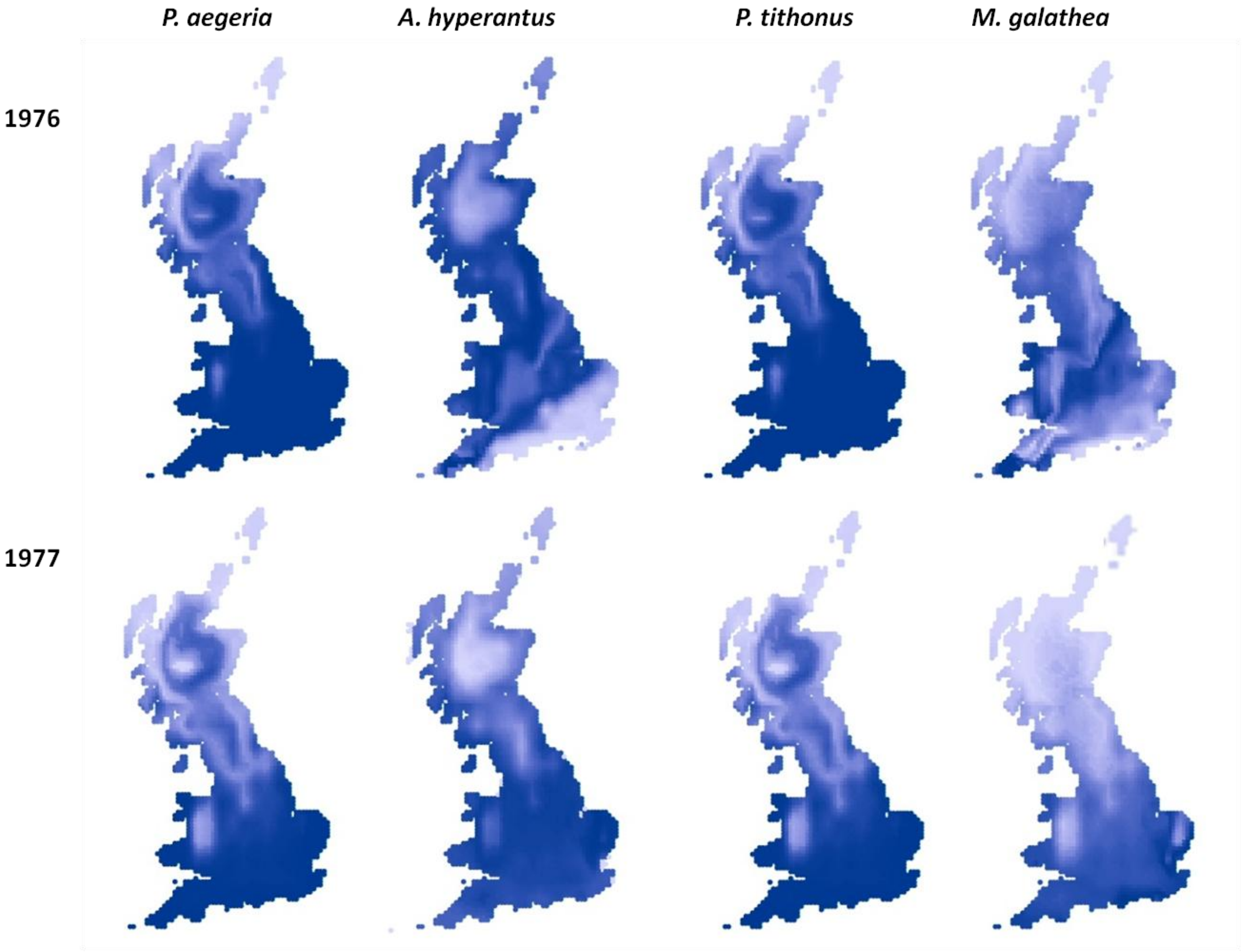


Figure 3.3: Examples of climate suitability grids in years 1976 and 1977 for the four study species. Darker areas indicate areas of higher suitability.

Demographic parameters

Characterisation of model parameters was achieved using annual butterfly abundance data from readily available field data from UKBMS transects, at survey sites located throughout a species range (refer to Chapter 2, section 2.2 for further details). Intrinsic rate of increase and species and habitat specific mean densities are shown in Table 3.1. Mean density of butterflies under variable climates was not estimated in this study and so the mean density used for models run under climate suitability grids was set to the highest mean density observed in those habitats used in the formation of the habitat suitability grids, for example 92 per hectare for *P. aegeria* and 244 per hectare for *A. hyperantus* (Table 3.1). Mean density for models run in unconstrained environment (i.e. the landscape is entirely suitable) was also set to the maximum observed mean density in occupied habitats. This approach was taken as it is likely that a habitat supporting the highest observed mean density of individuals is most representative of densities that might be observed in an unconstrained environment. It was assumed that all females get the chance to breed, so the probability of breeding was set to 1 for all model runs. *A. hyperantus, P. tithonus and M. galathea* all develop through one generation per year whilst *P. aegeria* typically develops through 1.5 to 2 generations per year (Hill *et al.,* 2001). However, generations in *P. aegeria* are not discrete and parameter values for carrying capacity and intrinsic rate of increase were calculated on an annual basis (Chapter 2, methods sections 2.2.3 and 2.2.4). As such it was appropriate to set the model time step to one year for all studied species. This was achieved by setting the probability of adult survival for all four species to 0.

Dispersal

Previous research has utilised dispersal data from Hill *et al.* (1996) when modelling the range shifts in generalist butterflies (Hill *et al.* 2001; Willis *et al.,* 2009b). The study by Hill *et al.* (1996) investigated the dispersal ability of specialist Hesperiid butterfly, *Hesperia comma,* and although studies utilising these dispersal data had relative success, it is likely that the dispersal ability of generalist butterflies can be better represented. It is well documented that dispersal ability of generalist butterflies surpasses that of more geographically restricted specialist butterflies. In order to better gauge the dispersal ability of the study species, a thorough literature search of dispersal ability in butterflies was undertaken, focusing on members of the family Nyphalidae and subfamily Satyrida, the family to which the four species under investigation are from. In a meta-analysis of dispersal in butterflies Stevens *et al.* (2010) found high heterogeneity in dispersal data across studies both at the inter and intra-specific levels. Many studies reported variable dispersal ability even between populations of the same species; Gilbert and Singer (1973) reported variable movement patterns of adult *Euphydryas* *editha* butterflies at both local and regional scales. They also found that probability of movement varied inter-annually from 0.129 to 0.514.

Since individualistic dispersal data was not available for each of the study species and very little is known about the dispersal ability of butterflies at a species-specific level, the effects of varying the probability of dispersal on model fit were tested. To achieve this, a dispersal kernel that was flexible with regards to probability of dispersal was used and all models were tested under a progression of dispersal probabilities from 0.0 to 1.0 at intervals of 0.2 (Figure 3.4). It has been noted that estimates of maximum dispersal distance are particularly difficult to gauge accurately and generally biased by the distance over which respective studies have taken place (Gilbert and Singer, 1973). Auckland *et al.* (2004) recorded a long-distance dispersal event in *Parnassius clodius* male of 12km. Baguette (2003) reported dispersal distances much larger than previously reported for butteflies. From 1995-1997 he recorded long-distance dispersal movements of the Nymphalid butterfly, *Boloria aquilonaris,* from 0.5 to 13.5km with an average of 5.9km. In view of the literature maximum dispersal distance was set at 10km for all species; 10km is large enough to allow for long distance dispersal to occur in line with the probability of dispersal, and not so large as to produce unrealistic predictions. The number of butterflies that disperse this distance is directly related to the probability of dispersal input into model as shown in Figure 3.4. Note that when probability of dispersal is set to zero, individuals will still move if the maximum density of a cell is reached.

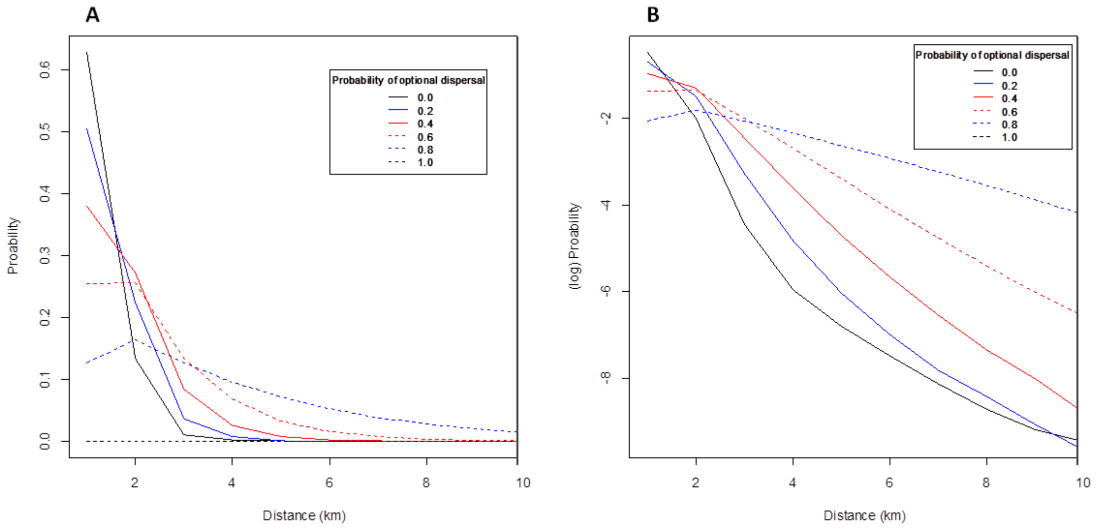
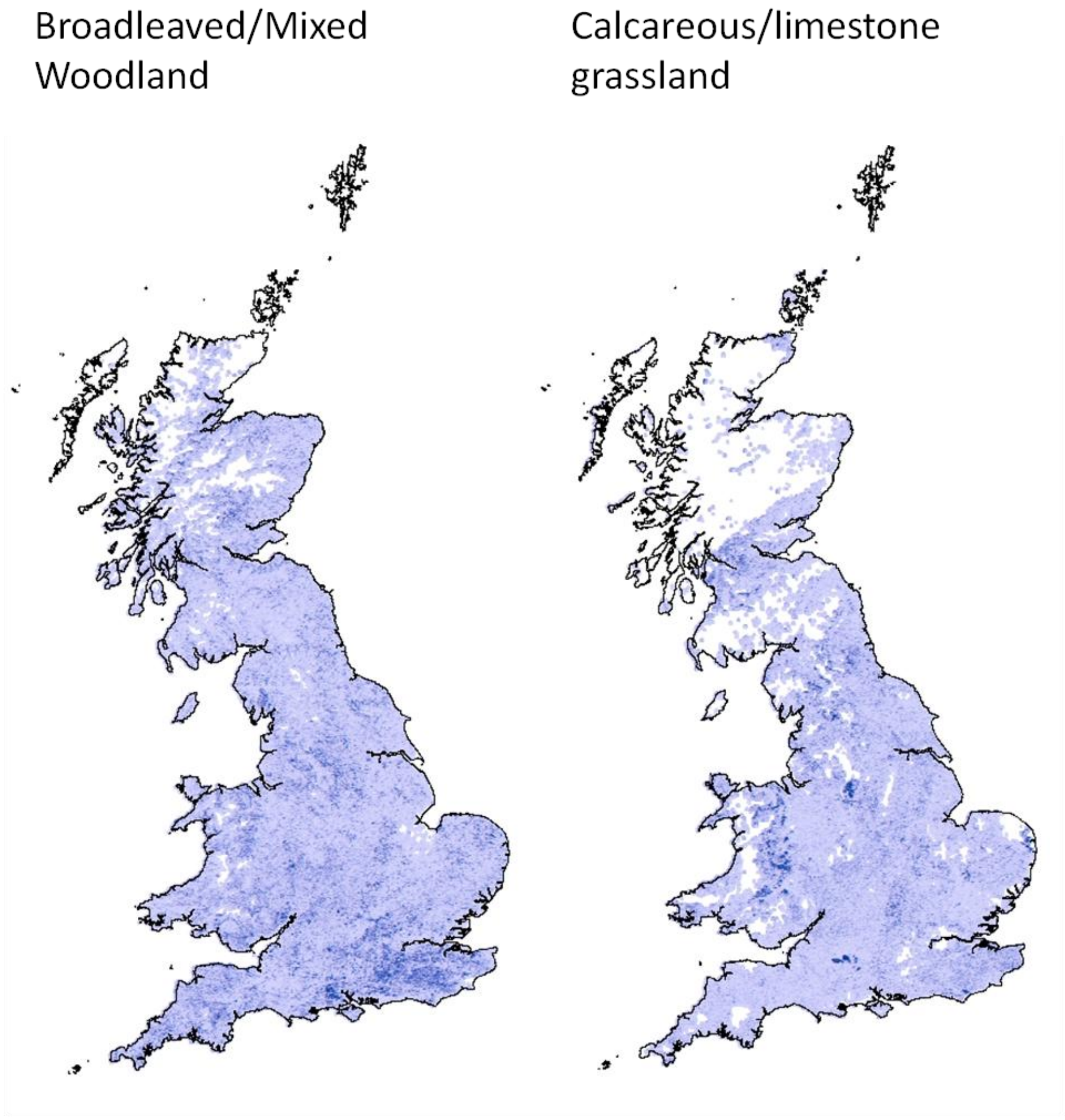


Figure 3.4: Butterfly dispersal kernel under variable probability of dispersal. Panel B shows probability densities at log scale. Optional dispersal refers to the ability for the modeller to manipulate the probability of dispersal input into the model.

3.2.4 Model simulations

Firstly, recent spread of species were simulated using spatial dispersal models across a gridded landscape of Great Britain, where cell suitability is modified between 0-1 according to (1) habitat suitability, (2) climate suitability or (3) all cells are given an equal suitability of unity. Herein models run on habitat suitability grids will be referred to as habitat only models, models run on climate suitability grids will be referred to as climate only models and models run on an entirely suitable grid with no limits to spread will be referred to as unconstrained models. Since climate suitability data were only available up to and including 2009, all model simulations were run between 1970 and 2009. Secondly, two of the best fitting habitat only models, *P. tithonus* and *M. galathea,* were chosen spread for these two species into the future to 2060 was simulated. These models did not consider any potential habitat change over the next 50 years and were only capable of simulating future spread under present-day habitat suitability. These models are herein referred to as 'future simulations'. A fourth suitability grid, combing both habitat and climate suitability, was generated for *P. tithonus,* which had no significant difference in carrying capacity across habitats (Chapter 2, section 2.3.1). Thirdly, models for *P. tithonus* were simulated on a combined habitat and climate suitability grid from 1970 to 2009. This model is herein referred to as the combined habitat and climate model.

Both *P. aegeria* and *M. galathea* occur most commonly in a single habitat type. *Pararge aegeria* is primarily a woodland butterfly (Hill *et al.,* 2001; Willis *et al.,* 2009a) whilst *M. galathea* thrives on calcareous grassland where its larval host plants are abundant (Asher *et al.,* 2001; Willis *et al.,* 2009b). Both occur in other sub-optimal habitats (Chapter 2, Figure 2.1). To assess the relative importance of including sub-optimal habitats in predictive models of spread for these two species, I ran models on habitat suitability grids representative of optimal habitat only (Figure 3.5) and assessed the impact on subsequent goodness of fit. Optimal habitat grid for *P. aegeria* comprised CEH landcover subclass ‘broadleaved/mixed woodland’. Optimal habitat grid for *M. galathea* comprised the ‘calcareous/limestone grassland’ subclass.



Broadleaved/Mixed Woodland

Calcareous/limestone grassland

Figure 3.5: Alternative habitat suitability grids for *P. aegeria* (mature broadleaved and mixed woodland) and *M. galathea* (calcareous/limestone grassland), representative of optimal habitats only.

3.2.5 Assessing model performance

Each model outcome was validated by examining how well it simulated recorded spread between 1970 and 2009. Model outputs were compared with present day distribution data compiled by the CEH Records Centre and Butterfly Conservation for the period 2005-2010 (Figure 3.6). Goodness of fit between observed and simulated species distributions was determined at a 10km grid scale, following presence-absence model predictions, using the true skills statistic (TSS; Allouche *et al.,* 2006) following methods detailed in Allouche *et al.* (2006). In order to avoid artificially inflating assessment of model fit, 1970 seed cells were removed from model outputs before generating a value for TSS. TSS was used preferentially over the kappa statistic, a popular measure of goodness of fit for models generating presence absence predictions, because TSS is independent of prevalence (Allouche *et al.,* 2006). Since each of the four study species varies in prevalence, it was appropriate to use a test which accounted for this. TSS ranges from +1 to -1 where +1 indicates perfect agreement with present day presence-absence distribution data, whilst any result ≤0 indicates random model performance.

In order to assess whether these models are subject to stochasticity 100 habitat only model replicates were run for *P. tithonus* at probability of dispersal 0.8. Both species and probability of dispersal were chosen at random. Habitat only model replicates were run in favour of climate only or unconstrained models as habitat only models took the least amount of time to run. Resultant TSS values were compared to assess the amount of variation in TSS values among model outputs. Mean TSS after 100 replicates was 0.862 with a minimum value of 0.857 and a maximum value of 0.866 (Appendix Table A12). Since variation in TSS across 100 replicates was < 0.01, 10 replicate runs for each model was deemed sufficient to represent any stochasticity among simulations.

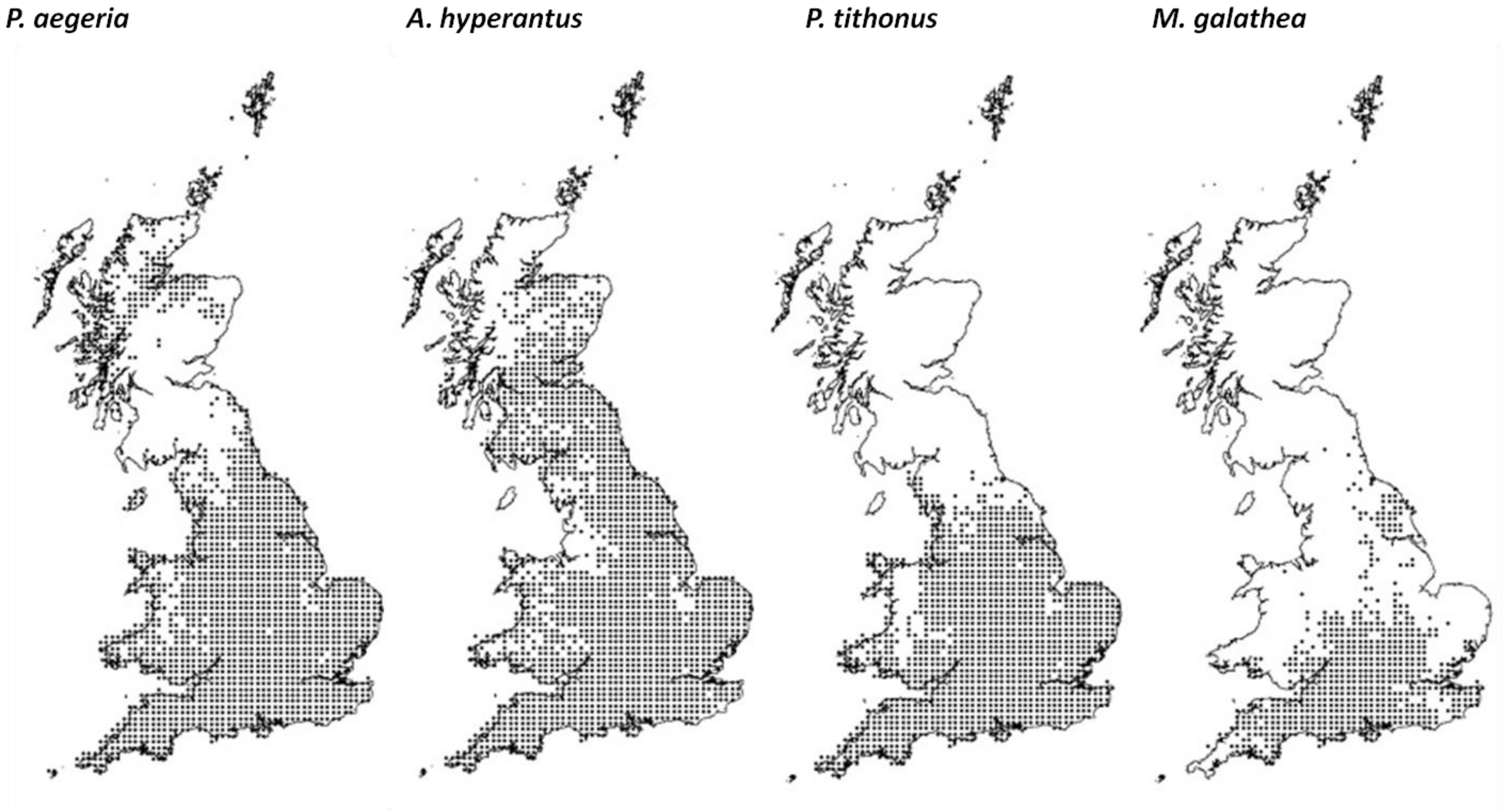


Figure 3.6: Present day distribution of the four study species at a 10km scale. Data compiled by CEH Records Centre and Butterfly Conservation for the period 2005-2010.

3.3 Results

3.3.1 Simulating 1970-2009 spread

Simulated range extent of four study species for habitat only, climate only and unconstrained models are depicted in Figure 3.7 (*P. aegeria*), 3.8 (*A. hyperantus*), 3.9 (*P. tithonus*) and 3.10 (*M. galathea*). Corresponding TSS goodness of fit measures are shown along with observed distributions of the respective species in 1970 and 2010. TSS goodness of fit values for model replicates are shown in appendix tables A6-A8. Note that TSS goodness of fit scores may appear equal for models that have resulted in either over or under simulation (that may appear markedly different in terms of final simulated distribution) since scores are derived from the number of incorrectly assigned grid cells.

Pararge aegeria

Simulated occurrence of *P. aegeria* under both climate and habitat suitability between 1970 and 2009 was accurately predicted by the model (Figure 3.7). There was limited variation in TSS values between comparable habitat only and climate only models (maximum difference in TSS 0.04). TSS goodness of fit for climate only models declined with increased probability of dispersal between 0.6 and 1.0 as a result of over-simulation of *P. aegeria* into cells outside of its observed range (Figure 3.7). Simulated spread in an unconstrained environment produced reasonable goodness of fit when probability of dispersal was set between 0.0 and 0.4 (TSS 0.62 to 0.59 respectively). When probability of dispersal was increased beyond 0.4 TSS values were substantially reduced as a result of over-simulation.

Aphantopus hyperantus

Present day distribution of *A. hyperantus* was most accurately simulated at probability of dispersal 0.8 using a model considering only habitat availability (TSS 0.66; Figure 3.8) whereby 86% of grid cells were correctly assigned. Over-simulation occurred for climate only models as probability of dispersal was increased (Figure 3.8). Unconstrained models produced poorer fitting models than either habitat and climate suitability models due to over-simulation (Figure 3.8).

Pyronia tithonus

Present day distribution of *P. tithonus* was simulated equally well for both habitat only and climate only models but at different probabilities of dispersal (Figure 3.9). Simulated present day distribution of *P. tithonus* for both habitat only and climate only models produced the best fitting models out of all four study species (TSS > 0.79 corresponding to >89% of grid cells correctly assigned). Simulated model fit under climate suitability produced well fitting models with model fit declining as probability of dispersal was increased (Figure 3.9). The reduction in model fit with increasing probability of dispersal is the result of over-simulation north of the present day distribution of *P. tithonus.* Even at high probabilities of dispersal, simulated fit in an unconstrained environment was highly accurate (mean TSS after 10 runs 0.84-0.71 probability of dispersal 0.0 to 1.0 respectively; Figure 3.9). This suggests *P. tithonus* is currently able to keep track of both suitable climate and habitat. Simulating spread of *P. tithonus* under a combined habitat and climate suitability grid had very little effect on mean TSS fit values after 10 replicates (Table 3.2). TSS values under combined habitat and climate suitability were most similar to climate simulations with TSS fit values declining with increasing probability of dispersal (Table 3.2; Figure 3.9).

Table 3.2: Mean TSS values after 10 replicates (Appendix Table A9) for *P. tithonus* for habitat, climate and combined habitat and climate suitability models.

	Probability of Dispersal					
Suitability Grid	0.0	0.2	0.4	0.6	0.8	1.0
Habitat	0.84	0.85	0.85	0.86	0.86	0.86
Climate	0.86	0.85	0.85	0.84	0.81	0.79
Habitat and Climate	0.85	0.85	0.85	0.84	0.82	0.78

Melanargia galathea

Present day distribution of *M. galathea* was most accurately simulated using habitat only models and at low probabilities of dispersal (mean TSS 0.78 corresponding to 89% grid cells correctly assigned; Figure 3.10). Model fit was reduced for climate only models and further still for unconstrained models (Figure 3.10). The reduced model fit in both cases was the result of over-simulation, particularly in the Welsh part of this species range, although model fit TSS values were still reasonably accurate (TSS ≥ 0.64; Figure 3.10). Under all alternative suitability grids (habitat, climate and unconstrained) model fit was greatest at low probabilities of dispersal (0.0-0.2).

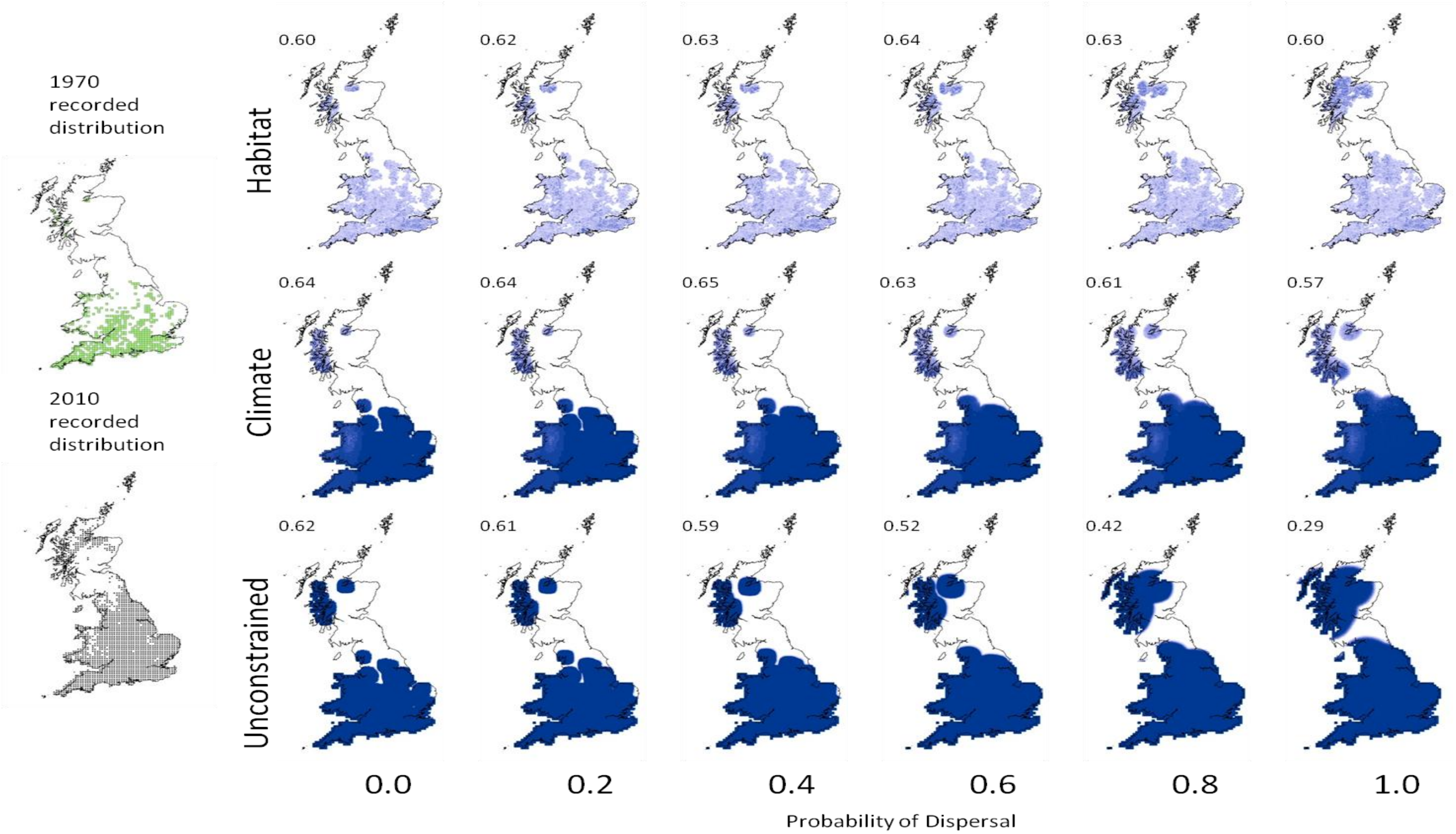


Figure 3.7: Simulated spread between 1970 and 2009 for *P. aegeria* for habitat only, climate only and unconstrained models with associated mean TSS values after 10 model replicates (top left of respective maps) under variable probability of dispersal. Darker shades indicate higher simulated density of butterflies. Recorded distributions in 1970 (representing records from 1940-1970) and 2010 (representing records from 2005-2010) at the 10km grid scale are also shown for comparative purposes (CEH Records Centre and Butterfly Conservation).

