

FROM MICROHABITAT TO METAPOPOPULATIONS:
A MODEL SYSTEM FOR CONSERVATION UNDER
CLIMATE CHANGE

Callum Robert Lawson

Submitted by Callum Robert Lawson to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, January 2013.

This thesis is available for Library use on the understanding that it is copyrighted material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

X

Callum Lawson

Abstract

Climate change is having important and widespread effects on global biodiversity. Species' geographic distributions are shifting as populations become extinct in the warmest parts of their range, and expand into cooler parts of their range that are becoming climatically suitable. Developing a holistic understanding of how climate affects ecological processes will improve our capacity to anticipate and ameliorate the impacts of climate change on biodiversity. In this thesis, I study the silver-spotted skipper butterfly *Hesperia comma* at its expanding upper latitude range margin in the UK to investigate the ecological effects of climate change. I examine how fine-scale variation in microclimate influences the spatiotemporal dynamics of range expansion and habitat use, and provide empirical tests of the extent to which different conservation actions can facilitate range shifts. I also develop a framework for analysing the predictive performance of species distribution forecasts under climate change. My principle findings are: (1) range expansions are vulnerable to setbacks, with patterns of local extinction related to spatial patterns of microclimate variation; (2) conservation actions at both local and landscape scales can enhance colonisation and population survival in range expansions; (3) current protected area networks combined with active conservation measures can offer effective means to facilitate range shifts; (4) fine-scale and short-term variation in climate interacts with microclimates generated by vegetation to drive changes in habitat use; and (5) current methods to assess range shift projections result in information loss, and predictions would be improved by the uptake of alternative performance metrics. These findings show how fine-scale variation in microclimate alters responses to climate change, but provide encouragement that existing conservation policy and practice, despite being originally designed to protect pre-existing populations, may transfer well to facilitate range shifts under global warming.

Contents

Abstract.....	2
Contents.....	3
Acknowledgements.....	9
Author’s declaration	11
Chapter 1: General introduction.....	13
1.1. Rationale	13
1.2. Ecological responses to climate change	13
1.3. The importance of climate change ecology.....	17
1.4. Challenges for conservation under climate change.....	19
1.5. Predicting the impacts of climate change on species’ distributions.....	22
1.6. Microclimate matters: the impact of spatial resolution	23
1.7. The silver-spotted skipper butterfly: a model system for conservation under climate change	25
1.8. Aims and structure of thesis	27
1.9. References	29
Chapter 2: Local and Landscape Management of an Expanding Range Margin under Climate Change	
.....	45
2.1. Summary	45
2.2. Introduction	46

2.3. Methods.....	49
2.3.1. Study system	49
2.3.2. Survey methods	50
2.3.3. Variable collation	51
2.3.4. Analyses	52
2.4. Results.....	55
2.5. Discussion.....	57
2.5.1. Determinants of extinction and colonisation	57
2.5.2. Implications for managing a range expansion	60
2.6. Conclusion.....	62
2.7. References	63
Chapter 3: Active conservation enhances metapopulation expansion under climate change	77
3.1. Summary	77
3.2. Introduction	77
3.3. Methods.....	79
3.4. Results.....	81
3.5. Discussion.....	83
3.6. References	85

Appendix to Chapter 3	92
3A.1. Null model structure.....	92
3A.1.1. Colonisation	92
3A.1.2. Survival.....	92
3A.2. Mixed models to test for spatial autocorrelation effects.....	93
3A.3. Detail on method for predicting colonisation and survival probabilities	93
3A.4. Comparison of original and mixed model results.....	94
3A.4.1. Colonisation	94
3A.4.2. Survival.....	94
3A.5. Relationships between management categories and variables in null models	95
3A.5.1. Colonisation data	95
3A.5.2. Survival data	96
Appendix 3 Tables.....	97
Appendix 3 Figures.....	100
Chapter 4: Climate drives changing microhabitat associations in a butterfly	102
4.1. Summary	102
4.2. Introduction	102
4.3. Methods.....	105

4.3.1. Study species.....	105
4.3.2. Sampling design	106
4.3.3. Variables.....	107
4.3.4. Model-fitting	108
4.3.5. Statistical tests	110
4.3.6. Model predictions.....	110
4.4. Results.....	111
4.5. Discussion.....	112
4.6. References	116
Appendix to Chapter 4	128
4A.1. Model selection tables including host plant-temperature interaction	128
Appendix 4 Figures.....	130
Chapter 5: Prevalence, thresholds, and the performance of presence-absence models	134
5.1. Summary	134
5.2. Introduction	135
5.3. Conceptual framework and literature review	137
5.3.1. Conceptual framework	137
5.3.2. Literature review.....	139

5.4. Discrimination and the importance of prevalence	140
5.5. The disadvantages of “threshold-dependent” metrics.....	143
5.6. Simulated conservation example.....	144
5.7. Discussion and recommendations	147
5.8. References	150
Appendix to Chapter 5	164
5A.1. Literature review methods	164
5A.2. Description of performance metrics.....	166
5A.2.1. Additional notation.....	166
5A.2.2. Description of performance metrics.....	166
5A.2.3. Skill scores.....	166
5A.3. Analytical demonstrations.....	171
5A.3.1. Proof that AUC is equivalent to TSS for binary models	171
5A.3.2. Proof that binary (confusion matrix) performance measures are improper	171
5A.4. Investigation of prevalence bias	174
5A.5. Additional information on simulation methods	176
5A.6. Demonstration of likelihood performance metrics.....	178
Chapter 6: General discussion	180

6.1. Summary	180
6.2. Chapter 2: patch-scale management prevents setbacks in range expansion	180
6.3. Chapter 3: current conservation practice can effectively facilitate range expansions.....	184
6.4. Chapter 4: habitat associations shift as climate changes in space and time	185
6.5. Chapter 5: a framework for metrics of species distribution model performance.....	188
6.6. Conclusion.....	190
6.7. References	191

Acknowledgements

I have received help and support from a great many people over the course of my PhD – more than a few paragraphs of thanks here can possibly cover. I will try and remember as much as I can, but there are bound to be omissions, so if you are missed out, please don't feel like I didn't appreciate your help!

My supervisor, Rob Wilson, has been a continual source of advice and encouragement throughout my PhD: enthusiastic about new ideas, patient when things don't go as planned, and supportive in everything I have done. Whenever I had a thought or a question about anything from writing a paper to applying for grants and jobs, I had the luxury of knowing that I could send Rob an email and expect a considered and helpful reply within hours. I will also take away fond memories of our research meetings, which often started out as brief discussion about something-or-other around lunchtime and ended up continuing in the pub because it was dark and everyone else had gone home.

Often present at those meetings was Jon Bennie, my unofficial second supervisor. To say that Jon has been generous with his time in helping me during my PhD is a huge understatement, and I dread to think how many hours he has spent writing replies to my emails or patiently explaining how to do something in ArcMap. Whether discussing ideas over a coffee in the Athenaeum or driving around in his camper van looking for silver-spotted skipper eggs, working with Jon has been a fantastic way to learn ecology, and always great fun.

Jenny Hodgson has been central to my scientific development and a constant inspiration to me during my research. Jenny invested considerable time in helping me to develop my statistical skillset and improve the clarity of my work, and there isn't an analysis in this thesis which hasn't benefitted from her input. I have also learned a great deal from the advice of Chris Thomas, who infallibly

identified the key missing ingredients from a manuscript, usually within about 30 seconds of reading it. My future research career will owe much to Jenny and Chris, and working with them has been both a privilege and a pleasure.

Thanks to Shane Richards for many interesting discussions about the testing of ecological predictions, and for imbuing me with a wealth of pragmatic statistical advice. I have also greatly enjoyed talking to Ilya Maclean about all things ecological, from microclimates to species-area curves. Karen Anderson has provided me with great deal of helpful advice on paper writing and spatial analyses, particularly on my first manuscript. I thank Owen Lewis for the time and effort he invested in my undergraduate research project and scientific development at Oxford, which gave me a fantastic experience of ecological research and encouraged me to begin a PhD.

To the students and staff at Tremough, thank you for providing an exciting and enjoyable environment in which to work, and for many fun days and evenings out. Thanks also to the students and staff in the Department of Biology at York for making me feel welcome and at home up North. I greatly appreciate the efforts of all those who assisted on the 2000 and 2009 silver-spotted skipper distribution surveys, especially Crispin Holloway, whose enthusiasm knew no bounds even when it was so overcast there was not a butterfly to be seen. Likewise, Bonnie McBride, Tracy Gray, Alice Daish, Michelle Bullock, Robyn Clark and Anna Rogers were all a great help in the field and assisted with the tedious business of data entry.

Last but by no means least, thanks to my friends, family (especially Lynn, Robert, and Jessica Lawson), and Victoria Davis for your constant support throughout my education, and for the countless hours of fun and enjoyment which helped me to remember that there are other things outside of ecology.

Callum, January 2013.

Author's declaration

This thesis involved collaboration with Rob Wilson (RJW), Jon Bennie (JJB), Jenny Hodgson (JAH), Chris Thomas (CDT), and Shane Richards (SAR). Additional assistance with data collection and collation was provided by Zoe Davies (ZD), Bonnie McBride (BM), Michelle Bullock (MB), and Crispin Holloway (CH), as well as the field assistants on the 2000 and 2009 *Hesperia comma* UK distribution surveys.

Chapter 1: General introduction

The writing of this chapter was supervised by RJW.

Chapter 2: Local and landscape management of an expanding range margin under climate change

This chapter employs data collected during the 2000 and 2009 *Hesperia comma* UK distribution surveys (supervised by RJW, CDT, and JJB). JJB assisted with digitisation of habitat patches. RJW, JJB, CDT, and JAH supervised the work. This chapter has been published in the *Journal of Applied Ecology*.

Chapter 3: Active conservation enhances metapopulation expansion under climate change

This chapter employs data collected during the 2000 and 2009 *Hesperia comma* UK distribution surveys (supervised by RJW, CDT, and JJB). JJB assisted with digitisation of habitat patches. RJW, JJB, CDT, and JAH supervised the work. This chapter is currently under review at *Conservation Letters*.

Chapter 4: Climate drives changing microhabitat associations in a butterfly

This chapter employs a physiologically-based microclimate model, the R code for which was originally conceived and written by JJB. RJW, JJB, CDT, and JAH supervised the work. The egg-laying data from the "Old Plantation" site in Surrey in years prior to 2010 was collected by ZD, CDT, RJW,

and BM. RJW, JJB, MB and CH assisted with the collection and collation of egg-laying data in 2010. Material from this chapter has been submitted for publication in the *Journal of Animal Ecology*.

Chapter 5: Prevalence, thresholds, and the performance of presence-absence models

The work in this chapter was supervised by RJW, JAH, and SAR. This chapter is currently under review at *Methods in Ecology and Evolution*.

Chapter 6: General discussion

The writing of this chapter was supervised by RJW.

Chapter 1: General introduction

1.1. Rationale

Climate change is having important and widespread effects on global patterns of biodiversity (Parmesan 2006, Cahill et al. 2013). Species' geographic distributions are shifting as populations become extinct in the warmest parts of their range, and expand into cooler parts of their range that are becoming climatically suitable (Wilson et al. 2005, Chen et al. 2011). Developing our understanding and prediction of species' responses to climate change will help to advance ecological theory and guide conservation management. In this thesis, I examine the ecological impacts of climate change on the silver-spotted skipper butterfly *Hesperia comma* at its expanding range margin in Britain. Using fine-scale data on the habitat associations and distribution dynamics of *H. comma*, I examine the role of microclimate in ecological responses to climate change, and assess the effectiveness of conservation measures for facilitating range expansions. In addition, I develop a framework for assessing the predictive performance of species distribution models under climate change.