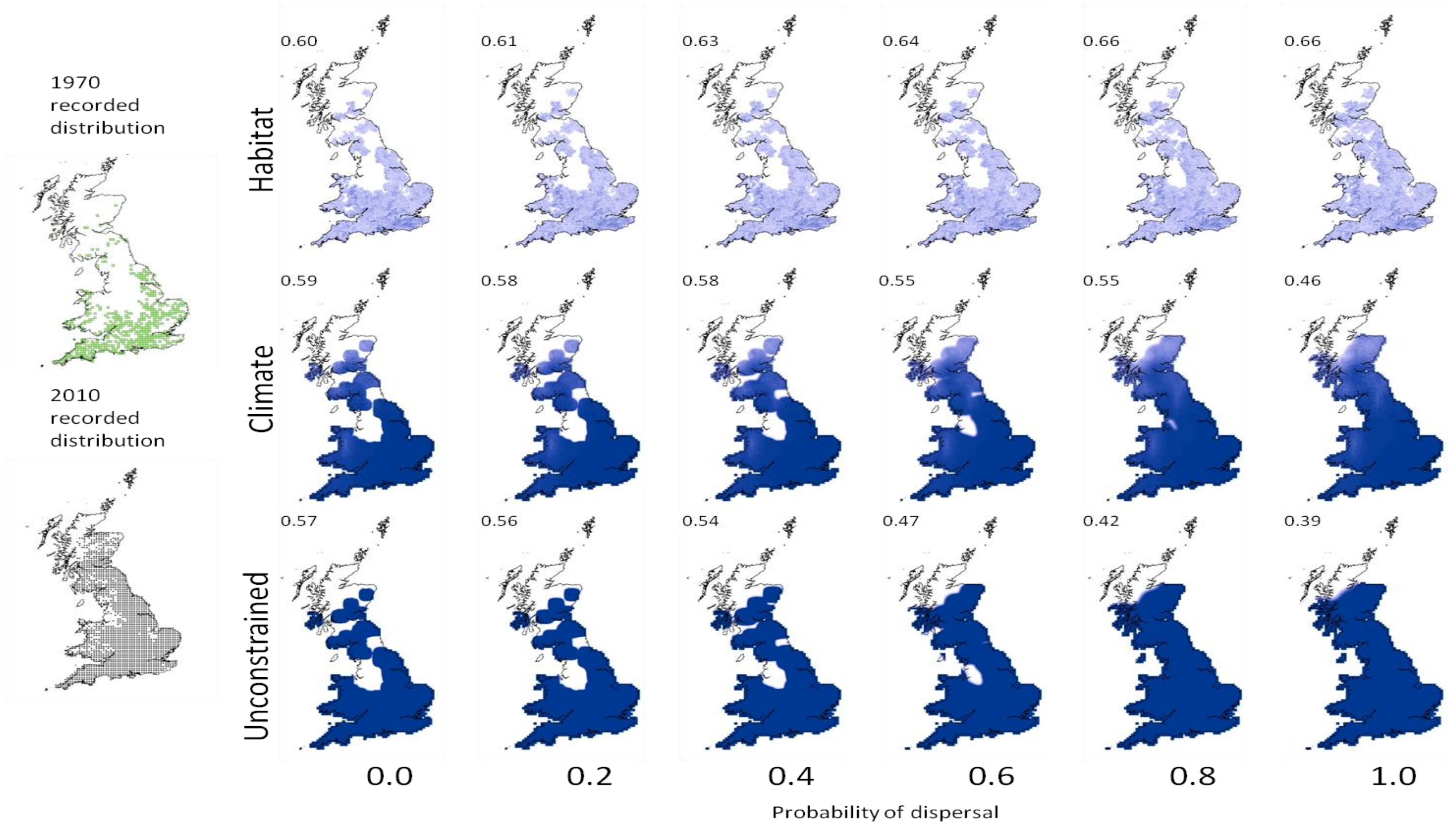


Figure 3.8: Simulated spread between 1970 and 2009 for *A. hyperantus* for habitat only, climate only and unconstrained models with associated mean TSS values after 10 model replicates (top left of respective maps) under variable probability of dispersal. Darker shades indicate higher simulated density of butterflies. Recorded distributions in 1970 (representing records from 1940-1970) and 2010 (representing records from 2005-2010) at the 10km grid scale are also shown for comparative purposes (CEH Records Centre and Butterfly Conservation).

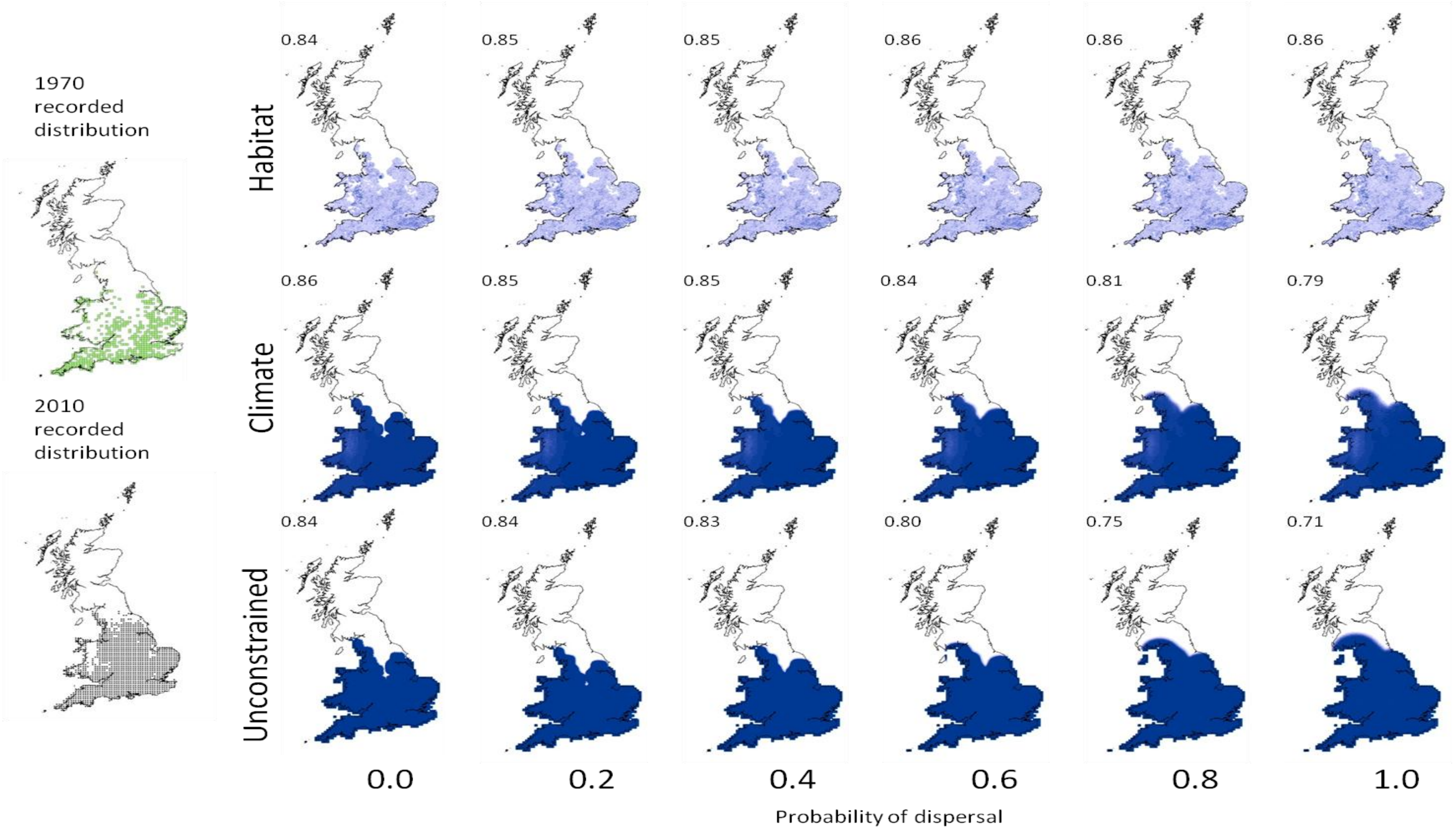


Figure 3.9: Simulated spread between 1970 and 2009 for *P. tithonus* for habitat only, climate only and unconstrained models with associated mean TSS values after 10 model replicates (top left of respective maps) under variable probability of dispersal. Darker shades indicate higher simulated density of butterflies. Recorded distributions in 1970 (representing records from 1940-1970) and 2010 (representing records from 2005-2010) at the 10km grid scale are also shown for comparative purposes (CEH Records Centre and Butterfly Conservation).

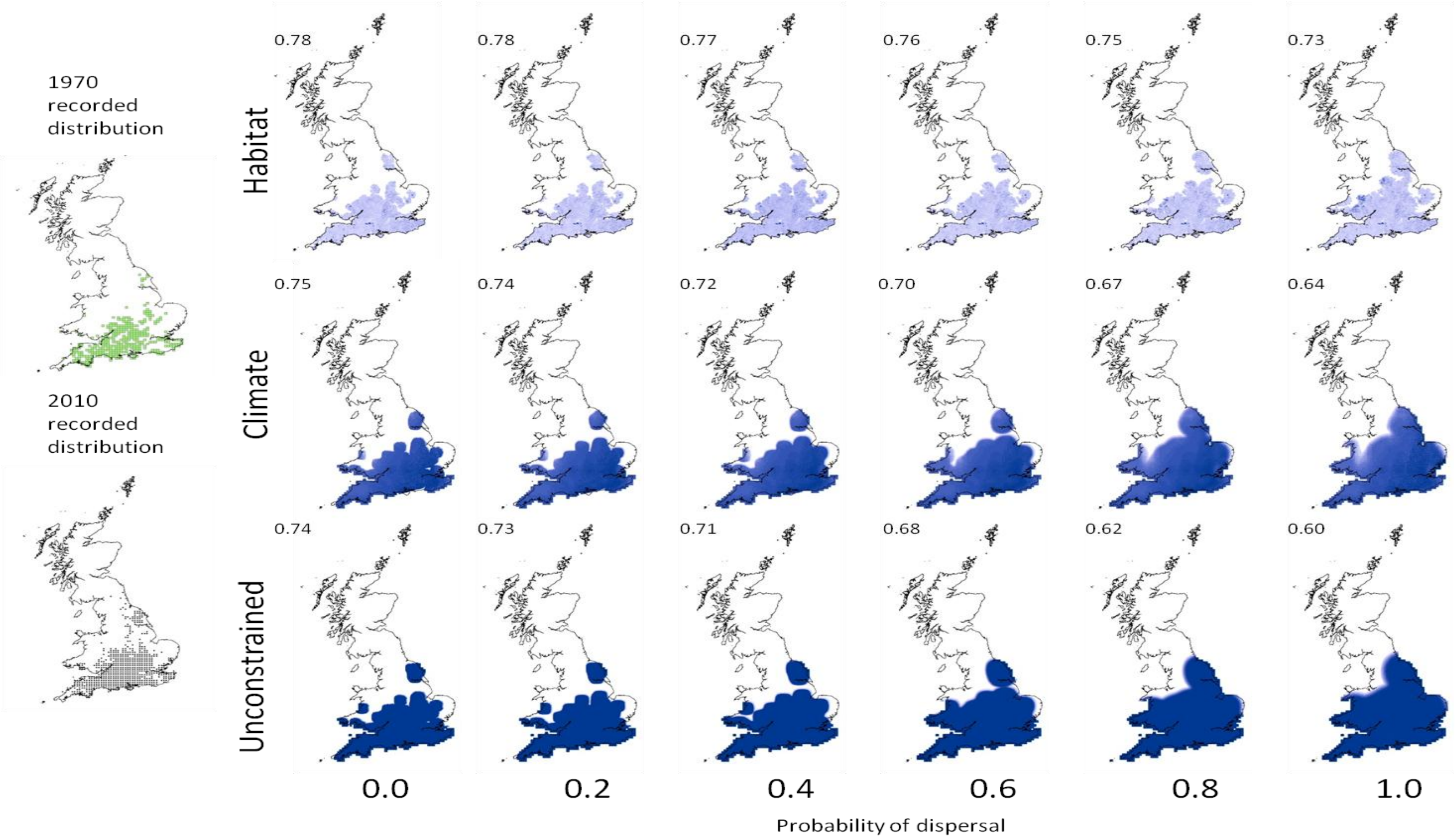


Figure 3.10: Simulated spread between 1970 and 2009 for *M. galathea* for habitat only, climate only and unconstrained models with associated mean TSS values after 10 model replicates (top left of respective maps) under variable probability of dispersal. Darker shades indicate higher simulated density of butterflies. Recorded distributions in 1970 (representing records from 1940-1970) and 2010 (representing records from 2005-2010) at the 10km grid scale are also shown for comparative purposes (CEH Records Centre and Butterfly Conservation).

3.3.2 Alternative habitat grid simulations for *P. aegeria* and *M. galathea*

Alternative model simulations for *P. aegeria* and *M. galathea,* incorporating habitat grids composed only of broadleaved/mixed woodland and calcareous/limestone grassland respectively, were run to assess the decision to include less suitable habitats, with lower maximum carrying capacities, in habitat suitability grids for default habitat model runs. Mean TSS values after 10 runs at each probability of dispersal are shown in Figure 3.11 and 3.12 (*P. aegeria* and *M. galathea* respectively; Appendix Tables A10-11).

Alternating between default and broadleaved/mixed woodland habitat grids had very little impact on overall TSS model fit values (Figure 3.11) for *P. aegeria*. Best fitting model simulations for *P. aegeria* were produced under the default habitat grid (Table 3.1; maximum mean TSS 0.64). When comparing the observed present day distribution of *P. aegeria* (Figure 3.5) with the spread depicted in Figure 3.11 it is clear that *P. aegeria* fails to spread throughout its occupied range in northern Scotland under the woodland grid. The default grid, particularly at mid to high probabilities of dispersal, does a far better job of predicting this spread (Figure 3.11), spread that may not be appreciated if TSS values alone were considered. Alternating between default and calcareous grassland habitat grids had very little impact on overall TSS model fit values (Figure 3.12) when simulating the spread of *M. galathea* between 1970 and 2009. As with *P. aegeria,* best model fit was achieved when simulating spread using the default habitat grid (Table 3.1; maximum mean TSS 0.78).

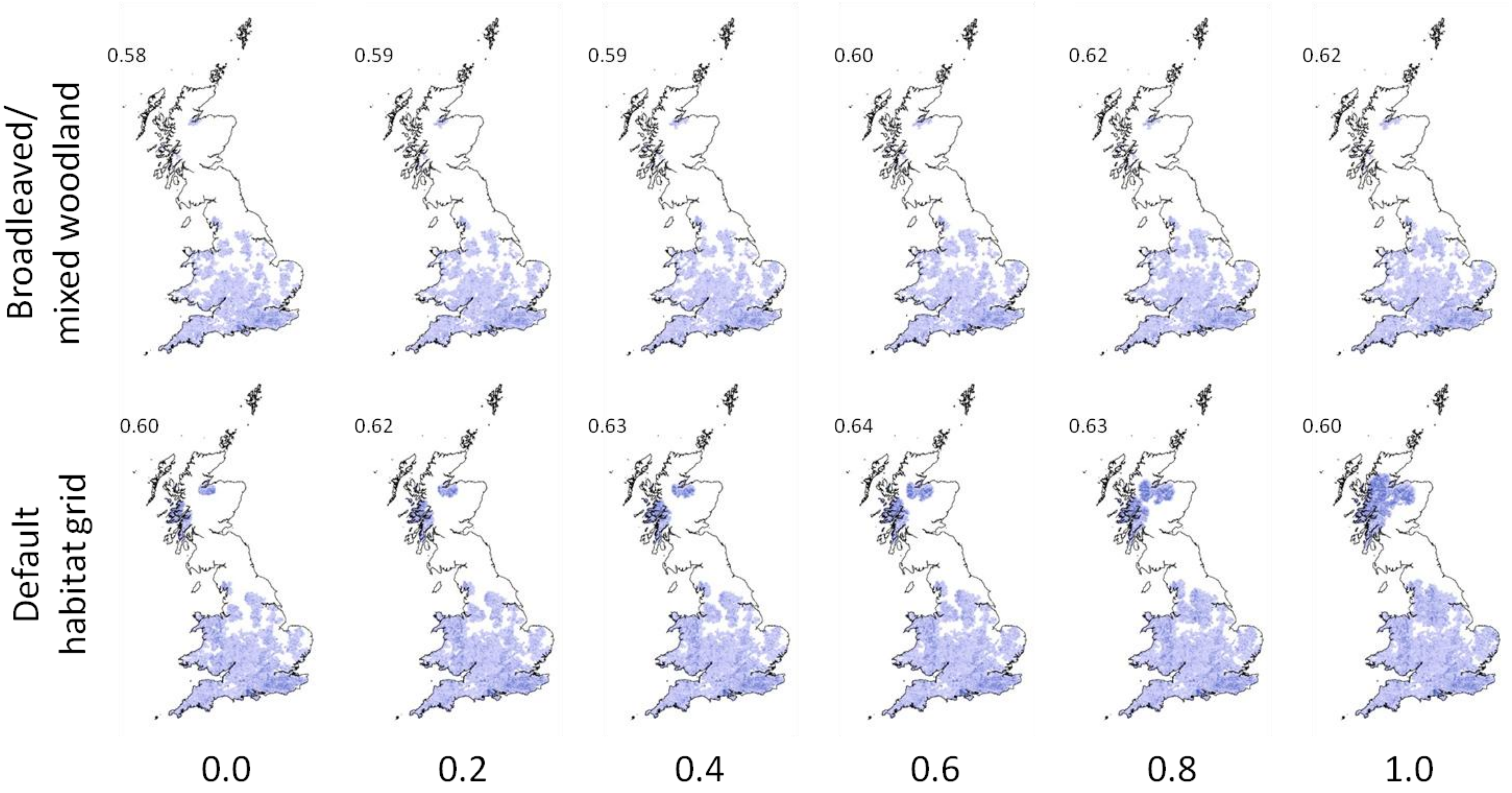


Figure 3.11: Comparison of mean TSS values (top left of respective maps) after 10 runs at variable probabilities of dispersal for *P. aegeria* under two habitat suitability grids, broadleaved/mixed woodland and all suitable habitats (Table 3.1).

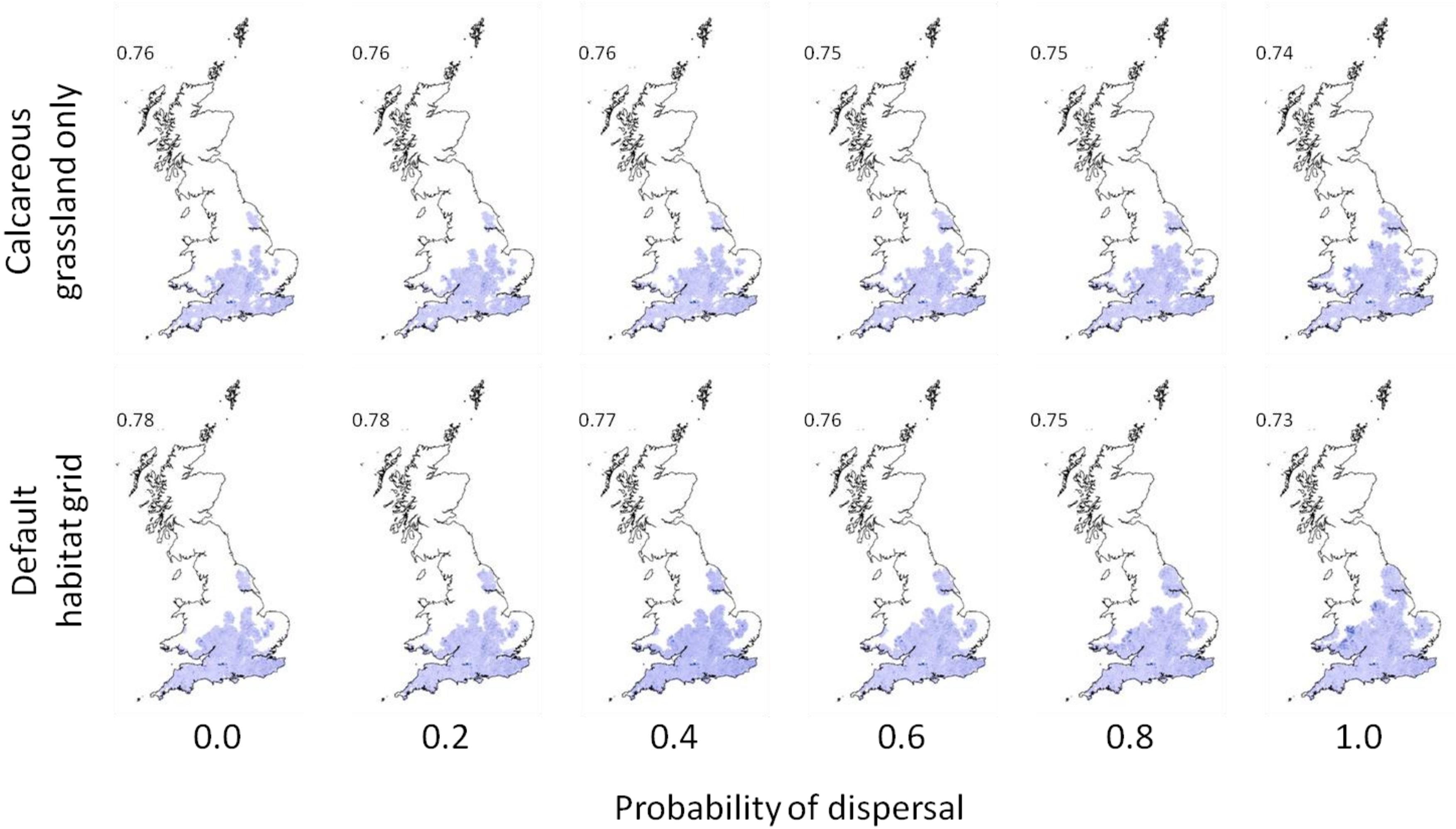


Figure 3.12: Comparison of mean TSS values (top left of respective maps) after 10 runs at variable probabilities of dispersal for *M. galathea* under two habitat suitability grids, calcareous grassland only and all suitable habitats (Table 3.1).

3.3.3 Future simulations

Habitat only model runs for *P. tithonus* and *M. galathea* produced the best model fit values (Figures 3.9 and 3.10 respectively) out of the four study species. I took the probability of dispersal that produced the best model fit (0.8 and 0.0 respectively) and ran these models for 90 years from 1970 to 2060.

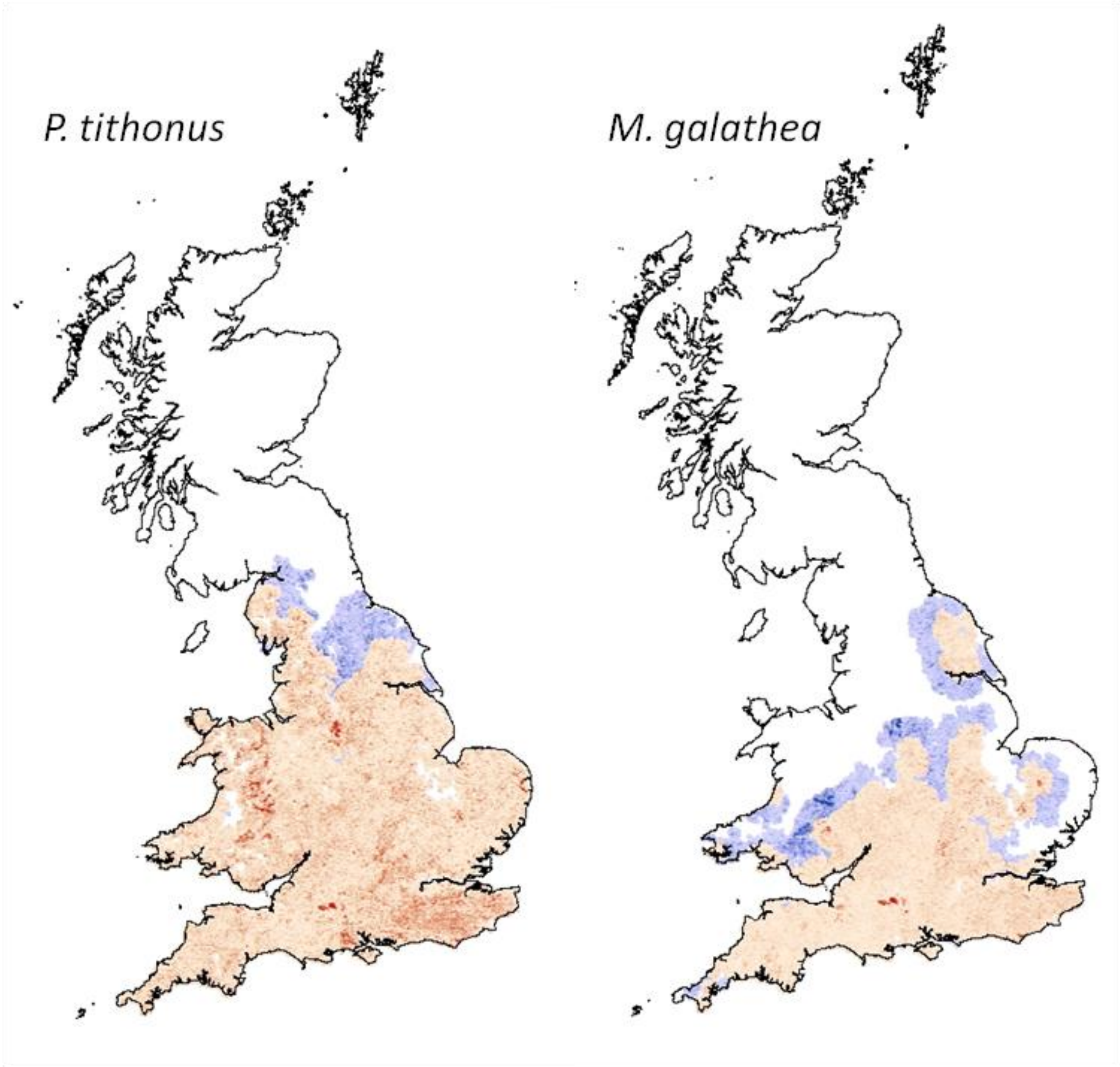


Figure 3.13: Final extent of simulated distribution of *P. tithonus* and *M. galathea* under present day habitat suitability at in from 1970-2009 (red) and 1970-2060 (blue).

Assuming habitat availability remains constant between the present day and 2060, model outcomes predict that the extent of *P. tithonus* will increase by 17928 1km squares (mean after 10 runs) corresponding to a 7.8% increase in range extent. It predicts that expansion will occur in Yorkshire, Humberside, County Durham, Cumbria and into NW Scotland (Figure 3.13). Future simulations for *M. galathea* suggest that this species will expand by 17674 1km squares (mean after 10 runs) corresponding to a 15.3% increase in range extent from 2009 to 2060 under present day habitat suitability. Model simulations suggest this species will expand further into East Anglia in the East and South Wales in the West. It also suggests that in the future populations currently occurring in isolation in Yorkshire and Humberside will expand to potentially join up with the southern population (Figure 3.13).

3.4 Discussion

This chapter has considered the importance of both macroclimatic and broad scale habitat characteristics in determining present day distribution patterns of four generalist butterflies resident in Great Britain. The present day distributions of these species were accurately predicted for habitat only models (maximum TSS>0.64) and climate only models (maximum TSS>0.59). Unconstrained models all resulted in over-simulation of species ranges, suggesting that these species are limited by both habitat and climate. There was very little variation in TSS values between habitat only and climate only models across these species (Figures 3.7 to 3.10), with only a slight variation in fit apparent between probabilities of dispersal. For all species model fit was reduced for climate only models as probability of dispersal was increased. This reduction in model fit was the result of over-simulation, i.e. the modelled species was simulated to occur in cells outside of its present day range. The fact that over-simulation did not occur to the same extent in habitat suitability models suggests that there is currently more suitable climate space available to these species than suitable habitat. This is in accordance with current research which suggests that many British butterfly species currently lag behind climate change (Menendez *et al.,* 2006) and that species are failing to colonise suitable climate space due to a lack of suitable habitat. The extent of over-simulation with increasing probability of dispersal for climate only models varies between species studied, and was most pronounced for *A. hyperantus* (TSS range 0.11) and least pronounced for both *P. aegeria* and *P. tithonus* (TSS range 0.07). These variable responses are most likely to do with the species specific demographic parameters used in the model (Table 3.1). These results suggest that models considering only habitat availability, incorporating habitat specific mean densities can reliably explain the current distributions of all studied species.

Analysis of transect survey data (Chapter 2, section 2.3-2.3) demonstrated that some of the study species occurred at variable densities across occupied habitats. By incorporating habitat specific mean densities into models, where it was appropriate, model fits were increased. Actual distribution of suitable habitat, as perceived by individuals and populations, is difficult to capture accurately. Even within the same habitat classification, habitat quality will vary across its distribution in relation to management practices and relative disturbance. In addition, the distribution of a given habitat type does not necessarily represent the distribution of important larval food plants (Thomas *et al.,* 1999), which often dictate where a particular species persists. A combination of these factor will determine the ability of butterflies to persist in a given habitat patch and such dynamics are not represented in the coarse habitat suitability grids used in these model simulations. If model predictions are to be improved, research efforts need to focus on assessing variability in population sizes both between and within habitat types. This would be beneficial when making predictions about the effects of land-use change and habitat fragmentation on butterfly distribution patterns.

The LCM2000 dataset was utilised in this chapter for the creation of habitat suitability grids as this was the most recent, readily available habitat data available at the time of study. Unfortunately, this dataset does not incorporate natural variability in habitat between years in the same way that annual variability in climate suitability was captured. As such, it was assumed that habitat suitability did not vary between years both for past and future model simulations. This assumption is unlikely to be true; it is likely that habitat suitability has changed quite markedly since 1970 and will continue to change into the future especially in light of a recent demand for housing in Great Britain and subsequent urban development. Whilst many areas have and will become increasingly urbanised, with subsequent negative effects on species range expansion (Wilson *et al.,* 2009), steps have also been made to increase the quality of habitats in rural parts of Great Britain. In 1991 the Countryside Stewardship Scheme was launched by Natural England which promoted enhancement of English landscapes and wildlife. Whilst this scheme has failed to abate the general decline of butterfly species associated with agricultural landscapes, it has been successful at slowing or reversing declines of 8 UK BAP(Biodiversity Action Plan) Priority Species (Warren *et al.,* 2007). In view of this mixed success a new scheme, the Environmental Stewardship Scheme, a more dynamic and flexible approach has been put in place with the hope of maximising benefits across a wide range of species (Warren *et al.,* 2007). Availability of suitable habitat in Great Britain in the future will in part be dictated by the success and continued uptake of these policies in the face of recent governmental budget cuts to key land managers, for example Natural England has had their budget cut by 21.5% for the period 2011-2015 representing a £44.2 m reduction in spending (www.naturalengland.org - Annual report and accounts 2011-2012). In addition to this, continued pressure on the government to meet housing demands, in 2007 the government set a target of 240,000 new homes by 2016 (www.parliament.co.uk), and the associated pressure this puts on greenfield land will have unknown consequences on availability of suitable habitat for butterflies. The effect of such anthropogenic, largely social factors, are hard to quantify and represent in predictive models of future distributions and must always be considered when assessing model outcomes and using predictions to make decisions about management of ecosystems.

The LCM2000 dataset is a thematic classification of spectral data recorded by satellite images. A comparison with field data from the Countryside Survey 2000 (CS 2000) was used to assess the accuracy of classifications based on satellite images using random sampling. Results suggested that whilst the LCM 2000 dataset records target classes with around 85% success, there is variability in the successful classification of different classes (Fuller *et al.,* 2002b). Whilst 'broadleaved and mixed woodland' showed near identical distributions to that of the CS 2000 dataset, distinction between semi-natural grasslands, that is calcareous, acidic and neutral, presented difficulties. This is because these habitats present no consistent spectral characteristic with which soil acidity can be determined using satellite data. At least one type of semi-natural grassland was incorporated into habitat suitability grids of the four study species (Table 3.1; figure 3.2) and as such inaccuracies in the classification of satellite data in the LCM 2000 dataset may have resulted in over or under-simulation of modelled range extents. Close inspection of the calcareous grassland habitat suitability grid (Figure 3.5) generated for the optimal habitat only model for *M. galathea* shows that key areas of chalk and limestone geology are missing, including the North and South Downs, Mendips, Cotswolds and Dorset chalk do not feature. Such errors will be limiting to the predictive power of models and in future it may be necessary to use ground-truth (collected in field) habitat data to generate habitat suitability grids for modelled species.

The LCM2000 dataset uses fewer classes to categorise habitat types than does the EUNIS habitat classification system utilised by UKBMS when classifying habitats. As such, when generating habitat suitability grids on the basis of UKBMS transect data some discretion was used when transitioning between the two different classification systems (Table 3.1). By using the LCM2000 dataset, the resolution of habitat grids input into model simulations has been restricted in this study. Some of the habitat types in which butterflies have been observed during UKBMS transect surveys are not represented by the LCM2000 dataset and so were not represented in habitat suitability grids generated for each study species. The most notable of these is post-industrial habitats, which were shown to host reasonably large populations of *P. aegeria* (Chapter 2, Figure 2.1). With the exception of *M. galathea,* all study species occupy hedgerows, green lanes and gardens (Asher *et al.,* 2001). These habitats are particularly difficult to represent accurately using the LCM2000 dataset, even at its finest resolution. It is likely that these, typically linear, habitats are particularly important in allowing species to cross between habitat patches that are increasingly surrounded by urban and suburban development (Collinge *et al.,* 2003). UKBMS data inherently biases against and underestimates the importance of these habitats to these species; the vast majority of UKBMS sites are located within protected areas and reserve networks. This is likely to both increase the estimated observed density of animals in these habitats, as active management presumably increases habitat quality, and under-represent those important, more linear habitats associated with human settlements.

Stevens *et al.,* 2010 suggest that understanding dispersal ability, both inter and intra-specifically, is paramount if we are to that if we are to understand the ability of, and the way in which species respond to both natural and anthropogenic environmental change. In this study, variation in probability of dispersal had very little impact on overall model simulations for the majority of model runs (Figures 3.7-3.10) suggesting this variable was of little importance to the simulated distribution of study species. This is perhaps due to the fact that only generalist species, known to be able to make use of a wider range of resources within a landscape, were studied. Such an observation may not have been made if specialists, species which depend on locally distributed resources, were the subject of study. More studies are needed to investigate the relative impact of and link between dispersal ability and distribution of resources required for survival on the ability of both generalist and specialist butterflies to spread.

Dispersal, as with all species ecological traits, is subject to evolutionary selection pressures (Thomas *et al.,* 2001). The selection pressures exerted on species traits inevitably vary across a species range in response to variable environments and as such result in variation in dispersal strategies and tendencies within a species and between populations (Thomas *et al.,* 2001; Dytham*,* 2009). Long-distance dispersal, for example, is more suited to core populations than marginal populations due to the respective distribution of suitable habitats. In a simulation study, Dytham (2009) found that both population demographics and habitat quality were found to influence evolved dispersal distances at the range margin. The cost of dispersal was found to have the greatest influence on dispersal strategy (Dytham, 2009), and clearly the cost of dispersal will vary depending on the quality and availability of suitable habitat in an individual's immediate surroundings. In a controlled experiment Merckx *et al.* (2003) demonstrated how individuals of the species *P. aegeria* originating from fragmented agricultural landscapes were less likely to disperse than those originating from less fragmented woodland habitat. Merckx and Van Dyck (2006) also went on to demonstrate that variation in the flight morphology of *P. aegeria* was influenced by both landscape of genetic origin and landscape of individual development. Gilbert and Singer (1973) found that adult movement and distribution patterns of *E. editha* varied significantly among individuals and populations, both at the local and regional scale. It was concluded that this difference was at least in part genetically based. Probability of movement has also been shown to vary between sexes; Auckland *et al.* (2004) found that probability of movement between 50m by 50m plots in females was almost double movement probability of males. This may be due to differences in resource needs in males and females; females for example require additional access to larval food plants for egg-laying whilst males only require access to adult food plants. Russell and Schultz, (2009) found that adult wing size was reduced in *Pieris rapae* (the small white) when treated with herbicides as larvae, with subsequent negative effects on the adults ability to disperse. These examples demonstrate how a single estimate of dispersal probability is unrealistic in butterflies and show that factors such as sex, genetics, quality of occupied habitat and position within range extent of a species can lead to differences in dispersal estimates.

Tracking this variability in dispersal, particularly long distance dispersal, is currently a challenge for evolutionary biology and ecology (Baguette, 2003); without a good understanding of such processes at a species specific level, predicting the effect of future and current change on patterns of species distribution will be difficult to do with confidence. Recent innovations in this field are improving our understanding of dispersal capacity in butterflies. Several recent studies have utilised harmonic radar to track butterfly movements (Cant *et al.,* 2005; Ovaskainen *et al.,* 2008). This enables movement distances and butterfly flight paths to be directly assessed using a signal emitted by radar. This approach removes the inherent bias of indirect mark-release-recapture experiments (Cant *et al.,* 2005), that are often restricted to a logistically reasonable study area. In the future, dynamic species population models would do well to include regional dispersal data. Such data collection is becoming more realistic in light of these recent radar studies.

There are several other factors other than habitat and climate that cause natural fluctuations in butterfly abundance and influence the success of populations in any given year. Such factors are difficult to parameterise and have not been represented within the modelling framework used in this study. The abundance of enemies such as predators and parasites can have measurable, typically short-term, effects on the relative abundance of butterfly populations across a species range (Dennis and Sparks, 2007). Predators of British butterflies include, but are not restricted to, birds, spiders, ants, wasps, dragonflies, reptiles such as adders, and amphibians such as the common toad and common frog. Butterflies are vulnerable to these predators at multiple stages in their lifecycle, for example as eggs, larva, during pupation and emergence and whilst basking. In the great "wasp year" of 1935, parasitism of larval broods of *Aglais urticae* (small tortoiseshell) and *Inachis io,* (European peacock butterfly) by the parasitoid wasp *Hyposoter horticola* in Great Britain caused dramatic declines in larvae populations and subsequent adult emergence (Beirne, 1955). Data assessing the long-term impact of such acute events on butterfly populations is lacking and are thus potential sources of error where not represented in predictive models.

The extent to which agrochemicals, such as insecticides, herbicides, fungicides and fertilisers, are used in the British landscape has changed markedly since the advent of agricultural intensification post-war. Increasingly mechanised intensive farming practices since 1945 have led to a 50% reduction in hedgerow stock (Robinson and Sutherland, 2002) in order to increase field size and allow access of heavy machinery (Longley and Sotherton, 1997). This coupled with an increase in the number and extent of agrochemicals used on farms along with an intolerance of non-crop species has led to widespread declines in farmland taxa with around a third of insects and half of plants experiencing declines (Robinson and Sutherland, 2002). These changes in agricultural practice have resulted in a decline in the abundance and distribution of butterflies thought to be the result of direct and indirect lethal and sub-lethal effects of agrochemicals on fecundity, survival and longevity (Longley and Sotherton, 1997), increasingly homogenous landscapes (Robinson and Sutherland, 2002; White and Kerr, 2007), habitat loss and reduction in habitat quality. It is likely that the historic distribution data of the study species (1940-1970) was dictated in some part by agricultural intensification at this time. Likewise recent expansion observed in the species studied may not only be the result of interactions with the climate. Recent agricultural policies are more sympathetic to conservation of biodiversity; the Environmental Stewardship scheme offers funding to farmers to manage their land in a way that is sensitive to the conservation of biodiversity, for example by creating and expanding hedgerows and other un-cropped edge habitats (Defra, 2005). Feber *et al.* (2007) found that significantly more butterflies were associated with non-cropped edge habitats than cropped habitats. In recent decades the use of many pesticides and herbicides has been banned in EU countries; most recently a EU ban on the use of neonicotinoid pesticides has been passed following concerns about its impact on bee populations in Europe (Goulson, 2013). These factors are likely to have resulted in both an increase in the abundance of butterflies and an increased ability of butterflies to disperse through the landscape by offering corridors of suitable habitat. Such factors must be considered when considering range expansion in butterflies.

It has become increasingly important to understand the ability of species to track recent climate change in view of increasing anthropogenic disturbance (Warren *et al.,* 2007; Fox *et al.,* 2010) and subsequent fragmented landscapes (Luoto *et al.,* 2002). If we are to successfully model such changes and make predictions about the impact of future change on species distributions, we must develop robust, ecologically valid models that incorporate species specific parameters. Although regional scale models of species distribution are useful tools for monitoring species responses to large scale variation/change in habitat and climate, it is what is occurring at finer resolutions that is important to the species (Underwood, 2007). At present models are not explicit enough to represent fine scale changes in populations, for example, due to the broad habitat data we feed in to such models. Until we develop a model framework that is able to factor in microclimatic and microhabitat conditions we may never truly represent the environment as it is experienced by the modelled species. None the less, as broad scale indicators of change these models are useful. In the future, field-based investigations into the ability of butterflies to cross man-made or unsuitable habitat barriers would be useful in furthering our understanding of the ability of these species to respond to climate and habitat change. In addition it is important to consider how factors other than climate and habitat, such as the widespread use of agrochemicals in the post-war era, affected species at this time and how changing attitudes to such practices may improve the ability of species to respond to climate change in the future. If model outcomes are to reliably inform conservation management plans of the future, investigating factors other than climate and habitat that relate to species population status and range extent and finding ways to incorporate these findings into predictive models should be a priority.

Chapter 4

Phenology of *Melanargia galathea* in relation to a preferred nectar source, *Centaurea scabiosa,* across its UK range

Abstract

Background: Climate change induced spatial or temporal disruption or alteration of phenological processes may lead to changes in patterns of reproductive success and hence the survival of species. Phenological mismatch has been observed across a range of taxa in response to changing environmental conditions. Local and regional phenological interactions between an insect pollinator, *Melanargia galathea*, and its preferred nectar source, *Centaurea scabiosa*, were investigated across a north-south transect.

Methods: Phenological interactions were investigated at three study sites (Totternhoe Quarry, Bedfordshire; Brockadale Quarry, West Yorkshire; Wingate Quarry, County Durham) along a north-south transect in Great Britain. Data from the UKBMS dataset and in-field survey data collected in 2011 was used in this analysis. Temperature data loggers were positioned to sample the variety of topoghraphical characteristics within each study site. Patterns of local and regional heterogeneity were examined using a univariate, general linear model on mean maximum daily temperatures. Local and regional heterogeneity in the flowering phenology of *C. scabiosa* and emergence of *M. galathea* was investigated using log-likelihood modelling.

Results: There is evidence of within site microclimatic variation at each of the three study sites Mean maximum daily temperature is significantly different across sub-sites at Totternhoe. Mean maximum daily temperatures on south-facing aspects are significantly warmer than either north or east facing aspects at all surveyed sites. Heterogeneity in the local environment (i.e. variable aspect/topography) at each of the three study sites results in an extended flowering period with multiple peaks throughout the flowering season of *C. scabiosa*. There is evidence of inter-annual and inter-site variability in the phenology of *M. galathea* at the three sites, with variability in peak abundance, date of peak abundance and duration of the flight period evident.

Conclusions: Microclimatic conditions experienced by an individual organism can vary substantially from regional scale climate. Topographically diverse areas present a broader range of microclimates that can act to extend the flowering period of plants, increasing the amount of time nectar is available to pollinating insects. Topographically variability could thus act as a buffer to phenological mismatch induced by future climate change and could be used

as a reserve selection criterion for conservation organisations. Variability in the timing of flowering and emergence along a north-south transect demonstrate the need to take care not to when translocating individuals from one site to another in order to avoid phenological mismatch between insect and plant. Such considerations should be made when interfering with all coevolved systems.

4.1 Introduction

Phenology concerns the timing of major events, critical for many organisms and includes time-sensitive, ecological relationships and life history events such as adult emergence (in insects), migration, breeding and flowering (Weiss and Weiss, 1998; Fitter and Fitter, 2002; Stefanescu *et al.,* 2003; Williams and Aberton, 2004; Morecroft *et al.,* 2009; Miller-Rushing *et al.,* 2010; Tooke and Battey, 2010). Climate change induced spatial or temporal disruption or alteration of phenological processes may lead to changes in patterns of reproductive success and hence the survival of species (Weiss and Weiss, 1998; Miller-Rushing *et al.,* 2010; Potts *et al.,* 2010). Such may be the case when phenological mismatches arise between interacting species, such as plant and pollinator or predator and prey (Ibanez *et al.,* 2010; Miller-Rushing *et al.,* 2010; Potts *et al.,* 2010; Hodgson *et al.,* 2011). As such, understanding phenological processes, and the biotic and abiotic factors integral to the observed patterns, is essential if we are to predict future impacts of environmental change on our ecosystems.

In plants, flowering phenology is a complex process controlled by both environmental cues (Tooke and Battey, 2010) and developmental regulation (Mouradov *et al.,* 2002). In temperate regions, environmental cues such as incidence of solar radiation (Weiss and Weiss, 1998; Bennie *et al.,* 2008), temperature and photoperiod, act to attune flowering to appropriate seasonal conditions (Elzinga *et al.,* 2007; Tooke and Battey, 2010). The intimate relationship between phenological events and environmental cues makes phenology an area of research that is of concern to environmental change biologists (Chuine, 2010), particularly in the context of modern day climate change biology (Roy and Sparks, 2000; Ibanez *et al.,* 2010; Hodgson *et al.,* 2011). Flowering phenology, in particular, has been the focus of a large body of research since plant reproductive biology is central to many ecological relationships such as insect diapauses and emergence (Miller-Rushing *et al.,* 2008).

Research relating to landscape scale phenological responses of plants to climate change has received much attention recently (Penuelas and Filella, 2001; Roy *et al.,* 2001; Ahas *et al.,* 2002; Hepper, 2003; Dunne *et al.,* 2003; Menzel *et al.,* 2006). Although phenological responses are known to vary across taxa (Primack *et al.,* 2009; Ibanez *et al.,* 2010; Miller-Rushing *et al.,* 2010), the primary finding of such studies is that climate change is altering flowering times worldwide (Miller-Rushing *et al.,* 2008) with the overall trend of an advancing spring and earlier flowering in temperate regions (Williams and Aberton, 2004; Ibanez *et al.,* 2010; Tooke and Battey, 2010). Fitter and Fitter (2002) found that first flowering date (FFD), regarded as the first open flower seen, and representing records of initial emergence times (Tooke and Battey, 2010) had advanced by an average of 4.5 days in 385 British plant species, when compared with the previous four decades which had demonstrated minimal variation in flowering time. Following research conducted in the UK, Williams and Aberton (2004) also found that FFD in agricultural varieties of the white clover has advanced by approximately 7.5 days per decade since between 1978 and 2002, with this trend linked to warmer air and soil temperatures during this period. Despite this large body of research relating to large scale phenological change, research is still lacking with regards to phenological responses of organisms occurring at finer spatial scales, for example in relation to microhabitat and microclimatic conditions. This is in part due to the time consuming nature of such data collection.

If shifts in phenology are to be recognised, scientifically robust monitoring of natural systems is essential (Morecroft *et al.,* 2009). Most flowering phenological datasets are composed of FFD; FFD has traditionally been used as a method of monitoring flowering phenology as it is an easily recorded measure of flower emergence that allows for direct comparison of flowering between years, without the need for time consuming, intensive monitoring protocols. Some, however, argue that the FFD approach to recording flowering phenology ignores processes occurring at the level of the population, and is both subject to confounding effects such as population size and sampling frequency, and unable to capture either flowering period or mean flowering date (Miller-Rushing *et al.,* 2008; Primack *et al.,* 2009; Tooke and Battey, 2010). Miller-Rushing *et al.* (2008) found that confounding effects of population size and sampling frequency may substantially affect observed FFD and subsequent estimations of changes in FFD. They found that both smaller population size and reduced sampling frequency consistently resulted in later estimates of FFD. They suggest that, in order to avoid such effects, where possible, researchers should observe the flowering season in its entirety. In the first part of this study, local and regional heterogeneity in the flowering phenology of a favoured nectar source *Centaurea scabiosa* (greater knapweed) for the butterfly *Melanargia galathea* are investigated both intra and inter-annually. To achieve routine data on flowering within three study field sites along a north-south transect. Phenological patterns occurring both within and among three principle field sites throughout the entirety of the *C. scabiosa* flowering season were investigated. Inter-annual heterogeneity in flowering phenology was investigated utilising field data collected under the supervision of SGW for the years 2001 to 2008 at one of the study sites.

Habitats are heterogeneous at multiple spatial scales as a consequence of both natural and anthropogenic processes (Fahrig and Merriam, 1994; Morris *et al.,* 2004). Variation in microclimate as a result of local habitat heterogeneity is known to be a dominant factor influencing phenological variation in flowering observed in heterogeneous environments (Weiss *et el.*, 1988). For example, it is commonly observed that flowers growing at warmer sites flower earlier than equivalent plants growing at cooler sites (Miller-Rushing *et al.,* 2008). Incidence of solar radiation is known to be an important temporal driver of flowering phenology, determining the time at which flowers emerge, at both local and regional scales (Weiss and Weiss, 1998; Bennie *et al.,* 2008; Bennie *et al.,* 2010). Regional scale variability in flowering times, observed at latitudinal and altitudinal scales (Bennie *et al.,* 2008), can often be observed at local scales as a result of local variation in microclimate. At the local microclimatic scale, thermal microclimates may be far removed from those expected by prevailing average, macroclimatic conditions (Bennie *et al.,* 2008; Bennie *et al.,* 2010). At mid to high latitudes this local variability is often the result of topographically induced spatial variation in climate (Hasse, 1970; Weiss and Weiss, 1998; Bennie *et al.,* 2008) and can lead to temporal variation in flowering phenology (Jackson. 1966; Weiss and Weiss, 1998). Jackson (1966) championed microclimatic research with regards to flowering phenology, recognising how microclimate represents the actual abiotic conditions experienced by the plant and those which influence plant response. In an early study, she observed that flowering of plant patches on north facing slopes were retarded with respect to mean flowering date when compared to warmer, south facing slopes. In this chapter I will investigate how local heterogeneity in sub-site characteristics (i.e. variable aspect, shelter and/or topography) can influence local, fine-scale flowering phenology of plant patches in terms of date of peak flowering and duration of the flowering period.

Phenological shifts have also been observed in insect species in light of recent climate change (Roy and Sparks, 2000; Hodgson *et al.,* 2011). Among Lepidoptera, there have been confirmed reports of shifts both poleward and to higher elevations shifts (Konvicka *et al.,* 2003), advancement in first appearance date (Roy and Sparks, 2000; Roy and Asher, 2003; Stefanescu *et al.,* 2003) and in some cases increased incidence of multi-voltinism (Stefanescu *et al.,* 2003; Hill *et al.,* 2011; Poyry *et al.,* 2011) within a species. There is concern that such changes occurring as a consequence of recent climate change may lead to phenological mismatch between closely dependent species, such as insect-pollinator relationships (Elzinga *et al.,* 2007; Memmott *et al.,* 2007; Potts *et al.,* 2010). This mismatch is likely to be even more extreme when responses to climate change are differential between species (Elzinga *et al.,* 2007), with unknown consequences for the co-evolved ecosystems undergoing such changes.

Melanargia galathea is a Satyrid butterfly that favours chalk and limestone grassland habitats (Baguette *et al.,* 2000) and has a preference for *C. scabiosa* as a primary nectar source. To investigate the possibility of phenological mismatch occurring between *M. galathea* and its favoured resource plant *C. scabiosa* within its range, this study aims to map regional, inter-annual phenological emergence patterns of *M. galathea* at the three study sites. This is achieved using abundance data from three sources: transect surveys undertaken as part of the UKBMS; reserve led surveys conducted at study sites under the direction of SGW for the years 2001 to 2008; and personal data collected at the study sites during the 2011 field season. Since *M. galathea* relies on *C. scabiosa* across its range, it is expected that patterns of peak flowering of *C. scabiosa* observed at the regional scale will mirror regional peak emergence patterns observed for *M. galathea.*

In summary, this chapter investigates the local and regional patterns of temperature along a north-south transect in England and relates this to phenology of a chalk grassland specialist butterfly, *M. galathea,* and its preferred nectar source, *C. scabiosa*. I hypothesise that both regional and local-scale near surface air temperatures differ at the three primary sites. Secondly, I hypothesise that patterns of local and regional heterogeneity in the flowering phenology of *C. scabiosa* differ both inter and intra-annually. Thirdly, I hypothesise regional and inter-annual emergence phenology of chalk and limestone grassland butterfly *M. galathea* will differ.

4.2 Methods

4.2.1 Study Species

Knapweeds have been described as keystone nectar plants for butterflies in calcareous and limestone grassland ecosystems (Rusterholz and Erhardt, 1998). *Centaurea scabiosa,* is a medium to tall native perennial found on a variety of grasslands on dry, calcareous soils (Lack, 1976). Flowering is predominantly from July to September although flowers can be seen as early as June in some southern sites with good habitat (Grime *et al.,* 1988). It is usually absent from intensely managed meadows and pastures and is most often associated with taller swards but can occasionally be found in scrub land, woodland edges, road verges and waste ground. In common with many members of the daisy family, *C. scabiosa* is an important food source for a wide range of insects including butterflies.

Melanargia galathea, the marbled white butterfly, is a member of the family Nymphalidae, subfamily, Satyridae. This species produces one generation per year and exhibits a relatively short flight period from mid- June until mid-August with peak emergence occurring in July (Asher *et al.,* 2001). *M. galathea* utilises *C. scabiosa* as a primary nectar source in calcareous grassland habitats and is often seen festooning the flower heads in large numbers. While a preference for *Centaurea* spp is notable in calcareous grassland habitats, *M. galathea* will also feed on a number of purple flowering species (e.g. *Scabiosa* spp., *Cirsium* spp., *Carduus* spp. and *Centaurea* spp.) across its range, particularly where *Centaurea* spp. are less abundant, such as in mesotrophic and disturbed habitats. There is some dispute over the classification of *M. galathea* as a generalist (a wider countryside species) or specialist (a species with a restricted range, associated with semi-natural habitats) butterfly with differences of opinion evident in the literature (Pollard and Yates, 1993; Baguette *et al.,* 2000; Asher *et al.,* 2001; Willis *et al.,* 2009b). What is clear is that *M. galathea* is mostly restricted to, and certainly thrives on, unimproved calcareous and limestone grasslands (Baguette *et al.,* 2000; Van Swaay, 2002) where both its key nectar species (*Centaurea* spp.) and larval host plants (*Festuca* spp. and *Brachypodium pinnatum* L.) thrive. *M. galathea* is a relatively good disperser and although it is currently mostly restricted to the south (Fox *et al.,* 2008) it is expanding its range north in Britain (Willis *et al.,* 2009b). It was recorded in 66% more 10km grid squares during a census in 1995-1999 compared to the 1970-1982 census (Asher *et al.,* 2001).

4.2.2 Study Sites

To collect data from the core to the periphery of the species UK range, three study sites were chosen that roughly followed a north-south transect, spanning 378km from Bedfordshire to County Durham (Figure 4.1). These sites were chosen on the basis of good habitat (calcareous/magnesium-limestone grassland), location within current range of *M. galathea* and previous records of both a strong colony of *M. galathea,* and presence of *C. scabiosa*. The first study site was located in the core of the range of *M. galathea*, the second near to its natural northern range boundary, and the third was the site of a successful translocation study north of the current naturally occurring populations of *M. galathea* (Willis *et al.,* 2009b).