1.2. Ecological responses to climate change

There is overwhelming evidence that global temperatures are rising, and that anthropogenic increases in atmospheric concentrations of greenhouse gases are the cause (Stott et al. 2000, Hansen et al. 2012). In broad terms, climate change signifies a tendency towards hotter and drier conditions, but its realised impact on weather varies considerably amongst regions (Stott et al. 2000). Moreover, although temperatures are becoming hotter on average, many climates are characterised by substantial inter-annual fluctuations in temperature, such that over short (decadal)

timescales, differences in temperature between years dwarf the long-term warming trend (Fig. 1.1). Evidence from global climate change models and empirical observations suggests that global warming will also increase inter-annual variability in climate, in which the differences between “hot” and “cool” years will become accentuated and extreme events such as droughts or storms will occur more frequently (Easterling et al. 2000, Boyce et al. 2006). Global warming thus encompasses manifold impacts on climate, with the salient outcome being that without abrupt and concerted efforts to mitigate greenhouse gas production, climates experienced in the future will increasingly depart from those experienced in the recent past.

Climate has long been known to influence the physiology and geographic distributions of organisms. The idea that abiotic variables such as temperature can limit the conditions under which organisms are able to grow and reproduce laid the foundations for the concept of the “ecological niche” and catalysed the development of early ecological theory (Grinnell 1917, Soberón and Nakamura 2009, Peterson et al. 2011, McNerny and Etienne 2012). Thermal physiology has since developed into an important sub-discipline of ecology, in which vital rates such as the fecundity or survival of individuals are quantified under a range of temperatures, enabling thermal optima and tolerance ranges to be estimated (Bryant et al. 2002, Angilletta 2009, Buckley and Kingsolver 2012). Physiological traits determine rates of population growth at locations with a given climate, affecting population persistence rates and ultimately species’ geographic distributions (Buckley et al. 2010). The influence of climate on species’ geographic ranges is evident in latitudinal gradients in species diversity; in the early 1800s, Alexander von Humboldt observed that more species were found towards the equator (Von Humboldt 1808, Erwin 2009), and later Carl Bergmann recognised that climate gradients were linked to species’ traits (specifically, body size) at geographic scales (Bergmann 1847, Gaston 2000, Gardner et al. 2011). Climate thus forms a major axis along which ecological communities are assembled.

Because climate forms an important ecological constraint, climate change is resulting in widespread and multi-faceted changes to ecological communities (Parmesan and Yohe 2003, Root et al. 2003, Chen et al. 2011, Maclean and Wilson 2011). The ecological impacts of climate change can be understood at many different levels, from changes in metabolic processes within an individual organism (Angilletta 2009) to changes in biodiversity at continental scales (Thomas et al. 2004, Araújo and Rahbek 2006, Peterson et al. 2011). Nonetheless, abundance – the number of organisms belonging to a given group in a given area – traditionally forms the common currency of ecology (Begon et al. 1996), and the ecological impacts of climate change can be usefully conceptualised as changes in abundance through space and time.

Changes in spatial abundance distributions are amongst the most widely-cited impacts of climate change, and form a central theme of this thesis. For example, suppose that the growth rate of populations of a given species is dependent on temperature. At the warmest parts of its geographic distribution (“trailing margins” under current global warming, usually found nearer the equator and at lower elevations), rising temperatures would be expected to decrease population growth and survival rates, such that the species will occupy those locations less frequently. Conversely, at the coolest parts of its range (“leading margins”, usually found nearer the poles and at higher elevations), population survival rates are expected to increase, such that the species will occupy those locations more frequently. Thus, the expectation under climate change is that species’ distributions will shift towards warmer locations, predominantly polewards and upwards in elevation (Thomas et al. 2004, but see VanDerWal et al. 2012). There is now overwhelming evidence for climate-driven range shifts from across a wide variety of taxa (Konvicka et al. 2003, Wilson et al. 2005, Hickling et al. 2006, Chen et al. 2011, Tingley et al. 2012), with species becoming locally extinct from the warmest parts of their distributions (Hampe and Petit 2005) and colonising habitats which were previously too cool to occupy (Thomas et al. 2001, Chen et al. 2011).

Climate change is also driving changes in temporal abundance patterns. Many species use temperature, or related variables such as the timing of winter frost, as cues for behaviours (e.g. spawning: Phillimore et al. 2010, hibernation: Lane et al. 2012) or physiological processes (e.g. emergence from pupation: Weiss et al. 1988, budburst: Bennie et al. 2010, emergence from eggs: Bonebrake et al. 2010). If the timing of those cues changes, the timing of biological life-history events, known as phenology, may also change, with potential impacts on seasonal patterns of abundance (Hodgson et al. 2011, Lane et al. 2012). Phenological changes have been documented extensively, but are not investigated in this thesis; useful discussion can be found in Parmesan (2006) and Körner & Basler (2010).

The ecological impacts of climate change (whether spatial or temporal) are not restricted solely to direct impacts on the physiology, demography or distribution of individual species. Ecological communities are characterised by complex networks of interactions between species, such that a change in abundance of one species can have important impacts on the abundance of others (May 2001). Theoretically, climate change could alter food-web structure by altering both relative abundances or per-capita interaction strengths (Wells and O'Hara 2012). For example, the arrival of warm-adapted equatorial species could place competitive pressure on species inhabiting mid-range latitudes (Norberg et al. 2012); conversely, shifts in the geographic distribution of important food resources, such as insect host plants, could doom populations to extinction (Parmesan 2006). Changes to the phenology of one species, such as the flowering time of a plant, could force mutualistic species such as insect pollinators to alter their phenology in a compensatory manner (Weiss et al. 1988, Memmott et al. 2007, Cahill et al. 2013). This thesis will focus on the direct impacts of climate change on a single species, but empirical explorations of the indirect impacts of climate change represent an important topic for future research.

Species may respond to climate change through plastic and/or evolutionary processes. In plastic responses, species' relationships with climate variables remain constant, but their phenotypic traits, habitat associations, distributions, or phenology changes in response to the shifting patterns of climate variables (sometimes referred to as "niche tracking" or "climate sorting"; Visser 2008, La Sorte and Jetz 2012, Norberg et al. 2012). In evolutionary responses, species adapt to climate change *in situ*, altering their relationships with climate variables (Parmesan 2006, Schiffers et al. 2013). In reality, species' responses are likely to involve a combination of both ecological and evolutionary responses to climate change, with the potential for interaction to create eco-evolutionary dynamics (Ozgul et al. 2009, Burton et al. 2010, Kubisch et al. 2010, Ozgul et al. 2010, Kubisch and Poethke 2011, Norberg et al. 2012). Although responses to global warming will thus be influenced by evolutionary processes, I do not explicitly consider eco-evolutionary dynamics in this thesis, instead choosing to focus largely on ecological responses to climate change.

1.3. The importance of climate change ecology

Why study ecological responses to climate change? One of the primary reasons is that we can learn much about the fundamental ecological process underlying such responses. Climate change represents a global experiment which we can use to develop and test ecological theory (Thomas 2010). Climate change allows us to examine gradients in climate through time as well as space (see "Ecological responses to climate change"), providing an additional axis along which we can measure the ecological impacts of climate. By inducing biological responses to climate in a way that eliminates alternative explanations (e.g. resulting from spatial gradients in other important environmental variables that are correlated with climate), global warming provides extra information on how climate structures ecological communities, helping to tease apart ecological and

evolutionary processes (e.g. Hodgson et al. 2011). By studying ecological responses to climate change, we can thus improve our understanding of species' relationships with climate.

There is, nonetheless, a more pressing reason for studying climate change: it threatens species with decline and extinction (Thomas et al. 2004, Maclean and Wilson 2011, Cahill et al. 2013). There has occasionally been confusion about why climate change represents a threat to biodiversity, especially given that many paleoecological studies indicate that species have apparently tolerated changes in temperature of approximately equal magnitude to those predicted by global climate models (Willis and MacDonald 2011). However, there are two reasons why the threat to biodiversity from contemporary climate change may be greater than during previous glaciation cycles.

First, the rate of global warming is much faster than previously experienced (e.g. an order of magnitude faster than during the previous deglaciation period; Malcolm et al. 2002). It is unknown whether dispersal rates are sufficient to allow species' distributions to track such rapidly shifting zones of suitable climate, or whether evolutionary adaptation will be sufficiently fast to allow species to persist *in situ* (Willis and MacDonald 2011, Norberg et al. 2012). This is particularly an issue for species inhabiting relatively flat landscapes, where the velocity of climate shifts (in metres per year) will be especially fast (Loarie et al. 2009).

Second, human activity has degraded and fragmented natural habitats (Fahrig et al. 2011), reducing population sizes and increasing distances between suitable habitats. Habitat destruction could interact negatively and synergistically with climate change, creating an "anthropogenic cocktail" which slows rates of range expansion and ultimately increases extinction rates under global warming (Travis 2003, Thomas et al. 2004, Lindenmayer et al. 2010). Empirical evidence from observed range shifts suggests that species' abilities to track climate change are being hindered by habitat availability (Hill et al. 1999, Parmesan et al. 1999, Warren et al. 2001). Habitat loss and

fragmentation are likely to accentuate threats to populations at species' trailing margins (Lindenmayer et al. 2010, Larsen 2012). Thus, a key objective of ecological studies and biodiversity conservation in the coming decades will be to quantify and mitigate threats to species posed by climate change (Gillson et al. 2012, Pettoirelli 2012).

Ecological research can inform biodiversity conservation under climate change in two ways: by increasing our understanding of which conservation measures are likely to be most effective under a given set of circumstances; and by providing accurate forecasts of spatial and temporal changes in abundance or occupancy which allow the realised impacts of climate change to be anticipated. This thesis aims to contribute towards both of these goals. I now briefly review the issues facing conservation practitioners and policy makers under climate change, before moving on to a short discussion of the challenges in predicting climate-driven changes in species' distributions. Finally, I introduce a central issue in this thesis, the importance of spatial resolution in climate change studies, and discuss how studying fine-scale variation in climate – known as microclimate – can inform both the understanding and prediction of responses to climate change.

1.4. Challenges for conservation under climate change

Climate change necessitates a reappraisal of existing conservation policy in several ways. Principal among the decisions that biodiversity conservation must now address is the extent to which investments should be made in combating the additional threat of increasingly unsuitable climatic conditions at species' trailing range margins, versus improving species' capacities to colonise new habitats that are becoming climatically suitable at their leading range margins. Aiming to maintain species' current geographic distributions remains a tenable proposition in the near future, but as the magnitude of warming increases, there will be growing pressure to forgo the traditional approach of conserving ecological communities in their current state, and adopt a more pragmatic strategy of

facilitating range shifts (Lawler 2009, Thomas 2011). This thesis aims to develop understanding of methods to help species expand their leading margins, with the hope that complementary studies will investigate how to preserve populations at species' trailing margins (Hampe and Petit 2005, Wilson et al. 2005).

Species might fail to colonise habitats that become climatically suitable for a combination of two reasons: (a) their habitats are fragmented and "patchy", such that there may be large distances between occupied habitat patches and suitable but uncolonised patches (Hanski 1998), and (b) their dispersal abilities are limited, such that they may be unlikely to traverse the distances between habitat patches within a given time frame (Warren et al. 2001, Hill et al. 2002). Finding solutions to the combined issues of habitat fragmentation and dispersal limitation represents the key to successfully enhancing range expansions (Crooks and Sanjayan 2006, Lawler 2009). In practice, the proposed solutions have been many and varied (Heller and Zavaleta 2009), and, broadly speaking, have been characterised by two parallel debates.