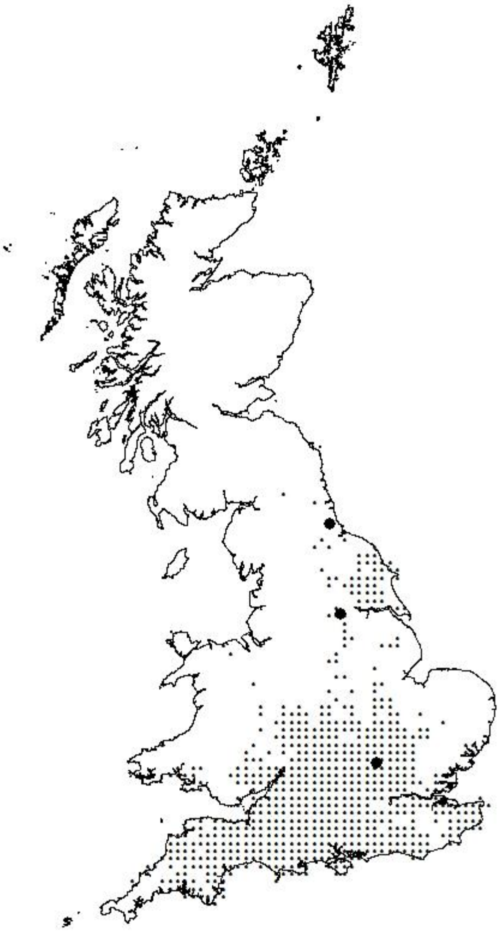


Figure 4.1: Location of field study sites (large black circles) in relation to observed present day (2010) distribution of *M. galathea* (small black dots); from south to north, Totternhoe Chalk Quarry Reserve, Bedfordshire; Brockadale Nature Reserve, West Yorkshire; Wingate Quarry, County Durham.

The southern-most study site, Totternhoe Chalk Quarry Reserve (Grid ref: SP 986 225), is located just outside Dunstable, Bedfordshire, England. This disused chalk quarry is located in the north-east of the Chiltern Hills (Area of Outstanding Natural Beauty) and has been managed by the Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire (BCN Wildlife Trust) since 2003. Quarrying has taken place here since medieval times leaving spoil heaps which have developed into highly diverse, flower-rich chalk grasslands (Newland, 2006). Today the area is largely made up of excavated chalk resulting in highly variable site topography (Turner *et al.,* 2009). The site is designated as a Site of Special Scientific Interest (SSSI) by Natural England recognising its rich flora and fauna as well as geological interest. Lowland calcareous grassland is a national priority habitat (UK Biodiversity Action Plan, 2007), with directives to maintain, restore and expand the habitat nationally (Turner *et al.,* 2009). The site's varied topography and vegetation make for a wide variety of microclimatic and microhabitat conditions within a small area, making it an ideal site on which to study the effect of habitat heterogeneity on flowering phenology of *C. scabiosa*.

Brockadale Nature Reserve (Grid ref: SE 503 174), near Wentbridge, West Yorkshire, England, is located near the natural northern edge of the distribution of *M. galathea.* It comprises the narrow, steep-sided valley created by the River Went, which has cut through a narrow belt of magnesium limestone rocks that stretch from north Nottinghamshire to County Durham. The site is managed by the Yorkshire Wildlife Trust and Natural England and has been designated a SSSI. The site extends nearly 3.2km, covering 50 hectares and is made up of several distinct habitat types including mature woodlands, riverside meadows and limestone grassland. The fertile, well-drained soil of the limestone grassland habitat is of particular conservation importance for both specialist flora and fauna and is maintained using traditional management methods such as sheep and cattle grazing and scrub removal. The calcareous grassland is located on steep valley sides and so has not been utilised as agricultural land. As such the meadows have developed undisturbed to produce a rich display of calcareous grassland specialist plants. These support a good range of butterflies including large colonies of *M. galathea*.

Wingate Quarry (Grid ref. NZ 373 375), Wingate, County Durham, the northernmost study site, is the site of a translocation study in which 500 *M. galathea* adults were translocated to the site from North Yorkshire in July, 2000 (Willis *et al.,* 2009b). This resulted in the establishment of an isolated population of *M. galathea* north of the current natural northern range boundary of the species and as such represents the northern most colony of *M. galathea* in the UK. This disused quarry was worked for magnesium limestone between the mid-18th century and 1930s and is one of the largest examples of magnesium limestone grassland in County Durham. Part of the site was declared a local nature reserve in 1980 and is known as Wingate Quarry Local Nature Reserve and managed by Durham County Council. The site was designated as a SSSI by Natural England in 1984. It supports a large number of species characteristic of limestone soils, several of which are otherwise uncommon in County Durham.

4.2.3 Part 1: Local and regional heterogeneity in microclimate

Temperature Data

To investigate microclimatic variation in temperature within and between study sites, iButton temperature loggers, version SL5IT, (distributor signatrol data logging solutions available at www.signatrol.com) were positioned so sample the variety of topographical characteristics within each of the study sites. Data loggers have a typical accuracy of recordings of ±1 °C. The loggers were placed in clear plastic 5cm pots with white screw fix lids. As the three study sites are all open access throughout, logger pots were positioned within the vegetation sward to minimise the risk of theft, displacement or tampering. Positioning the loggers in this way provides shading and therefore records ambient rather than exposed temperatures.. As all loggers were treated in this way, direct comparison of temperature data among sites was possible. Four loggers were set up at each site; temperature loggers at Totternhoe Quarry were set up at locations with east, west, south-west and south facing aspects and were set to record from 11/06/2011 until 22/07/2011. Loggers at Brockadale Reserve were set up at the top of north and south facing slopes at the valley top and at the base of these slopes at the valley bottom. Loggers at this site were set to record from 24/06/11 until 31/07/11. Temperature loggers at Wingate Quarry were set up on north, south, east and west facing slopes and ran from 16/06/11 until 27/07/11. Loggers were set to record at 30 minute intervals 24 hours a day. The first 12 hours of temperature data from all of the temperature loggers was disregarded to allow for loggers to equilibrate with the local temperature.

Statistical Analysis

To test for local and regional heterogeneity in temperature among sites a univariate, general linear model (GLM) was performed incorporating day as a random factor, on mean maximum daily temperature data collected throughout the survey period at each of the logger locations within each study site. Only data for days where temperature was recorded at all three sites (25/06/11 to 22/07/11) was used to ensure direct comparisons among sites could be made. Test for regional heterogeneity in temperature data (i.e. between sites) is restricted to southerly aspects as this aspect is represented at all three survey sites. Post-hoc Tukey's tests were performed to make multiple comparisons within and between sites. Maximum daily temperature was used as aspect induced variation in near-surface temperature is most apparent when solar radiation is most intense (Bennie *et al.,* 2010). All statistical analysis was conducted using IBM SPSS 20.0 statistical software.

4.2.4 Part 2: Heterogeneity in the flowering phenology of *Centaurea scabiosa*

Phenological Data

In 2011 phenological data for *C. scabiosa* was collected throughout each of the three study sites wherever the plant occurred. To investigate within-site variation of flowering phenology of *C. scabiosa* each of the sites was divided into sub-sites of differing aspect. At Totternhoe plants were allocated to one of six possible aspects: east, east-south-east, south-east, south, south-west and west facing. The distribution of *C. scabiosa* at Brockadale Quarry was fairly sparse, restricted to two south facing slopes (separated by a man-made fence line) and a flat, open ridge. These three locations comprised the phenological sub-sites for Brockadale Quarry.

Four Wingate Quarry sub-sites were categorised by aspect and were north-east, south-east, south and south-west facing. A further two sub-sites were categorised as flat open and flat sheltered; the flat sheltered sub-site was located in the bowl shaped base of the quarry and is sheltered on all four sides, the flat open sub-site is located outside of the quarry and is open on all four sides. Where possible at least 30 plants were surveyed per sub-site at random. Where fewer than 30 plants occurred on one sub-site all of the available plants were surveyed. On each survey date the number of closed capitula, open flowers (characterised by bright inflorescences and the presence of pollen) and past flowers (characterised as withering flowers and developing and spent seed capsules) were recorded per plant. For the purposes of this study, the sum of open flowers and past flowers are referred to as open capitula. Capitulum (plural capitula) is a term used to describe the type of inflorescence characteristic of members of the family Compositae. Plants at Totternhoe were surveyed 8 times between 11/06/2011 and 30/07/2011. Plants at Brockadale were surveyed four times between 24/06/2011 until 01/08/2011 and at Wingate plants were surveyed six times between 15/06/11 until 05/08/11.

Statistical Analysis

A model was developed to predict the mean proportion of open capitula on *C. scabiosa* plants, on a given day of the year, *p(x)*. The cumulative proportion of capitula open by day *x* is defined as *p(x)* where

$$p(x) = \frac{e^{\beta(x-\bar{x})}}{1+ e^{\beta(x-\bar{x})}} . \qquad \text{(Equation 4.1)}$$

$\bar{x}$ is the day when half the capitula have opened, and β is a parameter negatively related to duration over which capitula flower. For a given site, *I(x)* plants are sampled on day *x* where N_i is the total number of capitula formed on the i_{th} plant by time t and $n_i(x)$ is the number of capitula opened on plant i by day *x* where $0 \leq n_i \leq N_i t$. Since all plants likely differ in their phenology as a result of inherent genetic variation and/or biotic and abiotic environmental factors, the variation in the data about *p(x)* will be more variable across plants than predicted by the binomial distribution. To account for this extra source of variation in the data, it was assumed that the variation in the data about *p(x)* can be described by the beta-binomial distribution (Richards, 2008).

Maximum log-likelihood was used to fit the model of capitula emergence (Equation 4.1) to the recorded phenological time-series data. The likelihood of observing *n(x)* of the *N* capitula being open on day *x* is given by,

$$L(\vartheta \mid n, N) = \frac{\Gamma(N+1)\Gamma(a+b)\Gamma(n+a)\Gamma(N-n+b)}{\Gamma(n+1)\Gamma(N-n+1)\Gamma(a)\Gamma(b)\Gamma(N+a+b)}, \qquad \text{(Equation 4.2)}$$

where ϑ represents the set of model parameters that are estimated, i.e. $\bar{x}$, β and ϕ. Here $a = p(x)/\phi$, $b = [1-p(x)]/\phi$, and ϕ is a positive parameter (i.e. if ϕ is small expect less variation between plants). The log-likelihood of observing the capitula data collected on plants on day *x* is,

$$\begin{aligned} LL(\vartheta \mid n_i(x), N_i(x)) &= \ln\Gamma(N+1) + \ln\Gamma(a+b) + \ln\Gamma(n+a) + \ln\Gamma(N-n+b) \\ &- \ln\Gamma(n+1)\ln\Gamma(N-n+1)\ln\Gamma(a)\ln\Gamma(b)\ln\Gamma(N+a+b). \end{aligned} \qquad \text{(Equation 4.3)}$$

The log-likelihood of all the data collected throughout the season at a site is,

$$LL(\vartheta \mid data) = \sum_x \sum_{i=1}^{I(x)} LL\left(\vartheta \mid n_i(x), N_i(x)\right). \qquad \text{(Equation 4.4)}$$

Best parameter estimates were obtained by maximising Equation 4.4. Maximum-likelihood estimates were obtained using the SOLVER add-in on Microsoft Office Excel 2010. Firstly, evidence of a local sub-site effect on *p(x)* for each site was sought, indicating fine-scale effects such as microclimate. This was achieved by first estimating ϑ for all plants in a site combined (simple model). Values for ϑ were then estimated separately according to sub-site (complex model). The log-likelihood ratio test was then used to determine whether the complex model was significantly better at explaining the observed data than the simple model, indicating that sub-site was significant.

Secondly, following the same protocol, evidence of regional variation in flowering phenology on south-facing aspects was invesitigated. Since southerly aspects were consistently surveyed at all three study sites regional scale analysis was restricted to data from south facing aspects. Log-likelihood ratio test was used to compare model fits.

Thirdly, evidence of year and sub-site affect on flowering phenology of *C. scabiosa* at Wingate Quarry was sought. Phenological data for *C. scabiosa* was available for seven (non-sequential) years at Wingate Quarry, County Durham; 2001, 2003, 2004, 2005, 2006, 2008 and 2011. Flowering phenology data for *C. scabiosa* was only available for flat sub-sites in years 2001, 2003 and 2008, and for flat, northerly and southerly sub-sites in years 2004, 2005, 2006 and 2011. These annual data were collected using the same surveying technique employed in the 2011 survey season. In order to allow for variation in $\bar{x}$ and β between years two extra parameters, a_y and b_y respectively, were incorporated into the model of capitula emergence

(Equation 4.1). The probability capitula have opened in year y by day x is described by $p_y(x)$ where,

$$p_y(x) = \frac{e^{(\beta+b_y)(x-\bar{\mathrm{x}}+\mathrm{a_y})}}{1+ e^{(\beta+b_y)(x-\bar{\mathrm{x}}+\mathrm{a_y})}} \ . \qquad \text{(Equation 4.5)}$$

The following four models, denoted M_1 to M_4, were proposed to explain the data. K refers to the number of parameters estimated in each model. The first model, M_1, was the simplest model and assumed that data from all sub-sites and years had equal parameter values for ϑ whilst a_y and b_y were set to zero, K = 3. The second model, M_2, assumed sub-site, but not year played a role in the distribution of the observed data, K = 9 (parameter values for ϑ were allowed to vary across three sub-sites). The third model, M_3, assumed sub-site played no role but allowed variation in between years, K = 17 (model parameters, ϑ, remained constant across the three sub-sites whilst values for a_y and $b_y$varied across the 7 years of data). The final, most complex model, M_4, allowed all model parameters to vary both between years and sub-sites, K = 23 (parameter values for ϑ, and a_y and b_y varied across sub-sites and years respectively). Once again maximum log-likelihood was used (Equation 4.4) to fit my model of capitula emergence (Equation 4.5). Akaike's information criterion was used (AIC; Burnham and Anderson, 2002) to identify which of the proposed models was most consistent with the observed data. This method is suitable for assessing and selecting multiple process-based ecological modes (Richards, 2008). To avoid selecting overly complex models, all models with an ΔAIC within six units of the smallest ΔAIC value (i.e. ΔAIC ≤ 6) were selected and those with a ΔAIC > 6 were disregarded as inconsistent with the data (following Richards, 2008).

To estimate flowering duration at each sub-site, after fitting the model the cumulative function, *p*, was used to determine when 5-95% of capitula were predicted to be open (Figure 4.2).

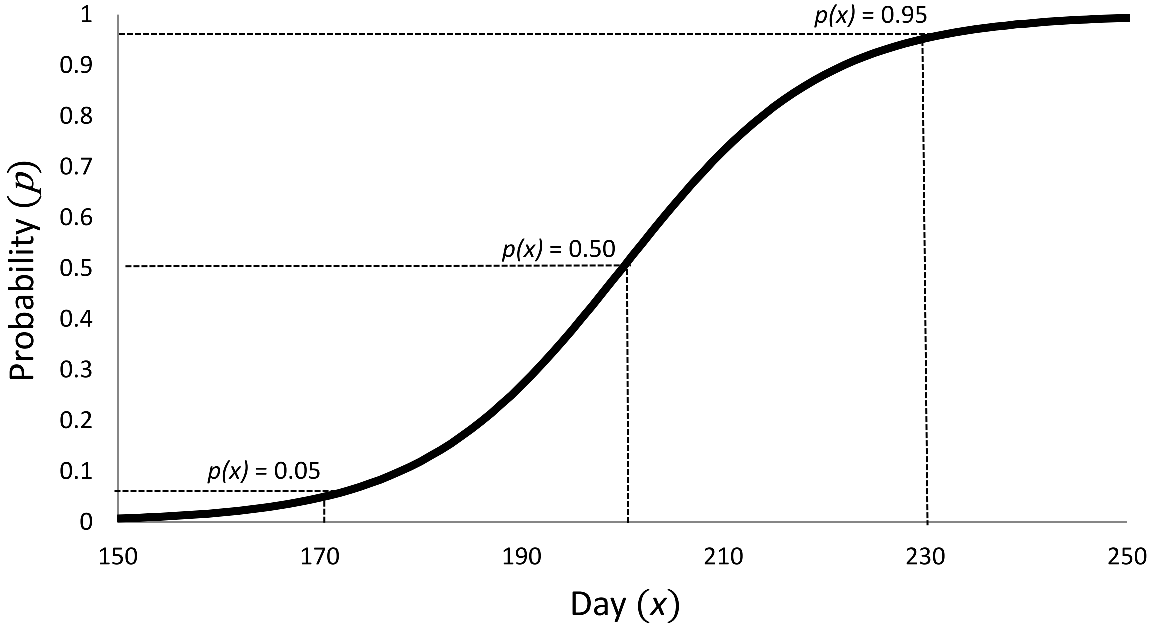


Figure 4.2: An example of the cumulative proportion of open capitula for *C. scabiosa* where *p* is the probability a capitula has opened by day *x*. The logistic curve presented here is described by the probability function presented in Equation 4.1, where $\overline{x}$ = 200, β = 0.1.

4.2.4 Part 3 Regional heterogeneity in the flight period of *Melanargia galathea*

Phenological Data

Two out of the three survey sites, Totternhoe and Wingate, are monitored by UKBMS; UKBMS transect survey data for *M. galathea* was utilised (recorded along set transect routes) from all years with available data for these two sites. For Totternhoe, this supplementary data was collected on 10 non-consecutive years between 1995 and 2009. For Wingate, these data comprised 5 years of data collected between years 2002 and 2009. The remaining survey site, Brockadale, is not subject to UKBMS transect monitoring, but has been monitored by staff and volunteers of the Yorkshire Wildlife Trust following standard UKBMS transect protocol. Survey data collected at Brockadale between years 2007 and 2008 was used for the purposes of this study. Data for Totternhoe and Wingate was supplemented with data recorded during my 2011 field season; adult *M. galathea* were surveyed along the same transect routes utilised by the UKBMS, throughout the flight season in 2011, from mid-June to early August. Butterfly transect data was recorded on as many days as possible when conditions were in line with those outlined by UKBMS as suitable for butterfly transect walking (Pollard and Yates, 1993). Adults were surveyed using traditional transect methods outlined by UKBMS (Pollard and Yates, 1993). Due to logistical constraints and poor weather on survey days I was unable to collate more than 2 data points for *M. galathea* abundance at Brockadale in the 2011 survey season and so data from 2011 was excluded from analysis for this site. Note that phenological flowering data was collected on all survey dates regardless of weather conditions.

Statistical analysis

A statistical model was developed to predict the mean abundance of *M. galathea* on a given day of the year. The expected number of *M. galathea* butterflies observed by time *t* is defined as *y(t)* where

$$y(t) = Y_{max} e^{\frac{-(t-\bar{T})}{2\sigma^2}}. \qquad \text{(Equation 4.6)}$$

where $\bar{T}$ describes the day on which peak abundance, Y_{max}, is reached (Figure 4.3) and the width of the distribution (duration of the flight period) is defined by term σ. If *I(t)* butterflies are recorded at a given site by time *t* where *N* is the total number of butterflies recorded at a site in a season and *n(t)* butterflies are recorded by time *t* then $0 \leq n \leq N$. The data analysed was Poisson count data with no upper bound and a lower bound of zero so it was appropriate to use the negative binomial function when calculating the likelihood of observing a data point. The likelihood of observing *n(t)* of the *N* butterflies by time *t* is,

$$L(\vartheta \mid n, N) = \frac{n+a}{\Gamma(n+1)\Gamma(a)} \left(\frac{a}{1+b}\right)^{a} \left(\frac{1}{1+b}\right)^{n}, \qquad \text{(Equation 4.7)}$$

where ϑ represents the set of model parameters that are estimated, i.e. $\bar{T}$, Y_{max} and σ. Here $a = y(t)/\phi$, $b = [1-y(t)]/\phi$, and ϕ is a positive parameter. The variance term, ϕ, was incorporated into all models and assumed to be of equal value for all years implying constant variation in counts across years. The log-likelihood of observing the abundance data at time *t* is,

$$LL(\vartheta \mid n(t), N(t)) = \ln\Gamma(n+a) - \ln\Gamma(n+1) - \ln\Gamma(a) + a\ln\left(\frac{b}{1+b}\right) - n\ln(1+b).$$

(Equation 4.8)

The log likelihood of all the data collected throughout the season at the site is,

$$LL(\vartheta| \, data) = \textstyle\sum_t LL\left(\vartheta| \, n(t), N(t)\right). \qquad \text{(Equation 4.9)}$$

Best parameter estimates were obtained by maximising Equation 4.9. Evidence of both site effect and year effect on *y(t)* was sought for each site indicating inter-site (regional) and inter-annual variability in peak abundance date. The following four models, denoted M_1 to M_4, were proposed to describe the data observed at each of the sites in each of the years with available data. The first model, M_1, was the simplest model and assumed that data from all years had equal parameter values for Y_{max}., $\bar{T}$, and σ. The second model, M_2, assumed Y_{max}., $\bar{T}$ remained constant between years while σ varied. The third model, M_3, assumed Y_{max}., σ remained constant between years while $\bar{T}$ varied. The final, most complex model, M_4, allowed all parameters, Y_{max}., $\bar{T}$, and σ, to vary between years. AIC (Burnham and Anderson, 2002) was used to identify which of the proposed models was most consistent with the data.

Following model selection, predicted model outcomes were used to estimate the duration of the *M. galathea* flight period; defined as the predicted number of days between which >1 butterfly has emerged and >1 butterfly still remains.

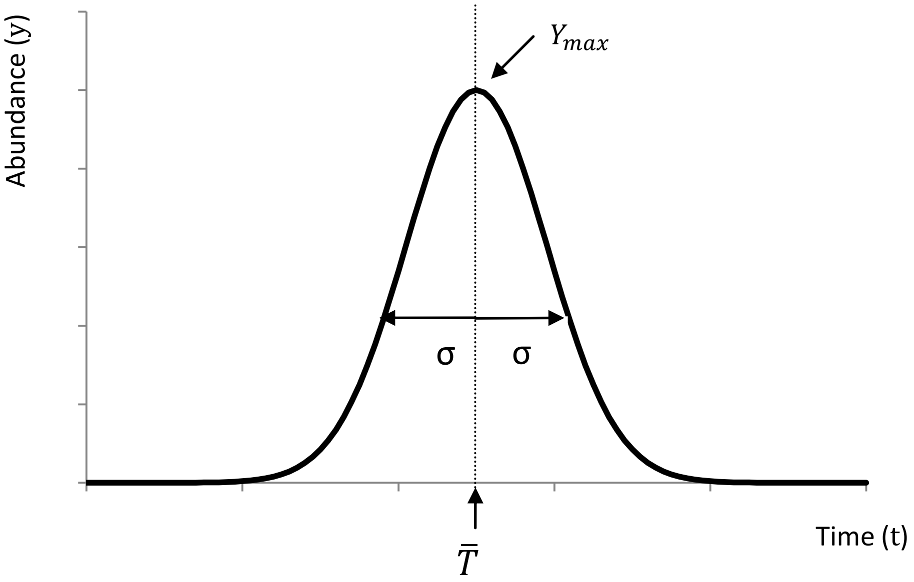


Figure 4.3: Functional form describing mean abundance data of *M. galathea.* See text for description of parameters.

4.3 Results

4.3.1 Part 1: Local and regional heterogeneity in microclimate

To directly compare temperature data from each of the sites a subset of overlapping data between the dates of 25/06/2011 and 22/07/2011 were extracted. There is evidence of within site microclimatic variation at each of the three study sites (Figure 4.4). Mean maximum daily temperature is significantly different across sub-sites at Totternhoe (GLM; $F_{3,\,81}$ = 36.29, P = <0.001), Brockadale (GLM; $F_{3,\,81}$ = 25.68, P < 0.001) and Wingate (GLM; $F_{3,\,81}$ = 49.15, P < 0.001).

Post-hoc Tukey's tests revealed whether some or all of the surveyed sub-sites differed in their daily maximum temperatures (Figure 4.4). Mean maximum daily temperatures on south-facing aspects are significantly warmer than either north or east facing aspects at all surveyed sites. At Totternhoe, south-westerly and west facing aspects were not significantly warmer than south facing aspects. At Wingate (the northernmost study site) the sequence of aspects from warmest to coolest based upon mean maximum daily temperature during the survey period was south, west, east, and north.

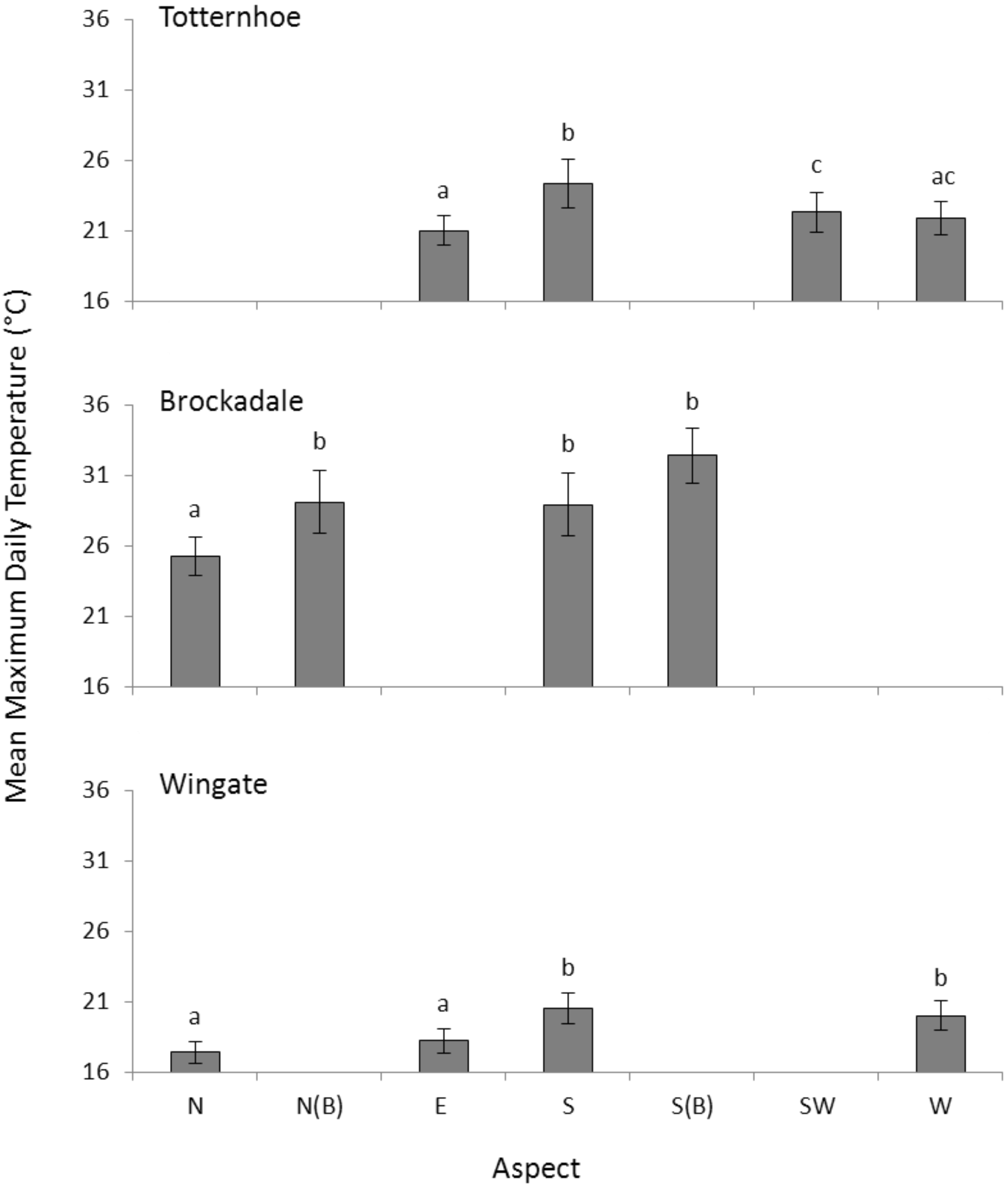


Figure 4.4: Mean maximum daily temperature at the three study sites. Aspect notations follow traditional compass notations. N(B) and S(B) refer to loggers positioned at the flat base of a north and south facing slopes respectively. Bars indicate 95% confidence intervals for the mean. Symbols indicate which means are statistically significant at α = 0.05.

Figure 4.5A shows a comparison of maximum recorded daily temperature on south facing aspects at each of the three study sites. Despite the fact that Brockadale is situated north of Totternhoe it occasionally had higher temperatures during the recording period (Figure 4.5A). There is a significant difference in mean maximum daily temperature on south facing slopes at the three study sites (GLM; $F_{2, 54}$ = 28.58, P = <0.001). A post-hoc Tukey test revealed which sites differed significantly (Figure 4.5B).