The first debate considers whether range shifts are best facilitated by (a) targeting existing habitat patches, to ensure the survival of existing populations, increase population sizes, and, ultimately, the number of emigrating individuals able to colonise new habitat (Clark et al. 2001, Hodgson et al. 2009), or (b) creating new habitats that "link up" existing habitat networks, making it easier for individuals to disperse between patches and expand their distributions (Crooks and Sanjayan 2006, Hannah et al. 2007, Krosby et al. 2010, Hodgson et al. 2012). Confusingly, option (b) is often referred to under the umbrella term of "increasing connectivity" (Crooks and Sanjayan 2006, Krosby et al. 2010), despite the fact that in metapopulation theory, connectivity refers to any means of increasing the colonisation of a given patch, and thus encompasses both options (a) and (b) (Hanski 1998, Hodgson et al. 2009). In general, increasing colonisation success by creating corridors or stepping stones of new habitat (Lovejoy and Hannah 2005, Crooks and Sanjayan 2006), or by directly

translocating individuals (Richardson et al. 2009, Thomas 2011), has emerged as the most widely-favoured means to increase connectivity and facilitate range shifts. However, this focus could divert attention away from more traditional approaches of increasing the size or quality of existing habitats, which are often advocated for the protection of populations at species' trailing margins, but frequently omitted from discussions of range expansion management (Pearce-Higgins et al. 2011, Oliver et al. 2012). Ideas for adapting conservation to climate change have until now been largely academic, with few detailed empirical studies of range shifts available to inform and test proposed actions (Heller and Zavaleta 2009). Chapter 2 tests the effectiveness of many of these conservation actions for facilitating range expansions.

The second (related) debate considers the extent to which pre-existing conservation policy and practice should be restructured to facilitate range shifts (Gaston et al. 2006, Hannah et al. 2007). The fear is that climate change renders existing networks of protected areas and management policies "out of date", because the original objective for which they were designed - to protect existing ecological communities in their current locations - is different to the role they must now play for newly-colonising species (Harris et al. 2006, Thomas 2011). This has prompted a number of theoretical and simulation studies testing the effectiveness of current protected area networks against new, adaptive conservation plans, in which protection and management effort shifts in anticipation of ecological responses to climate change (Lovejoy and Hannah 2005, Hannah et al. 2007, Araujo et al. 2011). However, the increased flexibility in these more adaptive conservation plans is likely to present considerable logistical and practical challenges (e.g. the difficulty of periodically buying and selling land regularly but cost-effectively), and may come at substantial cost to conservation resources. The first step should therefore be to use empirical data to assess the adequacy of current conservation measures for facilitating range shifts; this is the objective of Chapter 3.

1.5. Predicting the impacts of climate change on species' distributions

The effectiveness with which we conserve species under climate change may critically depend on our ability to anticipate their responses (Elith and Leathwick 2009, Peterson et al. 2011). The use of species distribution models (SDMs) to predict spatial patterns of species occurrence under future climate scenarios can potentially provide estimates of extinction risk from climate change, helping to prioritise the protection of those species which face the greatest threat (or, conversely, to save conservation resources which would otherwise be wasted on species which are doomed to extinction; Lawler 2009, Thomas et al. 2011). Moreover, with spatially explicit models of distribution change, the effectiveness of alternative conservation measures can be explored through simulations (Lovejoy and Hannah 2005, Hodgson et al. 2011).

Approaches towards species distribution modelling are many and varied (Peterson et al. 2011), but fall into two broad categories: correlative models, in which occupancy patterns are predicted on the basis of statistical associations with climate variables (Araújo and Peterson 2012); and process-based (or mechanistic) models, in which climate variables are used to parameterise relationships with biological meaning (e.g. activity patterns or fecundity; Buckley et al. 2010, Dormann et al. 2012). At present, correlative models are employed much more frequently than process-based models, perhaps because of the wide availability of automated modelling packages (e.g. BIOMOD: Thuiller 2003, MaxENT: Royle et al. 2012) and environmental layers from geographic information systems (e.g. satellite data).

The relative ease with which correlative SDMs can be fitted, coupled with their evident application to climate change predictions, has catalysed the growth of the SDM field to the point where one might reasonably argue that predictive species distribution modelling now forms one of the primary sub-disciplines of ecology. However, this presents an important challenge: how can we assess which

models provide the most reliable occurrence predictions, in order to refine and improve modelling efforts? Clearly, the way in which we assess predictive accuracy is important, because it will define which SDMs are applied to climate change conservation problems, and ultimately, the success of the solutions developed. The challenge of testing SDM predictions is the subject of Chapter 5.

1.6. Microclimate matters: the impact of spatial resolution

As in many areas of ecology, the conclusions from climate change ecology studies are often dependent on the spatial scale examined. Spatial scale can be broken down into two components: extent (the total area under study) and resolution (the size of the spatial units studied, also known as “grain”; Wiens 1989). Ideally, the spatial resolution of the study matches the resolution at which the study organism(s) perceives the environment, and hence the resolution at which the ecological processes of interest occur (Dutilleul and Legendre 1993, Wiens and Bachelet 2010). Typically, however, there is a trade-off between the spatial extent and spatial resolutions that can be studied (Wiens 1989). For example, collecting very fine-resolution data on the distribution of a species (reducing the size of the grid cells or quadrats) usually entails a greater collecting effort (there are more grid cells or quadrats in an area of a given size). Moreover, environmental data from geographic information systems or field surveys is of a fixed resolution, which often restricts the spatial resolution of modelling even if fine-scale patterns of abundance have been surveyed. Finally, records of species presence from historical records (e.g. museum collections) or as reported by the general public tend to have a maximum precision, such that the exact location of the record cannot be determined (Araujo and New 2007). For all these reasons, the data used to drive species distribution models tends to be of a resolution of 5km or more (sometimes much coarser, e.g. 50-100 km; Peterson et al. 2011).

Previous studies have argued that high spatial resolution may not be important for discerning species' relationships with climate (and consequently, predicting responses to climate change) because the majority of variation in climate occurs at coarse spatial scales (Pearson and Dawson 2003). In fact, however, fine-resolution patterns of topography and vegetation can generate ground-level differences in temperature equalling those observed across hundreds of kilometres at coarser scales (Bennie et al. 2008, Suggitt et al. 2011). These "microclimates" are averaged away by coarse-resolution species distribution models, but have biologically important consequences for organisms.

At the level of individuals, microclimates can affect behavioural decision-making and, potentially, patterns of habitat use. Moving amongst microclimates allows individuals to obtain body temperatures that are closer to their optimal requirements, increasing the efficiency of thermoregulation (Blouin-Demers and Weatherhead 2001, Angilletta 2009, Dubois et al. 2009), and providing conditions that are more suitable for processes such as egg maturation (Schofield et al. 2009) or egg-laying (Davies et al. 2006). Whether a given microhabitat-generated microclimate provides adequate thermal conditions depends on its temperature relative to the ambient, with the corollary that climate change could alter patterns of microhabitat use (Roy and Thomas 2003, Prinzing 2005, Davies et al. 2006). This possibility is the subject of investigation in Chapter 4.

By providing heterogeneity in temperature (and other climate variables) at fine spatial scales, microclimates can also have an important influence on species' responses to climate change. For example, microclimates that are cooler than ambient temperatures could allow species to survive warming temperatures at their trailing margins, providing "refugia" from climate change (Rowe 2007, Ashcroft 2010). Conversely, by providing unusually warm temperatures at species' leading margins, microclimates can accelerate rates of range expansion (Thomas et al. 2001, Wilson et al. 2010). These findings suggest that habitat management could potentially exploit microclimatic variation to deliver biodiversity conservation goals by providing heterogeneous microhabitats and

ensuring that some parts of the landscape will cater to the thermal requirements of all species of conservation concern (Opdam and Wascher 2004, Hodgson et al. 2009). Consequently, advancing our understanding of microclimate use and its impacts on species' distributional dynamics represents an important priority for climate change ecology, and one that this thesis aims to contribute towards.

1.7. The silver-spotted skipper butterfly: a model system for conservation under climate change

The previous section has highlighted how detailed, fine-resolution data on species' responses to climate change could help to guide ecological theory and conservation policy. Evidently, however, it is not possible to study all species to this level of detail. The solution is to select a small number of species to act as model systems, from which detailed information can be gathered and generalisable conclusions drawn. The model system studied in this thesis is the silver-spotted skipper butterfly (*Hesperia comma*; Fig. 1.2). There are a number of factors that make *H. comma* an excellent species with which to study the ecological impacts of climate change.

First, the habitat requirements of *H. comma* are well-known, allowing habitat to be clearly and easily defined. The primary requirement for *H. comma* populations is the availability of the host plant, sheep's fescue grass *Festuca ovina*, growing in heavily-grazed patches of unimproved calcareous grassland (Thomas et al. 1986). Eggs are laid almost exclusively on *F. ovina* plants in turf <10cm tall (Thomas et al. 1986), and calcareous grassland containing such host plants serves to delineate potentially suitable *H. comma* habitat throughout this thesis.

Second, *H. comma* is characterised by many of the traits that are thought to increase species' vulnerability to climate change. In Britain, where the studies presented in this thesis take place, the distribution of *H. comma* habitat is fragmented across the landscape due to the spatial distribution

of chalk geology, agricultural improvement, and grazing pressure by wild and farmed mammals (e.g. rabbits, livestock; Thomas et al. 1986). Because the habitat requirements of *H. comma* are highly specialised, populations cannot persist outside of these patches. Studies of the dispersal behaviour (Hill et al. 1996) and of large-scale distributional change (Thomas and Jones 1993, Davies et al. 2005) of *H. comma* have provided detailed information on its dispersal abilities, showing that individuals rarely disperse >300m (Hill et al. 1996) and that the majority of patches colonised over a nine-generation (nine-year) period are ≤ 2 km from a source population (although longer-distance colonisation events of up to 30km do occasionally occur within this period; Davies et al. 2005). The combination of fragmented habitats and limited dispersal abilities means that *H. comma* exists as a “metapopulation” in Britain, being composed of spatially separated populations linked by occasional dispersal events (Hanski 1998). Indeed, studies on *H. comma* have been instrumental in developing and testing metapopulation theory (Thomas and Jones 1993, Hanski and Thomas 1994, Hill et al. 1996b, Thomas and Hanski 1997). The factors that identify *H. comma* as a metapopulation – specialised habitat requirements, fragmented habitats, and limited dispersal - are precisely those that are thought to increase extinction risk under climate change (Parmesan et al. 1999, Warren et al. 2001, Travis 2003, Thomas et al. 2010).

Third, detailed, fine-resolution information on the distribution of *H. comma* habitat and populations in Britain is available. There have been four major surveys of the British distribution of *H. comma*, in which individual patches have been mapped and the occupancy of each patch recorded using surveys for eggs and/or adult butterflies (Thomas et al. 1986, Thomas and Jones 1993, Davies et al. 2005). These surveys have been conducted at nine-year (nine-generation) intervals, with the most recent survey prior to the data presented in this thesis (from 2009) taking place in 2000 (results of individual surveys reported in the following papers: Thomas et al. 1986, Thomas and Jones 1993,

Davies et al. 2005). The survey data provide unusually fine-resolution information on both distribution and metapopulation dynamics.

Fourth, and perhaps most importantly, the physiology and distribution of *H. comma* is strongly limited by climate. *H. comma* has a circumpolar distribution, extending as far north as Scandinavia (Forister et al. 2004). In Britain, the northern range limit of *H. comma* is strongly limited by climate, and based on its habitat associations and summer activity patterns, it is believed to be more limited by temperature than any other British butterfly (Thomas and Lewington 2010). A study of female *H. comma* showed that egg-laying rates increase with temperature, and that eggs are predominantly laid in warm microsites next to patches of bare ground, depending on the ambient temperature (Davies et al. 2006). Adult activity rates also increase with temperature, with a greater proportion of time spent in flying and courtship behaviour at higher ambient temperatures (Bennie et al., in prep). In recent decades, warming summer temperatures in Britain (Fig. 1.1) have facilitated a rapid range expansion, and between 1982 and 2000 the number of recorded *H. comma* populations in Britain increased by more than threefold. Furthermore, the warm microclimates generated by south-facing slopes have played an important role in this range expansion, being more likely to support the establishment of new *H. comma* populations than cooler north-facing slopes (Thomas et al. 2001). Phenological changes have also been documented, with adults emerging earlier in warmer summers (Wilson et al. 2007). All these factors indicate that *H. comma* is directly limited by temperature.

1.8. Aims and structure of thesis

The overarching objective of this thesis is to advance current understanding of ecological responses to climate change, using the silver-spotted skipper as a model system. My hope is that the work will both develop ecological theory and contribute to conservation practice.