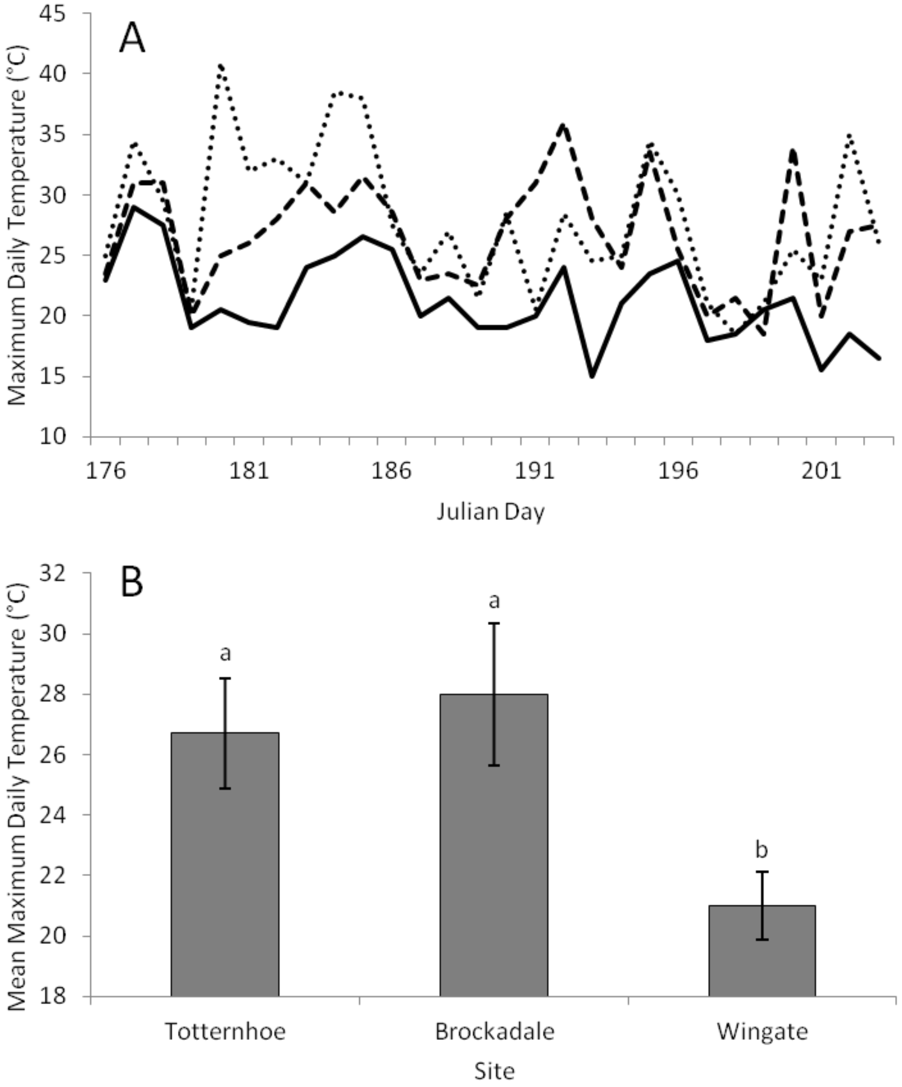


Figure 4.5: (A) Comparison of maximum recorded daily temperature on south facing aspects at each of the three study sites. Solid line, Wingate; short dashed line, Brockadale; long dashed line, Totternhoe. (B) Mean maximum daily temperature on south facing slopes at three study sites. Bars indicate 95% confidence intervals for the mean. Symbols indicate which means are statistically significant at α = 0.05

4.3.2 Part 2: Heterogeneity in the flowering phenology of *Centaurea scabiosa*

There was evidence that sub-site affected the flowering of *C. scabiosa* at the three sites during 2011 (Table 4.1); the best models for each sub-site had separate values of $\bar{x}$ (day when half the capitula have opened) and β (parameter negatively related to duration over which capitula flower; Table 4.1).

Table 4.1: Model fit and log-likelihood ratio test (LLRT) results comparing simple and complex models of *C. scabiosa* flowering phenology at the three study sites. LL Simple and LL Complex refer to the log-likelihood of the simple and complex models respectively. P-value follows the one-tailed probability of the chi-squared distribution at degrees of freedom (df). Site 'England' refers to the comparison of south facing slopes at each of the three study sites.

Site	LL Simple	LL Complex	LLRT	df	P-value
Totternhoe	-2951.4	-2816.7	269.5	10	<0.001
Brockadale	-430.0	-421.1	17.7	4	0.001
Wingate	-1867.3	-1770.1	194.3	10	<0.001
England	-1478.0	-1403.1	149.7	4	<0.001

There is evidence that heterogeneity in the local environment (i.e. variable aspect/topography) at each of the three study sites results in an extended flowering period with multiple peaks throughout the flowering season of *C. scabiosa* (Table 4.2). Peak flowering date ($\bar{x}$) at Totternhoe is predicted to be earliest at the south-westerly aspect (Julian day 180) and latest at the south-easterly aspect (Julian day 193; Table 4.2). Given the data, flowering period (time between which 5 and 95% of capitula have opened) at Totternhoe is predicted to be shortest at south west and westerly aspects (37 days) and longest at south-easterly aspects (55 days; Table 4.2). There is evidence of variable flowering phenology of *C. scabiosa* at two sub-sites both described as having a southerly aspect at Brockadale Nature Reserve (Table 4.2). This suggests that factors other than aspect are also influencing patterns of flowering across the site. Peak flowering at Wingate Quarry is predicted to occur later than that of either Totternhoe or Brockadale. In line with trends predicted for Totternhoe, peak flowering at Wingate is predicted to be earliest at the south-westerly aspect (Julian day 198) and flowering period predicted to be longest at the south-easterly aspect (77 days; Table 4.2).

Table 4.2: Julian day by which the model predicts 50% of capitula will be open ($\bar{x}$) and length of flowering period (FP) in days at each surveyed sub-site at Totternhoe, Brockadale and Wingate in the year 2011.

	Totternhoe		Brockadale		Wingate	
Sub-site	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP
North-east	~	~	~	~	209	37
East	188	44	~	~	~	~
East-south-east	188	46	~	~	~	~
South-east	193	55	~	~	200	71
South 1	188	51	191	44	201	51
South 2	~	~	189	52	~	~
South-west	180	37	~	~	198	58
West	182	37	~	~	~	~
Flat open	~	~	196	64	203	47
Flat sheltered	~	~	~	~	212	21

There is evidence that flowering phenology of *C. scabiosa* varied among sites. When fitting the model to data from south facing slopes at each of three sites model fit is significantly improved when $\bar{x}$ and β were allowed to vary between study sites (Table 4.1). Model fits for flowering phenology were very similar for the Brockadale and Totternhoe sites, with flowering at Wingate delayed relative to the other two sites (Figure 4.6). This suggests that Totternhoe and Brockadale share a more similar climate with one another than they do with Wingate. Peak flowering at Wingate is predicted to be much later than that at Totternhoe or Brockadale given the data (Figure 4.6). Figure 4.6 also demonstrates the high degree of variation in flowering times even within an aspect. This may be the result of a range of factors including inherent individual variation in age and genetics of plants in addition to biotic and abiotic environmental factors such as position with respect to other plants, moisture availability and presence of pests or disease.

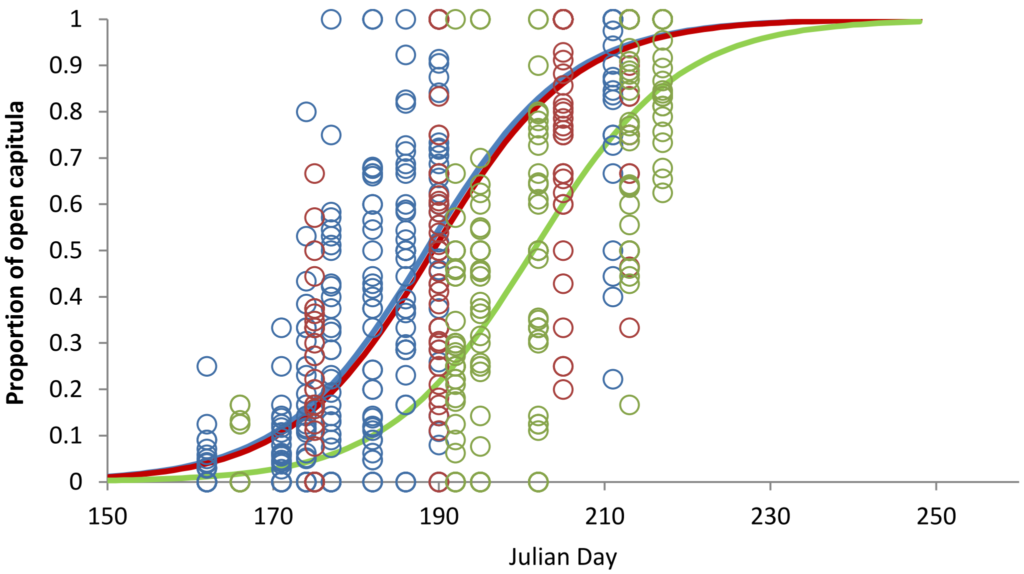


Figure 4.6: Comparison of flowering of *C. scabiosa* on south facing slopes at Totternhoe (blue circles), Brockadale (red circles) and Wingate (green circles) during 2011. Each data point is an individual surveyed plant. Fitted model curves of corresponding colour indicate predicted model fit, incorporating site effect.

Analysis focusing on sub-site and year effects at Wingate Quarry suggests that both peak flowering ($\bar{x}$) and length of flowering period (β) at Wingate are influenced by sub-site (i.e. variable aspect/topography) and year (Table 4.3; Figure 4.7).

Table 4.3: Model selection results from beta-binomial model fitted to flowering phenological data for *C. scabiosa* at Wingate Quarry. M_1-M_4 refer to models 1-4 outlined in section 2.2.4.

Model	K	Predictors	LL	ΔAIC
M_1	3	None	-7031.2	752.8
M_2	9	Sub-site	-6894.1	491.3
M_3	17	Year	-6745.5	209.5
M_4	23	Year and sub-site	-6634.8	0.0

Peak flowering of *C. scabiosa* is consistently predicted to be earlier at southerly aspects than either flat or northerly aspects. Flowering on north-facing aspects is predicted to peak 2 days later than flat sites and 8 days later than southerly aspects (Table 4. 4; Figure 4.7). There is evidence of variable flowering periods between years; flowering period from 2004 to 2006 declined by approximately 10 days a year with flowering periods of 80, 61 and 50 days on south facing slopes in years 2004, 2005 and 2006 respectively (Table 4.4). Flowering period on flat sites in 2001 is predicted to be 93 days, longer than any other predicted flowering period. Day of peak flowering also varies among years for a given sub-site.

Table 4.4: Variability in date of peak flowering and flowering period of *C. scabiosa* between years and sub-sites at Wingate Quarry, County Durham. $\bar{x}$ denotes the Julian day by which 50% of capitula are predicted to be open according to the beta-binomial model (Equation 4.4). FP denotes the length of the flowering period in days defined as the time between which 5-95% of capitula are predicted to be open by the beta-binomial model (Equation 4.4). ~ denotes missing data.

	Year													
	2001		2003		2004		2005		2006		2008		2011	
Sub-site	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP	$\bar{x}$	FP
Flat	207	93	199	53	210	76	212	60	207	49	220	38	207	46
North	~	~	~	~	212	78	214	60	209	50	~	~	209	46
South	~	~	~	~	204	80	206	61	201	50	~	~	201	48

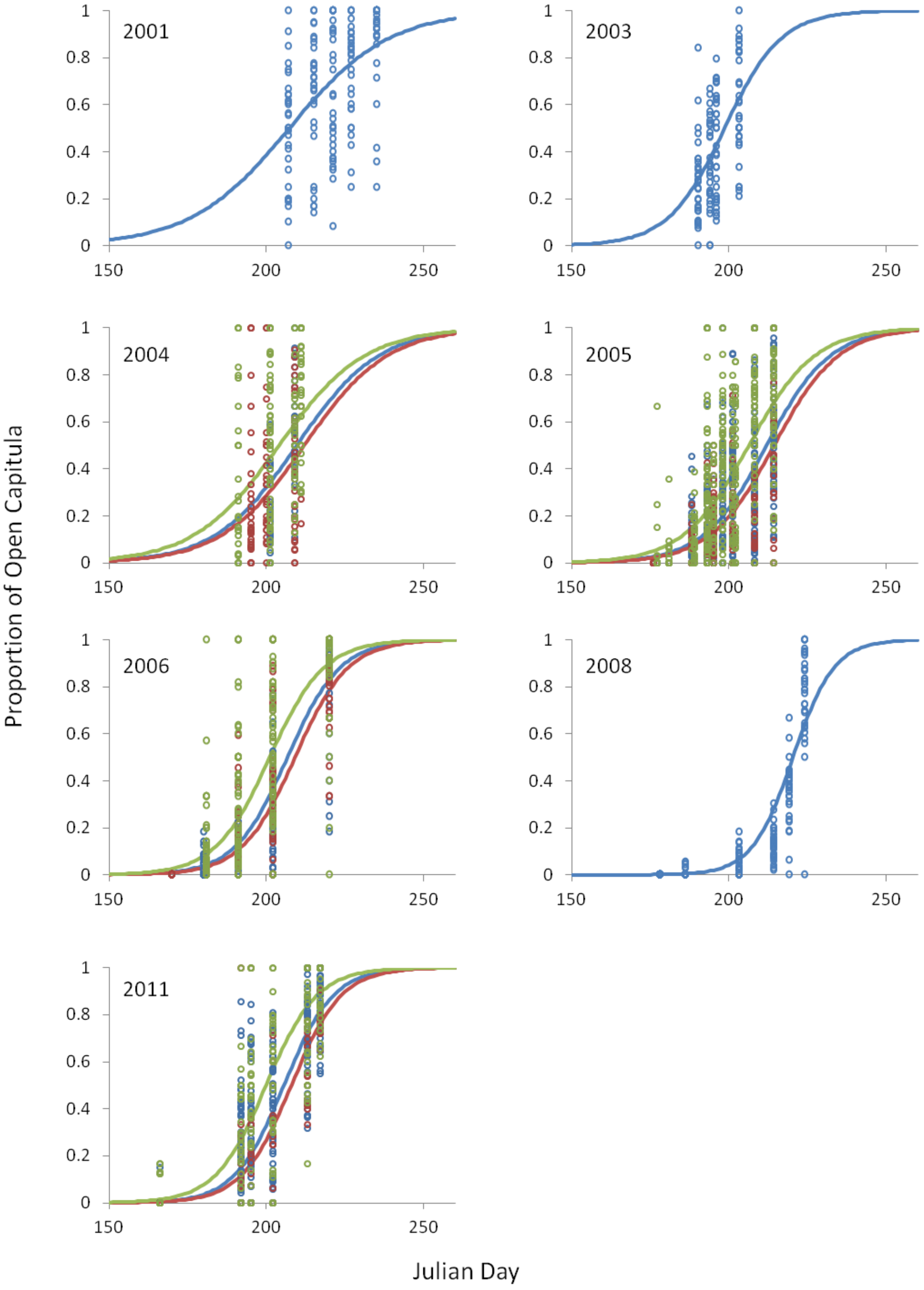


Figure 4.7: Inter-annual and inter-site variability in proportion of open capitula on *C. scabiosa* plants with time at Wingate Quarry, County Durham. Blue circles indicate flat survey sites, red circles north facing survey sites and green circles south facing survey sites. One circle represents a single surveyed plant. Fitted beta binomial model curves of corresponding colour indicate predicted model fit, incorporating year and site effects, for flat, north and south facing survey sites.

4.3.3 Part 3: Regional heterogeneity in the flight period of *Melanargia galathea*

There is evidence of inter-annual variability in the phenology of *M. galathea* at the three sites (Table 4.5). At Totternhoe there is evidence that peak abundance, date of peak abundance (Figure 4.8) and duration of the flight period of *M. galathea* differ inter-annually (Table 4.5; Table 4.6; Figure 4.8). *AIC* model selection criterion suggest that three alternative models are able to explain the observed data at Brockadale in years 2007 and 2008 with ΔAIC<6 (Table 4.5). Best model (*ΔAIC* = 0) as achieved when parameter σ remains constant across years suggesting limited variability in the duration of the flight period between years. Model selection suggests that best model fit for data observed at Wingate is also achieved when parameter σ remains constant across years but date of peak abundance was allowed to vary. This suggests that the flight period remains fairly constant but shifting in its timing between years (Figure 4.8).

Table 4.5: Model selection results from Poisson model fit to *M. galathea* abundance data at Totternhoe, Brockadale and Wingate. M_1-M_4 refers to models 1-4 outlined in part 2.2.5. $\bar{T}$ is the day on which peak abundance, Y_{max}, is reached. Term σ refers to the width of the distribution (duration of the flight period).

Site	Model	K	Predictors	LL	ΔAIC
Totternhoe	M_1	4	Null	-284.9	54.9
	M_2	24	$Y_{max,}\bar{T}$	-242.3	9.7
	M_3	24	$Y_{max,}\sigma$	-269	63.2
	M_4	34	$Y_{max,}\bar{T},\sigma$	-227.5	0.0*
Brockadale	M_1	4	Null	-82.6	28.4
	M_2	7	$Y_{max,}\bar{T}$	-66.4	0.0*
	M_3	6	$Y_{max,}\sigma$	-68.3	3.8*
	M_4	6	$Y_{max,}\bar{T},\sigma$	-66.4	2.0*
Wingate	M_1	4	Null	-78.4	23.9
	M_2	14	$Y_{max,}\bar{T}$	-56.5	0.0*
	M_3	14	$Y_{max,}\sigma$	-64.2	15.3
	M_4	19	$Y_{max,}\bar{T},\sigma$	-54.9	6.8

Date of peak abundance of *M. galathea* is on average earlier at Totternhoe when compared to Wingate (Table 4.6; Figure 4.8). In line with findings for date of peak flowering of *C. scabiosa* at Brockadale, peak abundance dates of *M. galathea* here are more similar to peak abundance dates predicted for data from Totternhoe than from the geographically closer Wingate study site. Data from Totternhoe in 2000 displays two peaks in abundance (Figure 4.8) which results in an abnormally long flight period (73 days). This data year may be influencing model selection results and may be the reason model fit is so greatly improved when parameter σ is allowed to vary between years (Table 4.5), in contrast to model selection results for both Brockadale and Wingate.

Table 4.6: Best model predictions (ΔAIC=0) for peak abundance (Y_{max}), day of peak abundance, ($\bar{T}$), measure of width of flight period (σ) and flight period in days of *M. galathea* (FPmg) at Totternhoe, Brockadale and Wingate between years. Flight period is defined as the predicted number of days between which >1 butterfly has emerged and >1 butterfly still remains.

	Totternhoe				Brockadale				Wingate			
Year	Y_{max}	$\bar{T}$	Σ	FPmg	Y_{max}	$\bar{T}$	σ	FPmg	Y_{max}	$\bar{T}$	σ	FPmg
1995	33	195	8.1	43	~	~	~	~	~	~	~	~
1996	102	203	5.6	34	~	~	~	~	~	~	~	~
1997	72	198	9.8	57	~	~	~	~	~	~	~	~
1998	40	203	10.6	57	~	~	~	~	~	~	~	~
2000	27	203	14.2	73	~	~	~	~	~	~	~	~
2001	72	195	8.8	51	~	~	~	~	~	~	~	~
2002	~	~	~	~	~	~	~	~	11	197	8.1	35
2004	~	~	~	~	~	~	~	~	7	207	8.1	32
2005	~	~	~	~	~	~	~	~	8	197	8.1	33
2006	98	192	9.4	57	~	~	~	~	6	202	8.1	31
2007	65	191	9.8	57	73	185	11.7	69	~	~	~	~
2008	35	198	11.4	61	261	192	11.7	78	~	~	~	~
2009	53	187	6.9	39	~	~	~	~	5	207	8.1	29
2010	~	~	~	~	~	~	~	~	~	~	~	~
2011	75	184	7.9	46	~	~	~	~	27	194	8.1	46

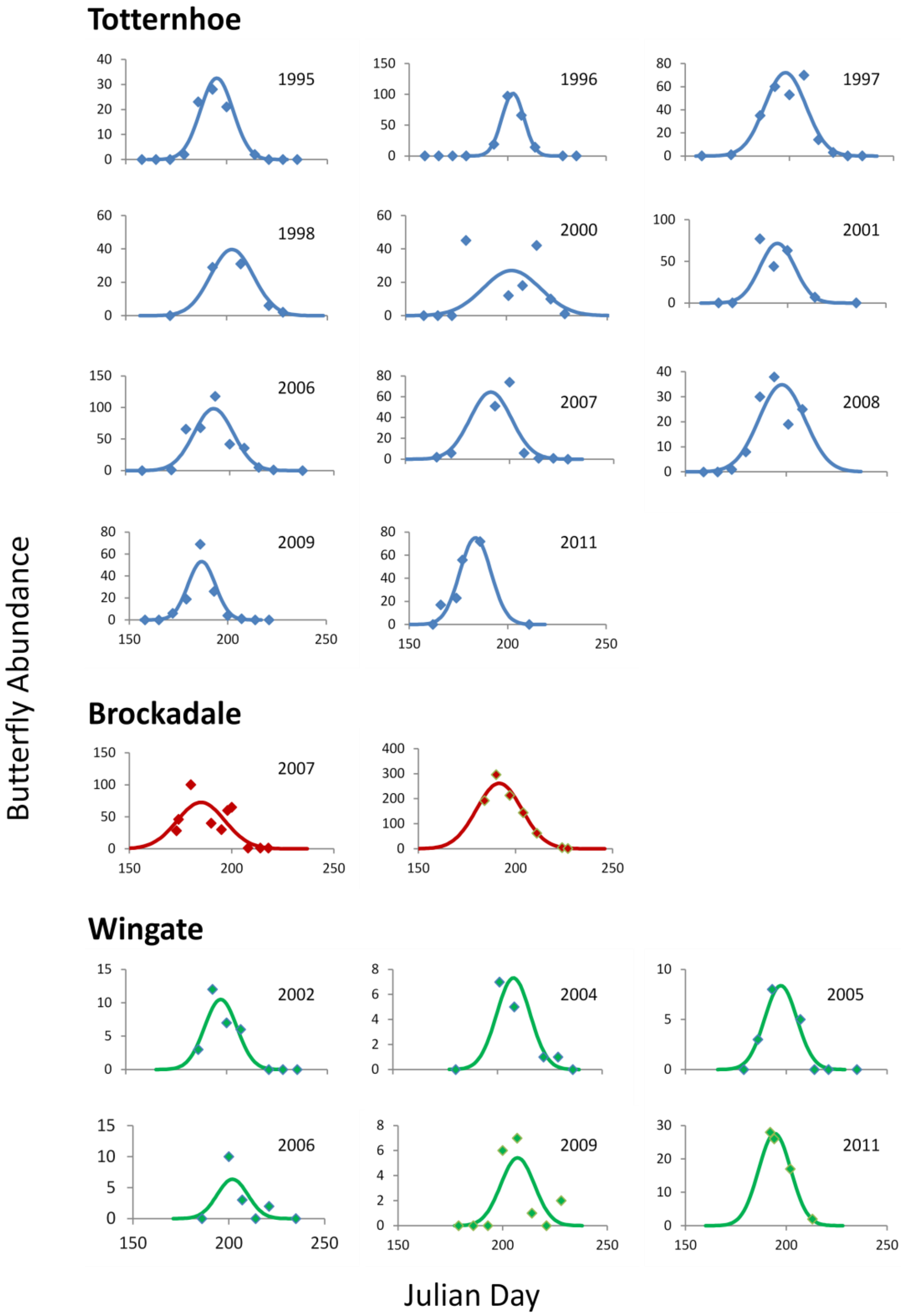


Figure 4.8: Inter-annual variability in *M. galathea* abundance data (diamonds) and best model fit ($\Delta AIC = 0$; solid line) at Totternhoe, Brockadale and Wingate between surveyed years.

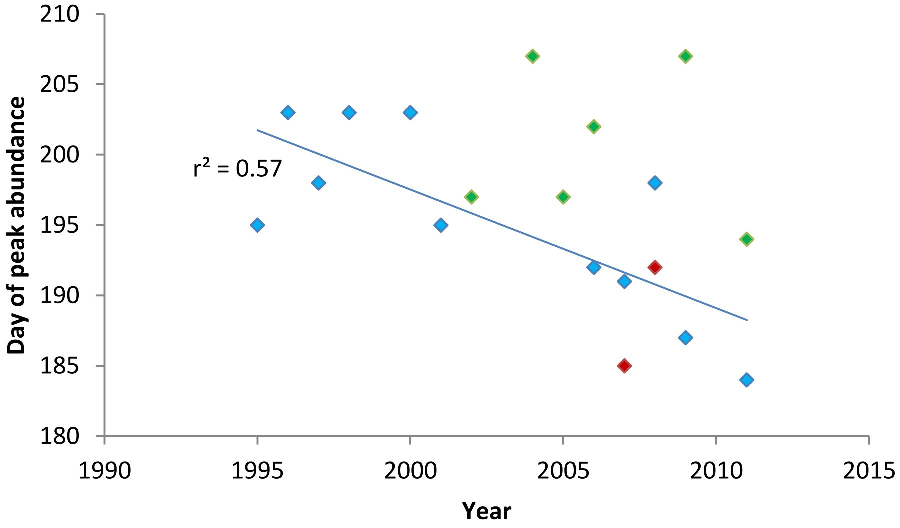


Figure 4.9: Variability in peak abundance date (Julian Day) of *M. galathea* at three study sites; Totternhoe (blue), Brockadale (red), and Wingate (green) as predicted by best fitting models. Linear regression line (blue) is fit to data for Totternhoe, $r^2 = 0.57$.

Figure 4.9 suggests that there is evidence that date of peak abundance of *M. galathea* has advanced at Totternhoe during the survey period (Table 4.6). Linear regression line with an r^2 value of 0.57 indicates a negative association between year and day of peak abundance of *M. galathea* at Totternhoe (Figure 4.9). The same pattern is not apparent in data for Wingate ($r^=$ 0.0089), and too few years were available for Brockadale. Table 4.8 compares modelled peak abundance of *M. galathea,* $\bar{T}$, and modelled peak flowering of *C. scabiosa*, $\bar{x}$, among years and sites for which both model parameters were estimated.

Table 4.7: Comparable years for which values for which both peak abundance of *M. galathea,* $\bar{T}$, and modelled peak flowering of *C. scabiosa*, $\bar{x}$, among years and sites were calculated. $\bar{x}$ values for a given year were calculated by averaging predicted best fitting modelled $\bar{x}$ across all surveyed sub-sites (refer to Tables 4.2 and 4.4 for Totternhoe and Wingate respectively).

Site	Year	$\bar{T}$	$\bar{x}$
Totternhoe	2011	184	186
Wingate	2004	207	209
	2005	197	211
	2006	202	207
	2011	194	207

Peak abundance of *M. galathea,* $\bar{T}$, is predicted to occur consistently earlier than peak flowering of *C. scabiosa*, $\bar{x}$, across comparable years and sites (Table 4.7). Wingate was the only site for which both annual *C. scabiosa* and *M. galathea* data were available. A comparison of modelled peak abundance of both *C. scabiosa* and *M. galathea* at Wingate among years suggests that predicted day of peak abundance of *M. galathea* is far more variable than predicted day of peak abundance of *C. scabiosa* (maximum difference 13 days and 4 days respectively; Table 4.7).

4.3.3 Synthesis of temperature, flowering and butterfly activity

Figure 4.10 shows inter-site variability in proportion of open capitula on *C. scabiosa* plants with time at Wingate (a and b) and Totternhoe (c and d) as predicted by best fitting beta-binomial models incorporating site effects. This is shown in conjunction with best fitting model predictions of abundance of *M. galathea* (ΔAIC = 0) and mean maximum daily temperature as recorded by all loggers positioned at a site.

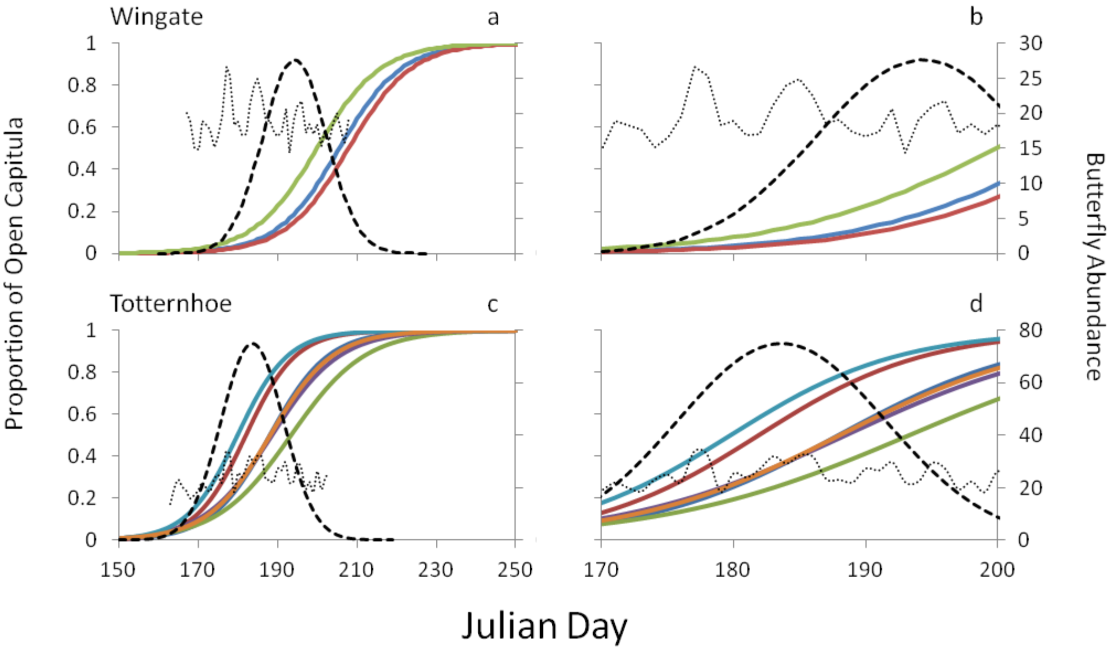


Figure 4.10: Proportion of open capitula (coloured lines), butterfly abundance (thick black dash line) and mean maximum daily temperature (thin black dash line) against Julian days in 2011 at Wingate (top - a and b) and Totternhoe (bottom - c and d). Coloured lines represent proportion of open capitula predicted by best fitting models at aspects surveyed at Wingate (south - green; north -red; flat - light blue) and Totternhoe (east - dark blue; east-south-east - orange; south-east - green; south - purple; south-west - light blue; west - red). Thick dash line represents the predicted butterfly abundance in 2011 (best model fit ΔAIC = 0).

Comparison of figures for Wingate (Figure 4.10 a and b) and Totternhoe (Figure 4.10 c and d) clearly show that date of first emergence and peak abundance of *M. galathea* occurs 10 days later at Wingate (Julian day 194), the northernmost site, compared to Totternhoe (Julian day 184) the southernmost site. Maximum butterfly abundance is predicted to be higher at Totternhoe than Wingate, 75 and 27 individuals respectively. Both show high variability in mean maximum daily temperature recorded at the sites, with greater fluctuations apparent at Wingate. Timing of peak flowering was also earlier at Totternhoe with peak flowering dates ranging from Julian day 180-193 with a mean of 186, in comparison to Wingate where day of peak flowering ranged from day 201-209 with a mean of 206. Date of mean peak flowering and peak butterfly emergence shows better synchrony at Totternhoe (days 186 and 184 respectively) than Wingate (days 206 and 194 respectively). This suggests that phenological mismatch may be occurring at Wingate. Given that individual butterflies live for approximately 3 weeks (www.wildaboutbritain.co.uk/marbled-white-butterfly - accessed 10.06.2013), this degree of mismatch (12 days) could have significant effects on adult feeding success during the flight period.

4.4 Discussion

This study investigated phenological patterns of flowering and insect emergence in an established insect-pollinator relationship at three calcareous/magnesium limestone grassland sites, along a north-south transect in England. Evidence of both intra and inter-annual variation in flowering phenology of the long-lived perennial *C. scabiosa* was found at both the local and regional scales. At the local scale these findings were in relation to observed variation in micro-habitat characteristics (in most cases aspect) and associated microclimatic conditions. Data from the 2011 field season demonstrated that peak flowering of *C. scabiosa* occurs 13 days earlier on south-westerly slopes when compared to south-east facing slopes at Totternhoe. Earlier peak flowering also occurred on south-west facing slopes at Wingate when compared with south-east slopes but only by two days. Given that adult *M. galathea* are on the wing for approximately 3 weeks, high variability in the timing of availability of nectar sources at Totternhoe could have biologically significant impacts on feeding adults. All sub-sites at Brockadale were south facing and so such a comparison could not be made. At Wingate, inter-annual, peak flowering of *C. scabiosa* was consistently predicted to be earlier on warmer south facing slopes than on flat areas and on cooler north facing slopes. This is in line with research by Jackson (1966), who found that flowering dates of 9 species were advanced by an average 6 days when compared to north facing slopes. This is also consistent with findings by Dunne *et al.* (2003) who found that experimental warming of plots advanced flowering, and that plants flowered earliest on south facing slopes in natural plots. Peterson (1997) also found that flowering phenology varied according to aspect, with delayed flowering observed on northerly aspects.

Dunne *et al.* (2003) found that flowering period was the longest on south facing plots; data from this study predicted that the flowering season of *C. scabiosa* at Totternhoe and Wingate was longest on south-east facing aspects, 55 and 71 days respectively. However, there were inconsistencies in the length of flowering season on other comparable aspects, for example the south-westerly aspect at Totternhoe had a relatively short 37day season, the shortest predicted flowering period at this site. Conversely, the same aspect at Wingate was predicted to have the second longest flowering period at this site of 58days. South-west facing aspects have been shown to experience the most intense solar radiation (Hasse, 1970; Bennie *et al.,* 2010). It is possible that the south-westerly aspects at Totternhoe, the southern-most site, are too warm and dry to allow extended flowering in these locations. Whilst at Wingate, the south-westerly aspects are just sufficiently warm and dry to allow for extended flowering at this more northern latitude. Wind is also known to affect plant growth by reducing soil moisture and water balance in leaves (Humphries and Roberts, 1964). Lapworth and Mcgregor (2008) showed that the prevalent wind direction across the majority of the UK in the autumn, winter and summer months is south-westerly while in the spring north-easterly and south-westerly winds are equally prevalent. The relative exposure of different aspects to these winds is another factor that should be considered when analysing timing of flowering in *C. scabiosa.* Since the predominant wind direction in summer is south-westerly, wind induced moisture stress on plants growing on south-west facing slopes at Totternhoe may have resulted in the short growing flowering season observed at this aspect (37 days).

This study has shown the potential for heterogeneous landscapes to reduce or extend (depending on the frequency of north and south facing aspects within a habitat) the flowering season of a key butterfly resource plant in calcareous/magnesium limestone grassland ecosystems. This finding has potentially important ramifications for reserve selection and reserve management practices; if the overall aim is to extend the length of time that nectar is available as a resource for insect pollinators then reserves with maximal topographical heterogeneity should be selected for use as wildlife sanctuaries. Management practices can also be put into place to encourage habitat heterogeneity at a site by manipulating levels of shading for example. This research has shown that consideration of spatial and topographic structure of habitats is of essential importance in research pertaining to the impacts of climate on species ecology at fine spatial scales.

Evidence of variation in date of peak abundance of *M. galathea* both intra and inter-annually was found at a regional scale. This is in line with findings by Stefanescu *et al.* (2003) who, in a study of 17 butterflies resident to the north-west Mediterranean Basin, found that, despite a tendency for earlier emergence from 1988-2002, there was no regular pattern discernible in the shape of the curve of adult emergence between years. The variation observed in the phenology of *M. galathea* at the regional scale is in line with variation in both micro-climatic temperature data analysis and patterns of phenological timing observed in *C. scabiosa* flowering. Both date of peak flowering and date of peak abundance of *M. galathea* were advanced at the southern site, Totternhoe, where temperature readings were on average higher, compared to the northern site, Wingate, where temperature readings were on average lower. This variation is in line with spatial variation in the sighting dates of British butterflies observed by Roy and Asher (2003). They found that in general, British butterflies were sighted 3-4 days later with every 100km shift north. At Brockadale, however, the situation seems a little more complex than the expected south-north variation might suggest. Patterns of flowering and butterfly emergence at Brockadale are much more in line with the warmer, southern site Totternhoe, than the cooler, and geographically closer, northern site Wingate. This finding is also in line with temperature data for this site which suggests much warmer microclimates than might be expected of this quite northerly site. It may be that the geographical designation of this site as a valley and subsequent protection from the wind is creating a far warmer microclimate than regional scale latitudinal climates might otherwise suggest.

Inter-annual peak flowering dates of *C. scabiosa* at Wingate range from an earliest predicted date of Julian day 199 on flat areas in year 2003, to the latest predicted date of day 214 in northerly facing locations in year 2005. There is evidence of declining duration of flowering period between years 2004 to 2006 (Table 4.4). This may be the result of inter-annual variability in climatic factors influencing flowering period or an artefact of the variable number of survey dates each year. Generally, peak flowering occurs earliest on south facing locations and latest at north facing locations. In comparable years, 2004, 2005, 2006 and 2011, both date of peak flowering and date of peak abundance of *M. galathea* at Wingate were predicted and compared. With the exception of year 2004, in which both peak flowering and peak abundance of *M. galathea* occur on Julian day 207, peak abundance seems to be occurring slightly earlier than peak flowering. This could be viewed as a mismatch that was greatest in years 2005 and 2011 when peak flowering occurred 13 and 12 days later than peak abundance of *M. galathea* respectively. However, in a review of the literature, Elzinga *et al.* (*2007*) found that pollinators tend to favour peak or early flowering, whilst Peterson (1997) found that butterflies were more often encountered in plant patches in full bloom (i.e. peak flowering). If *M. galathea* is a species that prefers early flowering, the plant and pollinator in this study may be well matched. However, if phenological mismatch is occurring at this site and this species in fact favours peak flowering, butterflies here are starting to die off before peak flowering is reached. This means that potentially, butterflies are missing out on peak production of nectar by one of their primary nectar sources at this site. On average, across all of the aspects surveyed in 2011 at Totternhoe, peak flowering of *C. scabiosa* occurs on Julian day 186, whilst peak abundance of *M. galathea* is predicted to occur by day 184 suggesting that at this site *M. galathea* favours peak flowering. This is, however, only a comparison of one year of data and findings must be treated as preliminary. The degree of synchrony between peak flowering and peak abundance of *M. galathea* at Wingate showed variation between years, solidifying the need to conduct long term surveys. For example peak flowering and peak abundance of *M. galathea* occurred on average by Julian day 209 and 207 respectively in 2004, and by Julian day 211 and 197 respectively in 2005.

If phenological mismatch is occurring between *C. scabiosa* and *M. galathea* at either the sites there will be ecological repercussions for both the plant and pollinator (Hodgson *et al.,* 2011). Many plants rely entirely or partially on insect pollination for successful reproduction (Elzinga *et al.,* 2007); temporal mismatches in plant-pollinator systems could reduce the seed set of the plants and the amount of food available to pollinators (Hodgson *et al.,* 2011). When modelling the potential impacts of raised CO_2 levels on phenological mismatch in plant-pollinator interactions, Memmott *et* al. (2007) found that floral resources available to pollinators were reduced by 17-50% as a consequence of simulated phenological shifts, and that reduced phenological overlap resulted in a decreased diet breadth in pollinators. It must be remembered however, that although *C.scabiosa* constitutes a primary nectar source in the diet of *M. galathea*, this butterfly can and will utilise a number of other nectar sources. As such the question of phenological mismatch between this species and its nectar sources is far more complicated that the timing of flowering in *C. scabiosa* alone. It is also important to remember that different plant resources are important at different stages in the flight season of these adult butterflies, with patterns of resource use differing between males and females (Auckland *et al.,* 2004). In line with this, synchronisation of the butterfly flight period with both larval host and adult nectar plants is important if reproductive success is to be optimised. As such to truly discern whether phenological mismatch is occurring between this species and its resource plants, more comprehensive data collection involving multiple plant species is necessary.

There was also evidence of annual variability in maximum abundance of *M. galathea* at each of the study sites. This is line with findings by Pollard (1991), who in an analysis of UKBMS transect survey data found there was evidence of annual population fluctuations of butterflies at monitored sites between years 1976-1989. This is best demonstrated by the Totternhoe site, for which 11 years of abundance data were available and maximum abundance predictions ranged from a low of 27 in 2000, to a high of 102 in 1996. A number of anthropogenic and environmental factors may have caused these fluctuations; the weather is a primary factor influencing annual abundance in butterfly populations (Woods *et al.,* 2008). Monthly rainfall and temperature have been shown to be important in predicting abundance patterns of British butterflies. For example, in an analysis of UKBMS transect data, Pollard (1988) found that high summer rainfall was always significantly associated with lower butterfly abundance. He also found that many butterfly abundance values were significantly higher during warm summers but that for some species the opposite was true, for example numbers of *A. hyperantus* and *P. aegeria* were reduced during high summer temperatures, highlighting the need for an individualistic approach to assessing weather patterns on butterfly numbers. Roy *et al.* (2001) found strong associations between the weather in current and previous summers and abundance patterns of *M. galathea*. Another factor that may influence local inter-annual variation in butterfly abundance is changing habitat quality (Clausen *et al.,* 2001), most likely resulting from anthropogenic intervention. Small changes in the management of a grassland site like Totternhoe, for example the degree of scrub control or grazing pressure exerted in a given year will alter habitat quality by increasing shading and presence of competitors in turn influence butterfly numbers. These changes may occur as a result of lack of resources or funding for management and may become increasingly important factors affecting abundance of butterflies in light of recent governmental budget cuts. Luoto *et al.* (2001) concluded that the most important environmental factors influencing abundance of *Parnassius mnemosyne* (clouded Apollo butterfly), were abundance of adult nectar plants and larval host plants, but that climate and topographic factors also played a role. Schultz and Dlugosch (1999) also found that size of butterfly populations is correlated with resource availability.

The importance of calcareous grassland to butterflies has been recognised in the research literature (Van Swaay, 2002). The ability of these grasslands to support viable populations of butterflies will vary with respect to management plan (grazing, control of scrub encroachment, use of herbicides to remove weed species), topography and position within the local landscape (for example proximity to agricultural fields or urban areas). The present study has demonstrated how heterogeneous landscapes within this ecosystem can potentially improve the productivity of the system by increasing the flowering season of *C. scabiosa,* a nectar plant utilised by 17 resident British butterfly species, from four families, including 4 species of conservation concern (Butterfly Conservation Online - accessed 25.07.2012). Many studies have highlighted the importance of plentiful nectar resources in butterfly ecology; Murphy (1983) and Murphy *et al.* (1983) demonstrated how stable population dynamics in *Euphydryas* butterflies*,* were closely linked to availability of nectar resources. Grossmueller and Lederhouse (1987) found that egg-laying in *Papilio glaucus* (tiger swallowtail butterfly) was concentrated in areas with plentiful nectar resources. Calcareous grassland is a flower-rich ecotype; if the same phenological response to topographic heterogeneity is true of other plants within this ecosystem, the potential benefits of preserving and promoting such heterogeneity within reserve systems could be far reaching. Although it has been recognised that species phenological responses to temperature are variable (Dunne *et al.,* 2003; Woods *et al.,* 2008; Primack *et al.,* 2009; Ibanez *et al.,* 2010; Tooke and Battey, 2010; Hodgson *et al.,* 2011) and as such it is important to assess to responses of plants to changing climates in an individualistic manner before broad conclusions are drawn. Not only is topographically induced microclimatic variation potentially important in extending the flowering period, it has also thought to play an important role in enabling species to persist near the edge of their range (Bennie *et al.,* 2008; Bennie *et al.,* 2010). In addition, habitat heterogeneity has been shown to promote and correlate with higher species diversity and density of species (Weibull *et al*., 2000), and has been increasingly linked with the stability of populations (Oliver *et al.,* 2010). These results in combination with the results of the present study suggest that conserving topographically diverse sites may help to conserve a greater range of biodiversity than flat sites and may aid in reserve selection decisions by land managers.

The present study has demonstrated the existence of microclimatic variation of air surface-temperature with regards to aspect at each of the study sites. Observed variation in air temperature from within surveyed sites can be explained in terms of the amount of solar radiation received by certain aspects during daylight hours; solar radiation estimates indicate that south facing aspects receive more annual solar radiation per unit area than do other aspects of the same slope in the Northern Hemisphere (Haase, 1970). This variation in microclimate may directly influence the timing of flowering in the study species. There are however, many other contributing factors that must be considered and future investigations should focus on disentangling those micro-climatic induced ecological variables that directly influence phenological processes (Bennie *et al.,* 2010). Despite this it is known that temperature does play a vital role in the timing of flowering (Weiss and Weiss, 1998; Fitter and Fitter, 2002); plants within the same population often flower asynchronously as a result of variation in the micro-environment they are exposed to (Elzinga *et al.,* 2007). This characteristic of flowering has been demonstrated at all three sites in this study and is an ecological trait that can be manipulated to favour longer flowering seasons for our pollinating insects. However, this is only a preliminary study and long term monitoring is essential if management objectives are to be effectively targeted and implemented in light of recent and predicted future environmental change (Morecroft *et al.,* 2009).

Phenological shifts are a realistic and observable means of tracking climate change at all spatial scales (Weiss and Weiss, 1998). There is already a large body of research focusing on phenological impacts of global change on phenological processes occurring at the regional scales. This study has demonstrated the importance of recognising that microclimatic conditions experienced by an individual organism can vary substantially from the broader regional scale climate as measured by meteorological networks (Bennie *et al*., 2008) with implications for both reserve selection and species translocation methodology. Findings in the present study suggest that topographically diverse areas present a broader range of microclimates that can act to extend the flowering period of plants, increasing the amount of time nectar is available to pollinating insects. Topographically variability could thus act as a buffer to phenological mismatch induced by future climate change and could be used as a reserve selection criterion for conservation organisations. Under future climate change predictions many species may require human intervention to disperse to new climatically suitable areas. This study has demonstrated how timing of events such as flowering and emergence vary along a north-south transect. As such care must also be taken when translocating individuals from one site to another in order to avoid phenological mismatch between insect pollinator and its larval host and adult food plants if translocation of individuals is to be a successful conservation measure.

Chapter 5

Final conclusions and challenges for the future

British butterflies are the most intensely studied insect fauna in the world (Warren *et al.,* 2007). With a wealth of readily available, comprehensive ecological field data pertaining to population trends and distribution status (Pollard *et al.,* 1993; Fox *et al.,* 2010), they represent a rare opportunity to assess the impacts of a wide range of modern issues facing biodiversity today. A notable sensitivity to both habitat and climate factors and relatively short generation times make butterflies a valuable indicator species for monitoring the effects of environmental change on ecosystems and biodiversity (Roy and Sparks, 2000; Stefanescu *et al.,* 2003; Warren *et al.,* 2007; Woods *et al.,* 2008). Anthropogenic pressures on butterflies over the past century, both in relation to habitats and climate, have resulted in substantial changes to the distribution status of many species (Parmesan *et al.,* 1999; Thomas *et al.,* 2001; Warren *et al.,* 2001; Hickling *et al.,* 2006; Sparks *et al.,* 2007; Fox *et al.,* 2010; Devictor *et al.,* 2012). Utilising UKBMS field data the first aim of this thesis was to identify and mathematically capture important variables that determine species range extent and simulate the present day range extent of four generalist butterfly species, *P. aegeria, A. hyperantus, P. tithonus and M. galathea*.

Many studies support the existence of variable population dynamic parameters at many spatial scales (Haddad and Baum, 1999; Thomas *et al.,* 2001; Auckland *et al.,* 2004; Underwood, 2007). In this thesis I have demonstrated how assumptions made about the ecology of modelled species have ill-represented population dynamics, possibly to the detriment of model outcomes. In the past models have assumed that density of generalist butterflies within the simulated landscape is homogeneous among variable occupied habitats (Hill *et al.,* 2001; Auckland *et al.,* 2004; Willis *et al.,* 2009a). Using UKBMS transect survey field data from multiple sites and multiple occupied habitats, I demonstrated how density in occupied habitats is heterogeneous for three out of the four habitat generalists studied (Chapter 2, section 2.3). In view of these findings, I proceeded to incorporate this knowledge into spatially explicit, dynamic population models with the aim of increasing the ecological validity of such models. Distributional change of four generalist British butterflies between the years 1970 and 2009 was modelled accurately in relation to both habitat (maximum TSS>0.64) and climate suitability (maximum TSS>0.59; Chapter 3, section 3.3).

Phenological responses of wildlife to climate change have become apparent across a wide range of taxa (Roy and Sparks, 2000; Viser and Holleman, 2001; Fitter and Fitter, 2002; Roy and Asher, 2003; Stefanescu *et al.,* 2003; Ibanez *et al.,* 2010; Wilson and Roy, 2011). Studies are already reporting incidences of phenological mismatch within our ecosystems. For example Viser and Holleman (2001) fond that egg hatching of the winter moth, *Operophtera brumata,* and bud burst of oak, *Quercus robur,* on which larvae feed showed poor syncrony in recent warm springs. Using an empirical model of plant-pollinator interactions Memmott *et al.* (2007) demonstrated the potentially far reaching ramifications of phenological mismatch on ecosystem functioning. When modelling phenological shifts between 1420 insect pollinators and 429 plant species expected from a doubling of atmospheric CO_2 they found that mismatches reduced plant resources available to 17-50% of insect pollinators. This thesis has demonstrated how heterogeneous landscapes (with regards to topography and aspect) could potentially mitigate against phenological mismatch occurring in an insect-pollinator system by increasing the duration of the flowering period, extending the time when nectar is available to pollinating insects (Chapter 4, section 4.3). Given that habitat heterogeneity is particularly amenable to anthropogenic manipulation through practical landscape management such as scrub control, hedge creation, woodland creation/removal, hand seeding of wild flower meadows and pond creation and (Oliver *et al.,* 2010), incorporating an understanding of these processes into predictive models of spread and subsequently management policy could aid in protecting species from the negative impacts of climate warming on phenology (Gillingham *et al.,* 2012).

Variable and complex responses of species to climate change are evident in the literature (Warren *et al.,* 2001; Walther *et al.,* 2002; Sparks *et al.,* 2006; Thomas *et al.,* 2006; Warren *et al.,* 2007; Gonzalez-Megias, 2008; Wilson and Roy, 2011) and highlight the importance of a dynamic approach to biodiversity conservation. UKBMS data has shown that many generalist butterfly species are expanding their range northwards, in keeping with predicted responses of generalists to modern-day climate change (Warren *et al.,* 2001). This observation is also in keeping with findings here; future simulation model predictions suggest that both *M. galathea* and *P. tithonus* will expand their range north by 15.3% and 7.8% respectively between 2009 and 2060 (Chapter 3, section 3.3.3). In contrast, recent analysis of UKBMS transects data shows that 93% of specialist species have declined since surveys began in 1976 (Warren *et al.,* 2007). Whilst some species are benefitting from a warming climate others are experiencing marked declines in range sizes. Many northern species, such as the northern brown argus (*Aricia agestis*) and mountain ringlet (*Erebia* epiphron), are become increasing isolated to fragments of suitable habitat as suitable climate space is pushed northwards (Warren *et al.,* 2007). Southern species on the other hand, particularly southern generalist species, have seen dramatic increases in range size since following range expansion northwards since 1976 (Asher *et al.,* 2001; Gonzalez-Megias, 2008).

Many climatic variables other than temperature influence butterfly life histories, both directly and via impacts on their larval and adult food plants (Woods *et al.,* 2008). Pollard (1988) identified significant associations between rainfall and reduced butterfly numbers in the current year. In addition, a positive association between rainfall early in the previous year and butterfly numbers in the current year was found. It was suggested that this is due to the positive effect of rain on subsequent larval and adult food plants (Pollard, 1988). Woods *et al.* (2008) found that counts were highest on warm days with moderate amounts of wind. He also concluded that both previous and current year's temperature and rainfall were important in determining butterfly numbers in the current year. He found a positive relationship between wet winters and butterfly numbers in the following summer and concluded this was the result of impact of precipitation on butterfly host plants. Whilst warm, dry weather may favour adult activity, warm damp weather favours larval development due to subsequent effects of weather on host plants. Heterogeneous landscapes that buffer against the effects of short-term changes in weather on butterfly communities are likely to be important in the future as climates become more erratic. Predictive models must take into account suitability of climate for all stages of the butterfly life cycle and perhaps most importantly the impact of climate on the distribution of larval and adult food plants.

If models are to be used to identify those species at risk and inform conservation strategies we must first appreciate the numerous responses to climate change observed among species. Incorporating the potential for physiological and morphological change in response to climate change (Dell *et al.,* 2005; Buckley *et al.,* 2010; Hill *et al.,* 2011) into predictive models will be a challenge for future research. Many studies have now observed variation in habitat associations (Thomas *et al.,* 2001; Oliver *et al.,* 2009), reproductive output (Hanski and Saccheri, 2006), flight morphology (Merckx and Van Dyck, 2006) and dispersal propensity and ability (Thomas *et al.,* 2001; Hughes *et al.,* 2003; Hagg *et al.,* 2005; Dytham, 2009; Hill *et al.,* 2011) among individuals and populations across a species range, particularly at the leading range edge (Thomas *et al.,* 2001). At present these factors are not considered in predictive models of spread, but may go a long way to explain the rate of range expansion witnessed in recent decades and act as an important determinant of future changes (Hill *et al.,* 2011). Identification of such variable responses to climate change among taxa also further solidify the need for a dynamic approach to conservation strategies.

There are many factors other than climate change that are impacting on the population and distribution status of butterflies in Great Britain and across the globe. Many of these factors relate to anthropogenic land use change in particular in relation to agricultural intensification and mechanisation post-war. Agriculture is currently the primary land use in Europe (Brittain *et al.,* 2010) and it has led to habitat fragmentation, loss of semi-natural habitats, reduction in habitat quality and increased inputs of agrochemicals such as pesticides, herbicides, fungicides and fertilisers (Geiger *et al.,* 2010). Traditional management practices of semi-natural grasslands for haymaking and stock grazing have largely been abandoned (Saarinen, 2002) leading to scrub encroachment and subsequent loss of wildflower and insect pollinator habitat. Polarisation of agriculture in Great Britain, with pastoral farming focussed in the west and arable farming in the east has also led to loss of habitat diversity (Robinson and Sutherland, 2002). This, coupled with loss of non-cropped field margins, removal of hedgerows to allow movement of machinery, loss of ponds and copes led to a dramatic reduction in habitat heterogeneity on farmland post-war resulting in large reductions in associated farmland biodiversity with around a third of insects and half of plants experiencing declines (Robinson and Sutherland, 2002).

Use of agrochemicals to maximise crop outputs by increasing soil fertility (chemical fertilisers) and suppressing non-crop plants and pests (herbicides and insecticides) has increased markedly post-war. Non-target organisms such as butterflies are exposed to such chemicals as a result of spray drift and direct overspray leading to dermal contact and ingestion (Russell and Schultz, 2009). There is still uncertainty about the ecological risks of agrochemicals on non-target species with conflicting findings reported from research and many species exhibiting variable responses to exposure (Brittain *et al.,* 2010). In a study which mimicked in-field herbicide treatment regimes, Russell and Schultz (2009) reported a reduction in survival of 32% when *Pieris rapae* (small white) larvae were exposed to the herbicide sethoxydin and 21% when exposed to fluazifop-*p*-butyl. The same herbicide treatments were not associated with a reduction in survival of the butterfly *Icaricia icarioides blackmorei* (puget blue). They also found that multiple life stages were affected, with both pupal weights and wing size of adult butterflies reduced in *P. rapae* when treated with herbicides as larva (Russell and Schultz, 2009). This variability in susceptibility has also been demonstrated for insecticides, with timing of life histories shown to determine which species are most susceptible (Robinson and Sutherland, 2002). These variable impacts across species highlight the importance of species specific toxicological screenings.