Chapters 2 and 3 provide empirical tests of the effectiveness of different conservation measures in facilitating climate-driven range expansions. Using data collected from a new survey of the British distribution of *H. comma* in 2009, these chapters examine the range expansion of *H. comma* between 2000 and 2009, analysing correlates of patch colonisation, population survival, and population density. Chapter 2 investigates how the differences in microclimate generated by slope and aspect can affect the process of range expansion. Chapter 2 also examines the relative roles of local management actions, such as increasing patch size or quality, and landscape-scale actions, such as increasing connectivity, in facilitating range expansions. Chapter 3 tests the extent to which current networks of protected areas can enhance range expansions, and investigates how protection status and active conservation interact to affect colonisation and population survival rates.

Chapter 4 explores how differences in macro- and microclimate can influence patterns of microhabitat use among populations. Using fine-scale surveys of egg locations from north- and south-facing sites across the UK, this chapter quantifies changes in microhabitat use across the range margin of *H. comma*, and tests whether microhabitat use varies predictably among populations according to the temperatures they experience.

Chapter 5 considers a more general problem in climate change ecology: how to measure the performance of species distribution models (SDMs). This chapter reviews current methods of SDM performance assessment, and develops a conceptual framework to assess the relative merits of different performance metrics, with the objective of improving the prediction of species' distributions under climate change.

Finally, Chapter 6 discusses the implications of the research presented in Chapters 2-5 for climate change ecology and conservation, and suggests potential avenues for future research.

1.9. References

- Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford.
- Araujo, M. and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* **22**:42-47.
- Araujo, M. B., D. Alagador, M. Cabeza, D. Nogues-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. *Ecology Letters* **14**:484-492.
- Araújo, M. B. and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**:1527-1539.
- Araújo, M. B. and C. Rahbek. 2006. How does climate change affect biodiversity? *Science* **313**:1396-1397.
- Ashcroft, M. B. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37**:1407-1413.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: individuals, populations and communities*. 3rd edition. Blackwell Science, Oxford.
- Bennie, J., J. A. Hodgson, C. R. Lawson, C. T. R. Holloway, D. B. Roy, T. Brereton, C. D. Thomas, and R. J. Wilson. In prep. Range expansion through fragmented landscapes under a variable climate.
- Bennie, J., B. Huntley, A. Wiltshire, M. O. Hill, and R. Baxter. 2008. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* **216**:47-59.

- Bennie, J., E. Kubin, A. Wiltshire, B. Huntley, and R. Baxter. 2010. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. *Global Change Biology* **16**:1503-1514.
- Bergmann, C. 1847. Über die Verhältnisse der warmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* **3**:595–708.
- Blouin-Demers, G. and P. J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* **82**:2882-2896.
- Bonebrake, T. C., C. L. Boggs, J. M. McNally, J. Ranganathan, and P. R. Ehrlich. 2010. Oviposition behavior and offspring performance in herbivorous insects: consequences of climatic and habitat heterogeneity. *Oikos* **119**:927-934.
- Boyce, M. S., C. V. Haridas, and C. T. Lee. 2006. Demography in an increasingly variable world. *Trends in Ecology & Evolution* **21**:141-148.
- Bryant, S. R., C. D. Thomas, and J. S. Bale. 2002. The influence of thermal ecology on the distribution of three nymphalid butterflies. *Journal of Applied Ecology* **39**:43-55.
- Buckley, L. B. and J. G. Kingsolver. 2012. The demographic impacts of shifts in climate means and extremes on alpine butterflies. *Functional Ecology* **26**:969-977.
- Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? *Ecology Letters* **13**:1041-1054.
- Burton, O. J., B. L. Phillips, and J. M. Travis. 2010. Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* **13**:1210-1220.

- Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, and O. Warsi. 2013. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* **280**.
- Chen, I., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* **333**:1024-1026.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *The American Naturalist* **157**:537-554.
- Crooks, K. R. and M. A. Sanjayan. 2006. *Connectivity conservation*. Cambridge University Press, Cambridge.
- Davies, Z. G., R. J. Wilson, T. M. Brereton, and C. D. Thomas. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation* **124**:189-198.
- Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**:247-256.
- Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X. Morin, C. Römermann, B. Schröder, and A. Singer. 2012. Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography* **39**:2119-2131.
- Dubois, Y., G. Blouin-Demers, B. Shipley, and D. Thomas. 2009. Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. *Journal of Animal Ecology* **78**:1023-1032.

- Dutilleul, P. and P. Legendre. 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. *Oikos* **66**:152-171.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* **289**:2068-2074.
- Elith, J. and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677-697.
- Erwin, D. H. 2009. Climate as a Driver of Evolutionary Change. *Current biology* **19**:575-583.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J.-L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* **14**:101-112.
- Forister, M. L., J. A. Fordyce, and A. M. Shapiro. 2004. Geological barriers and restricted gene flow in the holarctic skipper *Hesperia comma* (Hesperiidae). *Molecular Ecology* **13**:3489-3499.
- Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* **26**:285-291.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405**:220-227.
- Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, and W. E. Kunin. 2006. The ecological effectiveness of protected areas: the United Kingdom. *Biological Conservation* **132**:76-87.
- Gillson, L., T. P. Dawson, S. Jack, and M. A. McGeoch. In press. Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution*.
- Grinnell, J. 1917. The niche-relationships of the California Thrasher. *The Auk* **34**:427-423.

- Hampe, A. and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* **8**:461-467.
- Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5**:131-138.
- Hansen, J., M. Sato, and R. Ruedy. 2012. Perception of climate change. *Proceedings of the National Academy of Sciences* **109**:2415-2423.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* **396**:41-49.
- Hanski, I. and C. D. Thomas. 1994. Metapopulation dynamics and conservation - A spatially explicit model applied to butterflies. *Biological Conservation* **68**:167-180.
- Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. *Restoration Ecology* **14**:170-176.
- Heller, N. and E. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* **142**:14-32.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**:450-455.
- Hill, J., C. Thomas, R. Fox, M. Telfer, S. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**:2163-2171.