In recent years, attitudes towards agricultural practice have changed in the UK; organic farming has expanded massively since the 1990s and in 2011, 656,000 hectares of UK land was organically farmed (DEFRA - Organic Statistics 2011 - accessed online 08.06.2013). Organic farms exclude the use of synthetic chemicals, use traditional crop rotation system incorporating grass leys and generally have a greater area of uncropped habitat such as hedgerows (Feber *et al.,* 2007). Feber *et al.* (2007) found that organic farms had increased species richness and abundance of butterflies than non-organic farms and that the uncropped field margins were hosted the most individuals. Uptake of agri-environment schemes put in place by the government to provide incentives for conventional farmers to manage their land in a way that is sensitive to the conservation of biodiversity has also been encouraging, with nearly 3 million hectares of land brought under Environmental Stewardship in its first year from 2005-2006 (Defra, 2005; Defra, 2006). The advent of organic farming and schemes like Environmental Stewardship are likely to have played a role in the recent expansion of many of our butterfly species (Fox *et al.,* 2008), particularly the generalist species which have been shown to be typical of British farmland today (Robinson and Sutherland, 2002). Expansion and recovery of butterfly populations directly relating changes in agricultural practice is difficult to quantify and represent in models of range expansion. This is made harder still by the distinct lack of monitoring on agricultural sites which account for 77% of the UK's total land area (Angus *et al.,* 2009).This is an area of future research that must be explored if we are to accurately model range expansion of butterflies and indeed many other species across the British landscape.

Many of the habitats utilised by butterflies such as semi-unimproved grasslands, hedgerows, woodland rides and glades require intensive management if late successional stages such as scrub and woodland are not to take over. Maintenance of these habitats is a primary goal of nature conservation organisations and land owners such as Natural England, National Trust, the RSPB and the Wildlife Trusts. However such management requires extensive man hours and capital and in light of the recent recession many of these organisations have had their budgets cut and have been forced to reduce costs by way of staff cuts and reduced staff hours. For example Natural England, a government organisation, has had their budget cut by 21.5% for the period 2011-2015 representing a £44.2 m reduction in spending (www.naturalengland.org - Annual report and accounts 2011-2012). Whilst publically funded bodies such as the Wildlife Trusts and the RSPB, which rely primarily on public and business donations, lottery funding and government environmental stewardship grants have been hit by both governmental budget cuts and a reluctance of the public and local businesses to donate to charity in times of recession. The conservation sector is increasingly relying on volunteers and as such if volunteer recruitment fails to meet the deficit in staff levels many nationally important conservation sites may fall into unfavourable condition impacting species numbers and persistence.

Despite recent budget cuts, local and landscape scale habitat improvement schemes are in place which may benefit flora and fauna in the future. Recently, The Coronation Meadows Project has been announced. This project involves the recognition of nationally important wildflower meadow sites and their subsequent use as donor sites for the creation of new meadows across Great Britain (www.coronationmeadows.org.uk - accessed 06.06.2013). These sites will be highly valuable habitat for pollinators such as butterflies providing both larval host and adult nectar plants whilst increasing connectivity of existing habitat patches aiding in dispersal and range expansion. In response to recent habitat fragmentation primarily caused by urban sprawl and agricultural land use practices, The Wildlife Trusts have pioneered The Living Landscapes Scheme (www.wildlifetrusts.org.uk - accessed 06.06.2013). This scheme focuses on landscape-scale conservation and aims to create and restore habitat corridors through which disconnected species populations can colonise and re-colonise isolated habitats. At present there are 100 Living Landscape Schemes being carried out throughout Great Britain, one of which is the 'West Cambridgeshire Hundreds' a scheme which aims to link isolated fragments of ancient woodland across West Cambridgeshire through woodland and hedgerow restoration (www.wildlifebcn.org/westcambshundreds - accessed 06.06.2013). If successful, these schemes will undoubtedly improve the ability of butterflies to disperse through the landscape and may aid future range expansion. However, the relative ability of such schemes to combat the loss of habitat that will be associated increasing population pressure, for example in the UK the population is projected to increase from 62.3 million in 2010 to 73.2 million by 2035 (Office for National Statistics, 2012), is yet to be realised. If models of future range expansion are to be accurate in predicting future spread, human-induced changes to the landscape, both positive and negative, need to be considered.

The importance of landscape scale conservation in response to increasingly fragmented and isolated habitats (Dewenter and Tscharntke, 2000; Hill *et al.,* 2001) has been recognised (Warren *et al.,* 2007). At present butterfly conservation efforts in Britain are focussing on both maintaining and extending current habitat networks as a means of allowing species to respond to environmental change in a natural way (Warren *et al.,* 2007). This includes creating corridors of habitat in a fragmented landscape that will allow species to disperse between larger patches of suitable habitat (Haddad and Baum, 1999). If such measures are not plausible or effective enough in the short term, then translocations of species may become necessary to enable species to track environmental change (Hoegh-Guldberg, 2008; Caroll *et al.,* 2009). Assisted colonisation experiments have been met with success in recent years, both confirming how species are lagging behind suitable climate (Menendez *et al.,* 2006; Devictor *et al.,* 2012) and demonstrating how translocations could form a viable and valuable part of species conservation plans (Willis *et al.,* 2009b).

The community composition of many British butterflies' assemblages has changed since 1976 (Gonzalez-Megias, 2008). These changes have been characterised by an increase in the number of generalist species in communities whilst specialist species have declined (Gonzalez-Megias, 2008). Identifying and prioritising those species most at risk from environmental change is high on the agenda of conservationists and policy makers (Warren *et al.,* 2007). Dynamic population modelling incorporating demographic parameters and environmental data informed by observed ecological field data provide valuable insights into species responses to environmental change. A crucial next step in ecological modelling is to incorporate multiple species within the same modelling framework allowing each species their each own set of parameters. By doing so there is the potential to predict how species interact and persist as part of a dynamically changing community. These models would enable us to assess dominance within communities and identify which species will be able to coincide under variable environments.

Species ranges are in continual flux as a result of demographic, genetic and environmental variation (Buckley *et al.,* 2010). A broad understanding of how these factors influence distributions of species at both local and regional scales is necessary if to inform effective conservation strategies in view of a wide array of anthropogenic pressures (Morecroft *et al.,* 2009). Future research must continue to recognise the importance of an individualistic approach to forecasting responses of species to environmental change whilst expanding our knowledge of how species interact in a dynamically changing environment. Continued degradation and loss of key wildlife habitats as a result of anthropogenic land use change and climate warming pose serious threats to biodiversity and subsequent challenges to conservation policy makers (Warren *et al.,* 2007). Given the limited resources available for biodiversity conservation, ensuring conservation policies are targeted and effective (Warren *et al.,* 2007) by increasing the accuracy and robustness of predictive models is paramount (McPherson and Jetz, 2007; Zurell *et al.,* 2009).

References

Ahas, R., Assa, A., Menzel, A., Fedotova, V.G. & Scheifinger, H. (2002) Changes in European spring phenology. *International Journal of Climatology*, **22**, 1727-1738.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,* **43**, 1223-1232.

Angus, A., Burgess, P.J., Morris, J. & Lingard (2009) Agriculture and land use: Demand for and supply of agricultural commodities, characteristics of the farming and food industries, and implications for land use in the UK. *Land Use Policy,* **26**, 230-242.

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

Aukland, J.N., Debinski, D.M. & Clark, W.R. (2004) Survival, movement, and resource use of the butterfly *Parnassius clodius*. *Ecological Entomology*, **29**, 139-149.

Ayres, M.P. & Scriber, J.M. (1994) Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecological Monographs*, **64**, 465-482.

Baguette, M. (2003) Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography*, **26**, 153-160.

Baguette, M., Petit, S. & Queva, F. (2000) Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology,* **37**, 100-108.

Baguette, M. & Schtickzelle, N. (2003) Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology,* **40**, 404-412.

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

Beirne, B.P. (1955) Natural fluctuations in abundance of British Lepidoptera. *Entomological Gazette*, **6**, 21-52.

Bennie, J.J., Huntley, B., Wiltshire, A., Wilson, M. O. & Baxter, R. (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling,* **216**, 47-59.

Bennie, J.J., Wiltshire, Joyce, A.N., Clark, D., Lloyd, A.R., Baxter, R. & Huntley, B. (2010) Characterising inter-annual variation in the spatial pattern of thermal microclimate in the UK upland using a combined empirical-physical model. *Agricultural and Forestry Meteorology*, **150**, 12-19.

Bergman, K-O. (2001) Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. *Journal of Applied Ecology*, **38**, 1303-1313.

Birch, L.C. (1948) The intrinsic rate of natural increase in an insect population. *Journal of Animal Ecology*, **17**, 15-26.

Blanckenhorn, W.U. & Demont, M. (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: Two ends of a continuum? *Integrative and Comparative Biology*, **44**, 413-424.

Box, J. (1999) Nature conservation and post-industrial landscapes. *Industrial Archaeology Review,* **21**, 137-146.

Box, G.E.P. and Draper, N.R. (1987) *Empirical model building and response surfaces*. John Wiley & Sons Inc., USA.

Braschler, B. & Hill, J.K. (2007) Role of larval host plants in the climate-driven range expansion of the butterfly *Polygonia c-album*. *Journal of Animal Ecology*, **76**, 415-423.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J. & Potts, S.G. (2010) Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology,* **11**, 106-115.

Brook, B.W., Akcakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araujo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723-725.

Buckley, J., Bridle, J.R. & Pomiankowski, A. (2010) Novel variation associated with species range expansion. *BMC Evolutionary Biology*, **10**, 382-384.

Burnham, K.P. & Anderson, D,R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach, second edition*. Springer.

Cant, E.T., Smith, Reynolds, D.R. & Osbourne, J.L. (2005) Tracking butterfly flight paths across the landscape with harmonic radar. *Proceedings of the Royal Society B.,* **272**, 785-790.

Carroll, M.J., Anderson, B.J., Brereton, T.M., Knight, S.J., Kudrna, O. & Thomas, C.D. (2009) Climate change and translocations: The potential to re-establish two regionally-extinct butterfly species in Britain. *Biological Conservation*, **142**, 2114-2121.

Caughley, G. & Birch, L.C. (1971) Rate of increase. *The Journal of Wildlife Management,* **35**, 658-663.

Clausen, H.D., Holbeck, H.B. & Reddersen, J. (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation*, **98**, 167-178.

Chuine, I. (2010) Why does phenology drive species distribution? *Phil. Trans. R. Soc. B.,* **365**, 3149-3160.

Cleveland, W.S. & Devlin, S.J. (1988) Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, **83**, 596-610.

Collinge, S.K., Prudic, K.L. & Oliver, J.C. (2003) Effects of local habitat characteristics and landscape b context on grassland butterfly diversity. *Conservation Biology,* **17**, 178-187.

Conradt, L., Bodsworth, E.J., Roper, T.J. & Thomas, C.D. (2000) Non-random dispersal in the butterfly *Manioloa jurtina*: implications for metapopulation models. *Proc. R. Soc. Lond. B*, **267**, 1505-1570.

Crick, H.Q.P. & Sparks, T.H. (1999) Climate change related to egg-laying trends. *Nature,* **399**, 423-424.

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

Crozier, L. (2004) Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology,* **85**, 231-241.

Davies, C.E., Moss, D. & O'Hill, M. (2004) *EUNIS habitat classification revised 2004*. European Environment Agency, European topic centre on nature protection and biodiversity.

Davis, B.N.K., Lakhani, K.H., Yates, T.J. and Frost, A.J. (1991) Bioassays of insecticide spray drift: the effects of wind speed on the mortality of *Pieris brassicae* larvae (Lepidoptera) caused by difubensuron. *Agriculture, Ecosystems and Environment,* **36**, 141-149.

Defra (2005) *Environmental stewardship: higher level stewardship handbook.* PB10382. Rural development service, Defra, UK.

Defra (2006) http://statistics.defra.gov.uk/esg/statnot/orgeng.pdf - accessed online 08.06.2013.

Dell, D., Sparks, T.H., Dennis, R.L.H. (2005) Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly *Apatura iris* (Lepidoptera: Nymphalidae). *European Journal of Entomology,* **102**, 161-167.

Dennis, R.L.H. & Sparks, T.H. (2007) Climate signals are reflected in an 89 year series of British Lepidoptera records. *European Journal of Entomology*, **104**, 763-767.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliola, J., Herrando, S., Julliard, R., Kuussaari, M., Lindstrom, A., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., DeVries, M.W., Wynhoff, I & Jiguet, F. (2012) Differences in climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121-124.

Dewenter, I.S. & Tscharntke, T. (2000) Butterfly community structure in fragmented habitats. *Ecology Letters*, **3**, 449-456.

Diamond, S.E., Frame, A.M., Martin, R.A. and Buckley, L.B. (2011) Species traits predict phenological responses to climate change in butterflies. *Ecology,* **92**, 1005-1012.

Dunne, J.A., Harte, J. & Taylor, K.J. (2003) Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs*, **73**, 69-86.

Dunlap, B., Hannigan, A., Petersen, C., Boettcher, C., Bradbury, S., Evans, J., Keith, A., Nelson, A. and Warbler, J. (2000) The effect of humidity on the egg development and survivorship of the Monarch Butterfly (*Danaus plexippus)*. The Monarch Laboratory Website. [http://www.monarchlab.org/research/GD/Chan.htmp - accessed online 20.05.2013}.

Dytham, C. (2009) Evolved dispersal strategies at range margins. *Proceedings of Royal Society B*, **276**, 1407-1413.

Easterling, D.R., Evans, J.L., Groisman, P.Y., Karl, T.R., Kunkel, K.E. and Ambenje, P. (2000a) Observed variability and trends in extreme climatic events: A brief review. *Bulletin of the American Meteorological Society,* 417-425.

Eastering, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. and Mearns, L.O. (2000b) Climate extremes: observations, modelling and impact. *Science,* **289**, 2068-2074.

Ellis, J. (2006) *Brownfield sites of conservation importance for butterflies and moths in the West Midlands*. *Butterfly Conservation report,* S06-09.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E. & Bernasconi, G. (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology and Evolution*, **22**, 432-439.

Environment agency position statement (2003). *Brownfield land redevelopment: position statement* [www.environment-agency.gov.uk/research/library/position/41237.aspx - accessed online 24.05.2013]

Eyre, M.D., Luff, M.L. & Woodward, J.C. (2003) Beetles (Coleoptera) on brownfield sites in England: An important conservation resource? *Journal of insect conservation,* **7**, 223-231.

Fahrig, L. & Merriam, G. (1994) Conservation of fragmented populations. *Conservation Biology*, **8(1)**, 50-59.

Feber, R.E., Johnson, P.J., Firbank, L.G., Hopkins, A. & MacDonald, D.W. (2007) A comparison of butterfly populations on organically and conventionally managed farmland. *Journal of Zoology*, **273**, 30-39.

Fitter, A.H. & Fitter, R.S.R. (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689-1691.

Forister, M.L., and Shapiro, A.M. (2003) Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, **12**, 1545-1553.

Fox, R., Asher, J., Brereton, T.M., Roy, D.B. & Warren, M.S. (2008) *The state of butterflies in Britain and Ireland.* Pisces Publications, Oxford.

Fox, R., Warren, M.S., Brereton, T.M., Roy, D.B. and Robinson, A. (2010) A new Red List of British butterflies. *Insect Conservation and Diversity*, **4(3)**, 159-172.

Fuller, R. M., Smith, G.M., Sanderson, J.M., Hill, R.A., Thomson, A.G., Cox, R., Brown, N.J., Clarke, R.T., Rothery, P. & Gerard, F.F. (2002a) Land cover map 2000: A guide to the classification system (extract from final draft report). *Countryside Survey 2000 Module 7, Centre for Ecology and Hydrology.*

Fuller, R. M., Smith, G.M., Sanderson, J.M., Hill, R.A., Thomson, A.G., Cox, R., Brown, N.J., Clarke, R.T., Rothery, P. & Gerard, F.F. (2002b) Land cover map 2000: Final Report. *Countryside Survey 2000 Module 7, Centre for Ecology and Hydrology.*

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., part, T., Bertagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., thies, C., Flohre, A., Hanke, S., Fishcher, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control on European farmland. *Basic and Applied Ecology*, **11**, 97-105.

Gibbs, M., Van Dyck, H. & Breuker, CJ. (2012) Development on drought stressed host plants affects life history, flight morphology and reproductive output relative to landscape structure. *Evolutionary Applications*, **5**, 66-75.

Gilbert, L.E. & Singer, M.C. (1973) Dispersal and gene flow in a butterfly species. *American Naturalist*, **107**, 58-72.

Gillingham, P.K., Palmer, S.C.F., Huntley, B., Kunin, W.E., Chipperfield, J.D. & Thomas, C.D. (2012) The relative importance of climate and habitat in determining the distributions of species at different spatial scales: a case study with ground beetles in Great Britain. *Ecography*, **35**, 1-8.

Gonzalez-Megias, A., Menendez, R., Roy, D., Breretons, T. & Thomas, C.D. (2008) Changes in the composition of British butterfly assemblages over two decades. *Global Change Biology,* **14**, 1464-1474.

Goulson, D. (2013) Bees need Europe's pesticide ban, whatever UK says. *New Scientist*. http://www.newscientist.com/article/dn23465-bees-need-europes-pesticide-ban-whatever-the-uk-says.html - accessed online 09.06.2013.

Grime, J., Hodgson, J. & Hunt, R. (1988) *Comparative plant ecology: a functional approach to common British species*. 1st Addition. Unwin Hyman, London.

Grossmueller, D.W. & Lederhouse, R.C. (1987) The role of nectar source distribution in habitat use and oviposition by the tiger swallowtail butterfly. *Journal of Lepidopterists' Society*, **41**, 159-165.

Guisan, A. & Thuiller, W. (2005) Predicting species distributions: offering more than simple habitat models. *Ecology Letters,* **8**, 993-1009.

Gutierrez, D. and Menendez, R. (1998) Phenology of butterflies along an altitudinal gradient in northern Spain. *Journal of Zoology,* **244**, 249-264.

Haddad, N.M. & Baum, K.A. (1999) An experiment test of corridor effects on butterfly densities. *Ecological Applications,* **9,** 623-633.

Hagg, C.R., Saastamoinen, M., Marden, J.H. & Hanski, I. (2005) A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proceedings of the Royal Society B.,* **272**, 2449-2456.

Hanski, I., Eralahti, C., Kankare, M., Ovaskainen, O. & Siren, H. (2004) Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters,* **7**, 958-966.

Hanski, I. & Saccheri, I. (2006) Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biology,* **4**, e129.

Hasse, E.F. (1970) Environmental fluctuations on south-facing slopes in the Santa Catalina Mountains of Arizona. *Ecology,* **51**, 959-974.

Hepper, F.N. (2003) Phenological records of English garden plants in Leeds (Yorkshire) and Richmond (Surrey) from 1946 to 2002). An analysis relating to global warming. *Biodiversity and Conservation*, **12**, 2503-2520.

Helms, S.E., Connelly, S.J. & Hunter, M.D. (2004) Effects of variation among plant species on the interaction between a herbivore and its parasitoid. *Ecological Entomology*, **29**, 44-51.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology,* **12**, 450-455.

Hill, J.K., Collingham, Y.C., Thomas, C.D., Blakeley, D.S., Fox. R., Moss, D. & Huntley, B. (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters,* **4**, 313-321.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011) Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143-159.

Hill, J.K., Hughes, C.L., Dytham, C. & Searle, J.B. (2006) Genetic diversity in butteflies: interactive effects of habitat fragmentation and climate-driven range expansion. *Biology Letters,* **2**, 152-154.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. Lond. B,* **269**, 2163-2171.

Hill, J.K., Thomas, C.D. & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc. R. Soc. Lond.* B., **266**, 1197-1206.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crones, E.E. (2011) Predicting insect phenology across space and time. *Global Change Biology*, **17**, 1289-1300.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonisation and rapid climate change. *Ecology,* **321**, 345-346.

Holt, R.D. (2009) Bringing the Huntchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences USA,* **106**, 19659-19665.

Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A. & Taper, M.L. (2005) Theoretical models of species' borders: single species approaches. *Oikos,* **108**, 18-27.

Hughes, C.L., Hill, J.K. & Dytham, C. (2003) Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Trends in Ecology and Evolution*, **15(2)**, 56-61.

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

Huntley, B., Berry, P.M., Cramer, W. & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plant using climate response surfaces. *Journal of Biogeography*, **22**, 967-1001.

Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis* **148**, 8-28.

Hutchinson, G.E. (1978). An introduction to population ecology. *Yale University Press,* New Haven, CT.

Ibanez, I., Primack, R.B., Miller-Rushing, A.J., Ellwood, E. Higuchi, H., Lee, S.D., Kobori, H. & Silander, J.A. (2010) Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B.,* **365**, 3247-3260.

IPCC (2007) *Climate Change 2007: Working Group 1, the Scientific Basis.* Cambridge University Press, Cambridge.

Jackson, M.T. (1966) Effects of microclimate on spring flowering phenology. *Ecology*, **47**, 407-415.

Karl, T.R., Jones, P.D., Knight, R.W., Kukla, G., Plummer, M., Razuvayev, V., Gallo, K.P., Lindseay, J., Charlson, R.J. & Peterson, T.C. (1993) Asymmetric trends of daily maximum and minimum temperature. *Bulletin of the American Meteorological Society,* **74**, 1007–1023.

Keith, D.A., Akcakaya, H.R., Thuiller, W., Midgeley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araujo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560-563.

Kingsolver, J.G. & Huey. R.B. (2008) Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research,* **10**, 251-268.

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

Lack, A. (1976) Competition for pollinators and evolution in *Centaurea*. *New Phytologist,* **77**, 787-792.

Lawton, J.H. (1995) The response of insects to environmental change. In: *Insects in a Changing Environment* (eds R Harrington & N E Stork). Academic Press, London. pp. 3-26.

Linderholm, H.W. (2006) Growing season changes in the last century. *Agricultural and Forest Meteorology*, **137**, 1-14.

Longley, M. & Sotherton, N.W. (1997) Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. *Agriculture, Ecosystems and Environment*, **61**, 1-12.

Luoto, M., Kuussaari, M., Rita, H., Salminen, J. & von Bonsdorff, T. (2001) Determinants of distribution and abundance in the Clouded Apollo butterfly: A landscape ecological approach. *Ecography*, **24(5),** 601-617.

Luoto, M., Kuussaari, M. and Toivonen, T. (2002) Modelling butterfly distribution based on remote sensing data. *Journal of Biogeography,* **29**, 1027-1037.

McCauley, D.E., Schiff, N., Breden, F.J. & Chippendale, G.M. (1995) Genetic differentiation accompanying range expansion by the southwestern corn borer (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America*, **99**, 357–361

McLeod, S.R. (1997) Is the concept of carrying capacity useful in variable environments? *Oikos*, **79**, 529-542.

McPherson, J.M. & Jetz, W. (2007) Effects of species' ecology on the accuracy of distribution models. *Ecography*, **30**, 135-151.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710-717.

Menendez, R., Megıas, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the. Royal Society B*, **273**, 1465–1470.

Menzel A., et al. (2006) European phenological response to climate change matches the warming pattern*. Global Change Biology,* **12***,* 1969–197.

Merckx, T. & Van Dyck, H. (2006) Landscape structure and phenotypic plasticity in the flight morphology in the butterfly *Parage aegeria*. *Oikos*, **113**, 226-232.

Merckx, T. & Dyck, H.V. (2007) Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. *Animal Behaviour*, **74**, 1029-1037.

Merckx, T., Van Dyck, H., Karlsson, B. & Leimar, O. (2003) The evolution of movements and behaviour at boundaries in different landscapes; A common arena experiment with butterflies. *Proceedings of the Royal Society of London Series B,* **270**, 1815-1821.

Midgeley, G.F., Davies, I.D., Albert, C.H., Altwegg, R., Hughes, G.O., O'Halloran, L.R., Seo, C., Thorne, J.H. & Thuiler, W. (2010) BioMove - an integrated platform simulating the dynamic response of species to environmental change. *Ecography,* **33(3)**, 612-616.

Miller-Rushing , A.J., Hoye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Phil. Trans. R. Soc. B.,* **365**, 3177-3186.

Miller-Rushing, A.J., Inouye, D.W. & Primack, R.B. (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology*, **96**, 1289-1296.

Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Hart, J.D. & Moore, N.P. (2000) Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology*, **37**, 706-727.

Morecroft, M.D., Bealey, C.E., Beaumont, D.A., Benham, S., Brooks, D.R., Burt, T.P., Critchley, C.N.R., Dick, J., Littlewood, N.A., Monteith, D.T., Scott, W.A., Smith, R.I., Walmsley, C. and Watson, H. (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation,* **142**, 2814-2832.

Morrin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Biology Letters,* **4**, 573-576.

Morris, D.W., Diffendorfer, J.E. & Lundberg, P. (2004) Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection. *Oikos*, **107**, 559-575.

Morrison, J.I.L. and Morecroft, M.D. (2006) *Plant growth and climate change.* Blackwell Publishiing, Oxford.

Mouradov, A., Cremer, F. & Coupland, G. (2002) Control of flowering time: Interacting pathways as a basis for diversity. *The Plant Cell,* S111-S130 (Supplement).

Murphy, D.D. (1983) Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly, *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). *Environmental Entomology*, **12**, 463-466.

Murphy, D.D., Launer, A.E. & Ehrlich, P.R. (1983) The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oceologia*, **56**, 257-263.

Mousseau, T.A. (1997) Ectotherms follow the “Converse to Bergman’s Rule”. *Evolution,* **51**, 630-632.

Natural England Annual Report and Accounts 1 April 2011 to 31 March 2012 (2012) [publications.naturalengland.org.uk/publication/1738763 - accessed online 04.06.2013]

Newland, D.E. (2006) *Discover butterflies in Britain.* Princeton University Press.

Nicholls, C.N. and Pullin, A.S. (2003) The effects of flooding on survivorship in overwintering larvae of the large copper butterfly *Lycaena dispar batavus* (Lepidoptera: Lycaenidae), and its possible implications for restoration management. *European Journal of Entomology*, **100**, 65-72.

Nylin, S. & Svard, L. (1991) Latitudinal patterns in the size of European butterflies. *Holarctic Ecology,* **14**, 192-202.

Ockinger, E. Smith, H.G. (2006). Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia,* **149**, 526-534.

Office for National Statistics (2012) *Chapter 2: Results 2010 based NPP reference volume.* www.ons.gov.uk/ons/dcp171776_253934.pdf - accessed online 08.06.2013.

Oliver, T., Hill, J.K., Thomas, C.D., Brereton, T. & Roy, D.B. (2009) Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters,* **12**, 1091-1102.

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters,* **13**, 473-484.

Ovaskainen, O., Smith, A.D., Osborne, J.L., Reynolds, D.R., Carreck, N.L., Martin, A.P., Niitepold, K. & Hanski, I. (2008) Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *Proceedings of the National Academy of Sciences,* **105**, 19090-19095.

Pagel, J. & Schurr, F.M. (2011) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography,* **21**, 293-304.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *The Annual Review of Ecology, Evolution and Systematics*, **37**, 637-639.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T, Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional climate warming. *Nature*, **399**, 579-583.

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

Pearson, R.G. *&* Dawson, T.E. *(*2003*)* Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful*? Global Ecology and Biogeography,* **12***,* 361–372*.*

Pearson, R.G.*,* Dawson, T.E. *&* Liu, C. *(*2004*)* Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data*. Ecography,* **27***,* 285–298*.*

Pe'er, G., Saltz, D., Thulke, H.H. & Motro, U. (2004) Response to topography in a hilltopping butterfly and implications for modelling non-random dispersal. *Animal Behaviour,* **68**, 825-839.

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

Peterson, M.A. (1997) Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. *Ecological Society of America*, **78**, 167-180.

Peterson, A.T.*,* Ortega-Huerta, M.A.*,* Bartley, J.*,* Sánchez-Cordero, V.*,* Soberon, J.*,* Buddemeier, R.H. *&* Stockwell, D.R.B. *(*2002*)* Future projections for Mexican faunas under global climatic change scenarios*. Nature,* **416***,* 626–629.

Pollard, E. (1988) Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology,* **25**, 819-828.

Pollard, E. (1991) Changes in the flight period of the Hedge Brown butterfly *Pyronia tithonus* during range expansion. *Journal of Animal Ecology,* **60**, 737-748.

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

Pollard, E., Van Swaay, C.A.M., Yates, T.J. (1993) Changes in butterfly numbers in Britain and The Netherlands, 1990-91. *Ecological Entomology*, **18**, 93-94.

Pollard, E. & Yates, T. J. (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London.

Pollard, E. & Yates, T.J. (1996) Annual growth rates in newly established populations of the butterfly *Pararge aegeria*. *Ecological Entomology,* **21**, 365-369.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers*. Trends in Ecology and Evolution,* **25**, 345-353.

Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999) Biological responses to climate change on a tropical mountain. *Nature*, **398**, 611-615.

Poyry, J., Leinonen, R., Soderman, G., Nieminen, M., Heikkinen, R.K. & Carter, T.R. (2011) Climate-induced increase in of moth multivoltinism in boreal regions. *Global Ecology and Biogeography*, **20**, 289-298.

Primack R. B., Ibáñez I., Higuchi H., Lee S. D., Miller-Rushing A. J., Wilson A. M. & Silander J. A. Jr. (2009) Spatial and interspecific variability in phenological responses to warming temperatures*. Biological Conservation,* **142***,* 2569–2577*.*

Pullin, A.S. (1995) *Ecology and conservation of butterflies.* Chapman and Hall, London.

Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, **45**, 218-227

Ricker, W. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559-623.

Robinson, A.R. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157-176.

Root, R.B. (1960) An estimate of intrinsic rate of natural increase in the planarian, *Dugesia tigrina*. *Ecology,* **41**, 369-372.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60

Roy, D.B. & Sparks, T.H. (2000) Phenology of British butterflies and climate change. *Global Change Biology,* **6**, 407-416.

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

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

Rundolf, M. and Smith, H.G. (2006) The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology*, **43**, 1121-1127.

Russell, C. & Schultz, C.B. (2009) Effects of grass-specific herbicides on butterflies: an experimental investigation to advance conservation efforts. *Journal of Insect Conservation*, **14**, 53-63.

Rusterholz, H.P. & Erhardt, A. (1998) Effects of elevated CO_2 on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. *Oecologia*, **113**, 341-349.

Saarinen, K. (2002) A comparison of butterfly communities along field margins under traditional and intensive management in SE Finland. *Agriculture Ecosystems and Environment*, **90**, 59-65.

Schultz, C.B. & Dlugosch, K.M. (1999) Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. *Oecologia*, **119**, 231-238.

Schwartz, M.W.*,* Iverson, L.R. *&* Prasad, A. *(*2001) Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing*. Ecosystems,* **4***,* 568–581.

Schweiger, O., Dormann, C.F., Bailey, D. & Frenzel, M. (2006) Occurrence pattern of *Pararge aegeria* (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure. *Landscape Ecology*, **21**, 989-1001.

Shima, J.S. & Osenberg, C.W. (2003) Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology*, **84**, 46-52.

Sparks, T.H., Dennis, R.L.H., Croxton, P.J. & Cade, M. (2007) Increased migration of Lepidoptera linked to climate change. *European Journal of Entomology*, **104**, 139-143.

Sparks, T.H., Huber, K. & Dennis, R.L.H. (2006) Complex phenological responses to climate warming trends? Lesssons for history. *European Journal of Entomology*, **103**, 379-386.

Stefanescu, C., Penuelas, J. & Filella, I. (2003) Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1494-1506.

Stefanescu, C., Torre, I., Jubany, J. & Paramo, F. (2011) Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation,* **15**, 83-89.

Stevens, V.M., Turlure, C. & Baguette, M. (2010) A meta-analysis of dispersal in butterflies. *Biological Reviews*, **85**, 625-642.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, m. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577-581.

Thomas, C.D., Thomas, J.A. & Warren, M.S. (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia,* **92**, 563-567.

Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution,* **21**, 415-416.

Thomas, J.A. (1984) The conservation of butterflies in temperate countries: past efforts and lessons for the future. *Biology of Butterflies: Symposium of the Royal Entomological Society of London No. 11,* pp. 333-353. Academic Press, London, UK.

Thomas, J.A. (1995) The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society,* **56** (Supplement), 55-72.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R. & Goodger, B. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society B.,* **268**, 1791-1796.

Thomas, J.A., Moss, D. & Pollard, E. (1994) Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography,* **17**, 215-200.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R. (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55-64.

Tooke, F. & Battey, N. H. (2010) Temperate flowering phenology. *Journal of Experimental Botany*, **61**, 2853-2862.

Thuiller, W., Albert, C., Araujo, M.B., Berry, P.M., Cabeza, C.N., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global changes impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137-152.

Turner, E.C., Granroth, H.M.V., Johnson, H.R., Lucas, C.B.H., Thompson, A.M., Froy, H., German, R.N. & Holdgate, R. (2009) Habitat preference and dispersal of the Duke of Burgandy butterfly (*Hamearis lucina*) on an abandoned old chalk quarry in Bedfordshire, UK. *Journal of Insect Ecology*, **13**, 475-486.

Underwood, N. (2007) Variation in and correlation between intrinsic rate of increase and carrying capacity. *American Naturalist,* **169**, 136-141.

Underwood, N. & Rausher, M.D. (2000) The effects of host-plant genotype on herbivore population dynamics in a model system. *Ecology*, **81**, 1565-1576.

Van Swaay, C.A.M. (2002) The importance of calcareous grassland for butterflies in Europe. *Biological Conservation*, **104**, 315-318.

Visser, M.E. & Holleman, J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. B.,* **268**, 289-294.

Walmsley, C. and Watson, H. (2009) The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation* **142**, 2814-2832.

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature,* **416**, 389-395.

Warren, M.S. (1992) The conservation of British butterflies. In: Dennis, R.H.L. (Ed.), The Ecology of Butterflies in Britain. Oxford University Press, Oxford.

Warren, M.S. (1995) Managing local microclimates for the high brown fritillary, *Argynnis adippe. Ecology and Conservation of Butterflies,* **55**, 707-719.

Warren, M.S. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.

Warren, M.S., Asher, J., Brereton, T.M. & Roy, D.B. (2007) *The state of Britain's butterflies 2007*. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.H., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature,* **414**, 65-69.

Wedell, N., Nylin, S. & Janz, N. (1997) Effects of larval host plant and sex on the propensity to enter diapauses in the comma butterfly. *Oikos*, **78**, 569-575.

Weiss, S.B., Murphy, D.D. & White, R.R. (1988) Sun, slope, and butterflies: Topographic determinants of habitat quality for *Euphydryas editha*. *Ecology,* **69(5)**, 1486-1496.

Weiss, S.B. & Weiss, A.D. (1998) Landscape-level phenology of a threatened butterfly: A GIS-based modeling approach. *Ecosystems,* **1**, 299-309.

White, P.J.T. & Kerr, T. (2007) Human impacts on environment-diversity relationships: evidence for biotic homogenization from butterfly species richness patterns. *Global Ecology and Biogeography*, **16**, 290-299.

Wiebull, A.C., Bengtsson, J. & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and habitat heterogeneity. *Ecography*, **23**, 743-750.

Wiklund, C., Wickman, P-O. & Nylin, S. (1992) A sex difference in the propensity to enter direct/diapauses development: a result of selection for protrandry. *Evolution,* **46**, 519-528.

Williams, T.A. & Aberton, M.T. (2004) Earlier flowering between 1962 and 2002 in agricultural varieties of white clover. *Oecologia,* **138**, 122-126.

Willis, S.G., Hill, J.K., Thomas, C.D., Hill, J.K., Collingham, Y.C., Telfer, M.G., Fox, R., & Huntley, B. (2009a) Dynamic distribution modelling: predicting the present from the past. *Ecography*, **32**, 5-12.

Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S. & Huntley, B. (2009b) Assisted colonization in a changing climate: a test study using two U.K. butterflies. *Conservation Letters,* **2**, 45-51.

Wilson, R.J., Davies, Z.G. & Thomas, C.D. (2009) Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society B.,* **276**, 1421-1427.

Wilson, R.J., Davies, Z.G. & Thomas, C.D. (2009) Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. *Ecography,* **33**, 73-82.

Wilson, R.J. & Roy, D.B. (2011) Butterflies reset the calendar. *Nature Climate Change*, **1**, 101-102.

Woods, J.N., Wilson, J. and Runkle, J.R. (2008) Influence of climate on butterfly community and population dynamics in western Ohio. *Environmental Entomolgy,* **37**, 696-706.

Worcestershire Biodiversity Action Plan (2008) *Grizzled Skipper Species Action Plan*, Worcestershire Biodiversity Partnership [Available online at: http://www.worcestershire.gov.uk, accessed 16.04.2012]

Zaviezo, T., Grez, A.A., Estades, C.F. & Perez, A. (2006) Effects of habitat loss, habitat fragmentation, and isolation on the density, species richness and distribution of ladybeetles in manipulated alfalfa landscapes. *Ecological Entomology*, **31**, 646-656.

Zhou, X., Harrington, R., Woiwod, I.P., Perry, J.N., Bale, J.S. & Clark, S.J. (1995) Effects of temperature on aphid phenology. *Global Change Biology*, **1**, 303-313.

Zurell, D., Jeltsch, F., Dormann, C.F. & Schroder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32**, 733-744.

Appendices

Appendix list of tables

Table A0-1: UKBMS transect sites from which data was used to calculate separate values for intrinsic rates of increase for each of the four study species. Study species populations at all sites utilised were classified as increasing (regression slope is positive and $p<0.05$) by UKBMS at the time of data extraction (www.ukbms.org).

Species/Site lists

Pararge aegeria	***Athantopus hyperantus***	***Pyronia tithonus***	***Melanargia galathea***
West Hallam Ash Tip	Upper Teesdale	Friargate Station	Oxted Downs, Grangers Hill
Friargate Station	Smardale Gill	Beane Hill	Kingley Vale
Holkham	Ryton Wood	Roudsea	Knapp and Papermill
Holme Dunes	Newton Links	Rostherne Mere	Avon Gorge
Gibraltar Point	Avon Gorge 2	Castle Hill	Banstead Downs
Saltfleetby	Balls Wood	Catherington Down	Botley Wood 2
Perry Wood	Bedelands Farm NR	Perry Wood	Bunkers Park
Moor Farm	Brickett Wood	Ryton Meadows	Crabtree
Roudsea	Perry Wood	West Hallam Ash Tip	Juniper Hill
Butterfly Lane St Ives	Ryton Meadows	Winnal Moors	Lydden

Table A0-2: UKBMS transect sites with associated habitat classifications from which data was used to calculate separate values for mean density in occupied habitats for *Pararge aegeria*. Populations at all sites utilised were classified as stable (regression slope p>=0.05, e.g. not significant) by UKBMS, www.ukbms.org.

Marshy grasslands	**Chalk/limestone grassland**	**Broadleaved woodland**	**Heathland/heather moorland**	**Post-industrial**	**Mixed woodland**
Pamphill Moors	Aldbury Nowers	Alice Holt	Sopley Common	Ufton Fields1	Chambers Farm Wood
Itchen Valley CP meadows	Hod Hill (NT)	Eaves Wood	Bartley Heath New 1	Sovell Down (DTNC)	Crabtree
Moors Valley	Headley Heath	Denge Wood	Ashdown Forest, Warren car park	Portland Broadcroft (DBC)	Crowdhill Copse
Mount Fancy Combined	Dundon Beacon	Foxholes	Cavenham Heath	Portland Perryfields	Dancersend
Bentley Station Meadow	Deep Dean	Garston Wood	Chobham Common	Old Burghclere Lime Quarry	Botley Wood 2
Powerstock North (DTNC)	Farthing Down	Haugh Wood, South	Buckland Wood	Aston Brickyard Plantation	Morris' Wood
West Sedgemoor	Frog Firle Farm	Ebbor Gorge	Higher Hyde Heath (DTNC)		Lineover Wood
Coed Maidie B Goddard	Headley Warren	Brickett Wood	Hothfield Common		Langford Heath
	Bredon Hill	Green Lane Wood	Kinson Common		Finemere Wood
	Badbury Rings (NT)	Bovey Valley	Upton Heath North		Firestone Copse
			Tadnoll		Bentley Wood North
			Pitts Wood		Bentley Wood South
					Shabbington Wood
					Powerstock Poorwood
					Piddle's Wood (DTNC)
					Pickett Wood
					Wyre Forest

Table A0-3: UKBMS transect sites and associated habitat classifications from which data was used to calculate separate values for mean density in occupied habitats for *Aphantopus hyperantus*. Populations at all sites utilised were classified as stable (regression slope p>=0.05, e.g. not significant) by UKBMS, www.ukbms.org.

Chalk/limestone grassland	**Broadleaved woodland**	**Mixed woodland**
Albury Nowers	Ryton Wood North	Bentley Wood - Compartment Four
Aston Clinton Ragpits	Ryton Wood East	Bentley Wood - North
Aston Upthorpe Downs	Bentley Wood Hawksgrove	Bentley Wood - South
Badbury Rings	Denge Wood	Grafton Wood
Bevendean B	Foxholes	Chambers Farm Wood
Bevendean C	Grendon and Doddershall Woods	Oakley Woods
Box Hill, Viewpoint	Luckett Wood	Potton Woods
Box Hill, Zig Zag	Nagshead	
Bratton Castle Earthworks (EH)	Newton - Walters Copse	
Cissbury Ring	Alice Holt	
Cole Kitchen	Bradfield Woods	
Hackhurst Down	Shelfheld Coppice	
Headley Heath		
Headley Warren		

Table A0-4: UKBMS transect sites with associated habitat classifications from which data was used to calculate separate values for mean density in occupied habitats for *Pyronia tithonus*. Populations at all sites utilised were classified as stable (regression slope p>=0.05, e.g. not significant) by UKBMS, www.ukbms.org.

Chalk/limestone grassland	**Broadleaved woodland**	**Mixed woodland**
Albury Nowers	Alice Holt	Ampfield Wood
Aston Clinton Ragpits	Ashtead Common B	Bentley Wood - Compartment Four
Aston Rowant (N)	Avon Gorge 1	Bentley Wood - North
Aston Upthorpe Downs	Avon Gorge 2	Bentley Wood - South
Bevendean A	Balls Wood	Bevill's Wood
Bevendean B	Bovey Valley	Carsington Water
Bevendean C	Burnham Beeches (New walk)	Chambers Farm Wood
Boscombe Down O (WCC)	Church Place	Crabtree
Box Hill, Zig Zag		
Bratton Castle Earthworks (EH)		
Butler's Hangings		
Cheriton Hill		
Cleeve Prior		
Clubmens Down (NT)		
Cole Kitchen		
College Lake		
Common Hill		
Crickley Hill		
Crong		
Crook Peak		

Table A0-5: UKBMS transect sites and asociated habitat classifications from which data was used to calculate separate values for mean density in occupied habitats for *Melanargia galathea*. Populations at all sites utilised were classified as stable (regression slope p>=0.05, e.g. not significant) by UKBMS, www.ukbms.org.

Chalk/limestone grassland	**Neutral grassland**	**Marshy grassland**	**Broadleaved woodland**	**Mixed woodland**
Albury Nowers	Arlington Reservoir	Bentley Station Meadown	Bentley Wood Hawksgrove	Ampfield Wood
Aston Clinton Ragpits	Bannerdown	Farlington Marshes Route A	Bowdown (Baynes/Bomb Site)	Bentley Wood - Compartment Four
Aston Upthorpe Downs	Bentley Wood - Eastern	Itchen Valley CP Meadows	Bracketts Coppice (DTNC)	Bentley Wood - North
Badbury Rings	Castlemorton Common	Lower Test Marshes	Burnham Beeches (New walk)	Botley Wood 1
Beacon Hill, Sussex	Hartley Field	Middle Street Meadow, Salisbury	Crab Wood	Crowdhill Copse
Bevendean A	Hinkley Point Power Station	Moors Valley	Denge Wood	Dancersend
Bevendean B	Lorton Meadows	Mount Fancy Combined	Fifehead Magdafen Wood (WT)	Duncliffe Wood (WT)
Bevendean C	Lower Test - Testwood Park House	Pamphill Moors (NT)	Foxholes	Grafton Wood
Bonchurch Down	Lydlinch Common (Private)	Powerstock North (DTNC)	Grendon and Doddershall Woods	Lineover Wood
Boscombe Down O (WCC)	Medina Valley Centre	Winnal Moors	Gutteridge Wood	Oakley Woods
Box Hill, Viewpoint			Itchen Valley CP Woods	Piddle's Wood (DTNC)
Box Hill, Zig-Zag			Luckett Wood	Shabbington Wood
Bratton Castle Earthworks			Newton - Walters Copse	Shabbington Wood (new)
Bredon Hill			Perry Wood	Somerfield Common
Clubmens Down (NT)			Ryton Wood and Pool	Whippingham (Woodhouse)
Cole Kitchen			Sheepleas	
			Webb's Wood (FC)	

Table A0-6: Goodness of fit TSS values for each study species for habitat only models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
P. aegeria	1	0.604	0.620	0.629	0.637	0.623	0.598
	2	0.606	0.621	0.633	0.637	0.627	0.597
	3	0.604	0.617	0.632	0.642	0.630	0.597
	4	0.599	0.622	0.636	0.639	0.622	0.599
	5	0.601	0.618	0.631	0.637	0.631	0.597
	6	0.608	0.617	0.634	0.643	0.637	0.604
	7	0.606	0.613	0.631	0.637	0.626	0.607
	8	0.605	0.619	0.634	0.638	0.630	0.609
	9	0.609	0.624	0.629	0.634	0.626	0.604
	10	0.602	0.612	0.630	0.645	0.633	0.600
A. hyperantus	1	0.598	0.606	0.627	0.649	0.662	0.661
	2	0.594	0.610	0.628	0.640	0.661	0.662
	3	0.594	0.608	0.626	0.639	0.663	0.669
	4	0.595	0.607	0.626	0.647	0.663	0.664
	5	0.594	0.614	0.624	0.646	0.661	0.666
	6	0.602	0.612	0.624	0.642	0.663	0.663
	7	0.598	0.607	0.619	0.639	0.663	0.661
	8	0.592	0.606	0.627	0.642	0.665	0.663
	9	0.599	0.610	0.624	0.645	0.666	0.665
	10	0.588	0.607	0.630	0.646	0.661	0.665
P. tithonus	1	0.841	0.842	0.852	0.858	0.860	0.858
	2	0.843	0.845	0.852	0.857	0.866	0.861
	3	0.837	0.845	0.852	0.860	0.865	0.862
	4	0.838	0.847	0.855	0.858	0.861	0.861
	5	0.839	0.847	0.851	0.858	0.863	0.858
	6	0.841	0.847	0.850	0.857	0.862	0.859
	7	0.835	0.847	0.853	0.855	0.859	0.858
	8	0.843	0.847	0.852	0.861	0.861	0.862
	9	0.840	0.844	0.850	0.857	0.862	0.861
	10	0.837	0.844	0.852	0.858	0.865	0.857
M. galathea	1	0.794	0.781	0.776	0.770	0.754	0.732
	2	0.780	0.782	0.776	0.765	0.748	0.730
	3	0.787	0.778	0.772	0.765	0.757	0.735
	4	0.784	0.781	0.772	0.760	0.745	0.737
	5	0.784	0.786	0.772	0.762	0.750	0.736
	6	0.791	0.780	0.773	0.762	0.754	0.732
	7	0.786	0.781	0.773	0.764	0.756	0.739
	8	0.779	0.781	0.778	0.762	0.752	0.734
	9	0.785	0.779	0.778	0.766	0.751	0.734
	10	0.792	0.787	0.777	0.769	0.753	0.735

Table A0-7: Goodness of fit TSS values for each study species for climate only models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
P. aegeria	1	0.636	0.636	0.642	0.624	0.609	0.571
	2	0.640	0.640	0.643	0.631	0.607	0.565
	3	0.644	0.643	0.649	0.630	0.612	0.562
	4	0.636	0.635	0.645	0.638	0.607	0.577
	5	0.639	0.637	0.646	0.633	0.610	0.569
	6	0.637	0.639	0.646	0.630	0.608	0.569
	7	0.642	0.637	0.641	0.635	0.612	0.575
	8	0.636	0.641	0.647	0.630	0.616	0.573
	9	0.644	0.636	0.649	0.634	0.606	0.561
	10	0.647	0.639	0.647	0.638	0.614	0.571
A. hyperantus	1	0.587	0.584	0.575	0.545	0.484	0.460
	2	0.584	0.586	0.581	0.546	0.490	0.459
	3	0.588	0.586	0.577	0.550	0.485	0.460
	4	0.588	0.589	0.582	0.550	0.487	0.462
	5	0.592	0.587	0.579	0.550	0.488	0.459
	6	0.585	0.584	0.572	0.545	0.488	0.458
	7	0.581	0.581	0.575	0.548	0.481	0.461
	8	0.589	0.584	0.583	0.546	0.482	0.459
	9	0.589	0.584	0.578	0.557	0.810	0.461
	10	0.588	0.583	0.576	0.543	0.814	0.458
P. tithonus	1	0.855	0.852	0.847	0.840	0.809	0.783
	2	0.856	0.851	0.847	0.837	0.820	0.786
	3	0.857	0.852	0.848	0.840	0.814	0.788
	4	0.855	0.854	0.846	0.838	0.814	0.784
	5	0.855	0.851	0.850	0.840	0.814	0.792
	6	0.855	0.851	0.845	0.844	0.813	0.791
	7	0.856	0.849	0.844	0.837	0.815	0.792
	8	0.858	0.851	0.847	0.842	0.811	0.781
	9	0.855	0.851	0.845	0.838	0.817	0.794
	10	0.853	0.849	0.846	0.836	0.814	0.788
M. galathea	1	0.754	0.744	0.725	0.703	0.673	0.643
	2	0.753	0.746	0.722	0.702	0.671	0.642
	3	0.749	0.744	0.722	0.703	0.673	0.644
	4	0.753	0.746	0.726	0.705	0.674	0.643
	5	0.746	0.743	0.722	0.701	0.672	0.648
	6	0.750	0.742	0.723	0.702	0.672	0.642
	7	0.749	0.741	0.719	0.704	0.673	0.637
	8	0.752	0.740	0.721	0.698	0.672	0.642
	9	0.751	0.742	0.724	0.705	0.676	0.642
	10	0.750	0.743	0.721	0.707	0.674	0.648

Table A0-8: Goodness of fit TSS values for each study species for unconstrained models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
P. aegeria	1	0.617	0.615	0.595	0.529	0.414	0.277
	2	0.619	0.610	0.592	0.527	0.407	0.290
	3	0.622	0.612	0.594	0.526	0.416	0.296
	4	0.619	0.608	0.587	0.525	0.421	0.291
	5	0.618	0.613	0.587	0.526	0.424	0.287
	6	0.619	0.614	0.589	0.522	0.421	0.292
	7	0.621	0.617	0.588	0.519	0.412	0.284
	8	0.616	0.615	0.591	0.521	0.417	0.284
	9	0.616	0.612	0.594	0.523	0.422	0.279
	10	0.619	0.611	0.591	0.522	0.418	0.287
A.hyperantus	1	0.577	0.561	0.542	0.471	0.421	0.384
	2	0.582	0.555	0.546	0.472	0.410	0.387
	3	0.574	0.569	0.541	0.473	0.417	0.388
	4	0.580	0.561	0.539	0.473	0.420	0.383
	5	0.576	0.557	0.541	0.473	0.414	0.396
	6	0.578	0.558	0.548	0.475	0.415	0.394
	7	0.575	0.564	0.545	0.477	0.415	0.388
	8	0.572	0.566	0.540	0.475	0.415	0.394
	9	0.580	0.558	0.550	0.466	0.413	0.399
	10	0.577	0.562	0.537	0.470	0.413	0.380
P.tithonus	1	0.842	0.838	0.831	0.805	0.754	0.701
	2	0.845	0.836	0.831	0.804	0.753	0.715
	3	0.846	0.842	0.830	0.807	0.755	0.711
	4	0.846	0.836	0.828	0.802	0.746	0.710
	5	0.845	0.841	0.832	0.807	0.753	0.707
	6	0.844	0.836	0.831	0.804	0.760	0.707
	7	0.847	0.837	0.830	0.796	0.752	0.702
	8	0.844	0.838	0.828	0.802	0.761	0.708
	9	0.842	0.838	0.833	0.803	0.748	0.710
	10	0.844	0.837	0.828	0.805	0.754	0.727
M.galathea	1	0.737	0.730	0.709	0.677	0.625	0.603
	2	0.745	0.728	0.713	0.674	0.627	0.603
	3	0.742	0.731	0.708	0.678	0.620	0.601
	4	0.742	0.731	0.711	0.676	0.621	0.600
	5	0.742	0.737	0.709	0.676	0.625	0.599
	6	0.739	0.732	0.712	0.681	0.624	0.601
	7	0.748	0.733	0.708	0.682	0.625	0.599
	8	0.740	0.732	0.710	0.679	0.621	0.603
	9	0.746	0.733	0.709	0.675	0.625	0.598
	10	0.745	0.735	0.711	0.677	0.624	0.601

Table A0-9: Goodness of fit TSS values for *Pyronia tithonus* for combined habitat and climate grid models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
P. tithonus	1	0.856	0.849	0.844	0.838	0.818	0.780
	2	0.855	0.851	0.844	0.837	0.820	0.788
	3	0.855	0.850	0.848	0.842	0.816	0.783
	4	0.852	0.852	0.845	0.839	0.814	0.783
	5	0.858	0.852	0.846	0.834	0.817	0.786
	6	0.852	0.851	0.846	0.840	0.811	0.779
	7	0.858	0.852	0.847	0.838	0.812	0.788
	8	0.853	0.852	0.847	0.841	0.816	0.790
	9	0.856	0.850	0.844	0.836	0.812	0.789
	10	0.855	0.854	0.846	0.841	0.816	0.781

Table A0-10: Goodness of fit TSS values for *Pararge aegeria* for alternative woodland only habitat grid models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
P.aegeria	1	0.571	0.587	0.593	0.604	0.610	0.622
	2	0.575	0.581	0.601	0.595	0.616	0.629
	3	0.577	0.583	0.594	0.602	0.613	0.629
	4	0.574	0.581	0.602	0.602	0.611	0.628
	5	0.576	0.586	0.589	0.602	0.615	0.626
	6	0.574	0.587	0.593	0.577	0.619	0.631
	7	0.578	0.587	0.600	0.602	0.614	0.630
	8	0.570	0.592	0.596	0.601	0.614	0.625
	9	0.580	0.585	0.600	0.591	0.618	0.629
	10	0.576	0.587	0.587	0.604	0.615	0.623

Table A0-11: Goodness of fit TSS values for *Melanargia galathea* for alternative calcareous grassland only habitat grid models under forced probabilities of dispersal from 0.0 to 1.0 increasing at increments of 0.2. 10 model replicates were run per species per probability of dispersal.

		Probability of Dispersal					
Species	Run	0.0	0.2	0.4	0.6	0.8	1.0
M.galathea	1	0.757	0.754	0.755	0.742	0.746	0.739
	2	0.755	0.759	0.759	0.756	0.746	0.741
	3	0.763	0.759	0.753	0.753	0.748	0.741
	4	0.757	0.764	0.755	0.755	0.750	0.744
	5	0.754	0.752	0.758	0.748	0.747	0.743
	6	0.756	0.760	0.755	0.749	0.747	0.742
	7	0.749	0.756	0.757	0.754	0.750	0.746
	8	0.758	0.758	0.760	0.752	0.744	0.745
	9	0.751	0.759	0.753	0.751	0.749	0.739
	10	0.768	0.757	0.754	0.760	0.752	0.741

Table A0-12: Goodness of fit TSS values for 100 replicates of a habitat only model, probability of dispersal 0.8, species *Pyronia tithonus.*

Run	TSS
1	0.859
2	0.865
3	0.864
4	0.860
5	0.862
6	0.860
7	0.858
8	0.860
9	0.861
10	0.864
11	0.859
12	0.864
13	0.866
14	0.866
15	0.861
16	0.860
17	0.862
18	0.864
19	0.864
20	0.859
21	0.860
22	0.862
23	0.864

24	0.862
25	0.862
26	0.858
27	0.859
28	0.863
29	0.862
30	0.864
31	0.864
32	0.864
33	0.864
34	0.862
35	0.861
36	0.859
37	0.863
38	0.864
39	0.859
40	0.860
41	0.862
42	0.860
43	0.862
44	0.862
45	0.863
46	0.862
47	0.861
48	0.863
49	0.860
50	0.865
51	0.864
52	0.863
53	0.860
54	0.862
55	0.862
56	0.862
57	0.860
58	0.863
59	0.862
60	0.861
61	0.863
62	0.862
63	0.860
64	0.857
65	0.862
66	0.860
67	0.863
68	0.864
69	0.860
70	0.862
71	0.857

72	0.862
73	0.864
74	0.857
75	0.862
76	0.862
77	0.862
78	0.864
79	0.866
80	0.863
81	0.864
82	0.859
83	0.863
84	0.857
85	0.864
86	0.861
87	0.863
88	0.864
89	0.862
90	0.858
91	0.862
92	0.861
93	0.862
94	0.857
95	0.862
96	0.862
97	0.862
98	0.864
99	0.866
100	0.863