- Hill, J. K., C. D. Thomas, and B. Huntley. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**:1197-1206.
- Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of Habitat Patch Size and Isolation on Dispersal by *Hesperia comma* Butterflies: Implications for Metapopulation Structure. *Journal of Animal Ecology* **65**:725-735.
- Hodgson, J. A., C. D. Thomas, S. Cinderby, H. Cambridge, P. Evans, and J. K. Hill. 2011a. Habitat re-creation strategies for promoting adaptation of species to climate change. *Conservation Letters* **4**:289-297.
- Hodgson, J. A., C. D. Thomas, C. Dytham, J. M. J. Travis, and S. J. Cornell. 2012. The Speed of Range Shifts in Fragmented Landscapes. *Plos One* **7**:e47141.
- Hodgson, J. A., C. D. Thomas, T. H. Oliver, B. J. Anderson, T. M. Brereton, and E. E. Crone. 2011b. Predicting insect phenology across space and time. *Global Change Biology* **17**:1289-1300.
- Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* **46**:964-969.
- Konvicka, M., M. Maradova, J. Benes, Z. Fric, and P. Kepka. 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.
- Körner, C. and D. Basler. 2010. Phenology under global warming. *Science* **327**:1461-1462.
- Krosby, M., J. Tewksbury, N. M. Haddad, and J. Hoekstra. 2010. Ecological Connectivity for a Changing Climate. *Conservation Biology* **24**:1686-1689.

- Kubisch, A., T. Hovestadt, and H. J. Poethke. 2010. On the elasticity of range limits during periods of expansion. *Ecology* **91**:3094-3099.
- Kubisch, A. and H. J. Poethke. 2011. Range border formation in a world with increasing climatic variance. *Evolutionary Ecology Research* **13**:159-169.
- La Sorte, F. A. and W. Jetz. 2012. Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology* **81**:914-925.
- Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**:554–557.
- Larsen, T. H. 2012. Upslope Range Shifts of Andean Dung Beetles in Response to Deforestation: Compounding and Confounding Effects of Microclimatic Change. *Biotropica* **44**:82-89.
- Lawler, J. J. 2009. Climate Change Adaptation Strategies for Resource Management and Conservation Planning. *Annals of the New York Academy of Sciences* **1162**:79-98.
- Lindenmayer, D. B., W. Steffen, A. A. Burbidge, L. Hughes, R. L. Kitching, W. Musgrave, M. Stafford Smith, and P. A. Werner. 2010. Conservation strategies in response to rapid climate change: Australia as a case study. *Biological Conservation* **143**:1587-1593.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* **462**:1052-1055.
- Lovejoy, T. E. and L. J. Hannah. 2005. *Climate change and biodiversity*. Yale University Press, Michigan.

- Maclean, I. and R. J. Wilson. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences* **108**:12337-12342.
- Malcolm, J. R., A. Markham, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. *Journal of Biogeography* **29**:835-849.
- May, R. M. 2001. *Stability and complexity in model ecosystems*. Princeton University Press, Oxford.
- McInerney, G. J. and R. S. Etienne. 2012. Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? *Journal of Biogeography* **39**:2096-2102.
- Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. *Ecology Letters* **10**:710-717.
- Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille. 2012. Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change* **2**: 747–751.
- Oliver, T. H., R. J. Smithers, S. Bailey, C. A. Walmsley, and K. Watts. 2012. A decision framework for considering climate change adaptation in biodiversity conservation planning. *Journal of Applied Ecology* **49**:1247-1255.
- Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117**:285-297.
- Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**:482-U485.

- Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. *Science* **325**:464-467.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**:637-669.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**:579-583.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.
- Pearce-Higgins, J. W., R. B. Bradbury, D. E. Chamberlain, A. Drewitt, R. H. W. Langston, and S. G. Willis. 2011. Targeting research to underpin climate change adaptation for birds. *Ibis* **153**:207-211.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**:361-371.
- Perry, M. and D. Hollis. 2005. The development of a new set of long-term climate averages for the UK. *International Journal of Climatology* **25**:1023-1039.
- Peterson, A. T., S. J. R. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. *Ecological niches and geographic distributions*. Princeton University Press, Princeton, N.J. ; Oxford.

- Pettorelli, N. 2012. Climate change as a main driver of ecological research. *Journal of Applied Ecology* **49**:542-545.
- Phillimore, A. B., J. D. Hadfield, O. R. Jones, and R. J. Smithers. 2010. Differences in spawning date between populations of common frog reveal local adaptation. *Proceedings of the National Academy of Sciences of the United States of America* **107**:8292-8297.
- Prinzing, A. 2005. Corticolous arthropods under climatic fluctuations: compensation is more important than migration. *Ecography* **28**:17-28.
- Richardson, D. M., J. J. Hellmann, J. S. McLachlan, D. F. Sax, M. W. Schwartz, P. Gonzalez, E. J. Brennan, A. Camacho, T. L. Root, O. E. Sala, S. H. Schneider, D. M. Ashe, J. R. Clark, R. Early, J. R. Etterson, E. D. Fielder, J. L. Gill, B. A. Minter, S. Polasky, H. D. Safford, A. R. Thompson, and M. Vellend. 2009. Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences* **106**:9721-9724.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:57-60.
- Rowe, R. J. 2007. Legacies of land use and recent climatic change: the small mammal fauna in the mountains of Utah. *The American Naturalist* **170**:242-257.
- Roy, D. B. and J. A. Thomas. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia* **134**:439-444.
- Royle, J. A., R. B. Chandler, C. Yackulic, and J. D. Nichols. 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution* **3**:545-554.

- Schiffers, K., E. C. Bourne, S. Lavergne, W. Thuiller, and J. M. J. Travis. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**.
- Schofield, G., C. M. Bishop, K. A. Katselidis, P. Dimopoulos, J. D. Pantis, and G. C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology* **78**:14-21.
- Soberón, J. and M. Nakamura. 2009. Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences* **106**:19644-19650.
- Stott, P. A., S. Tett, G. Jones, M. Allen, J. Mitchell, and G. Jenkins. 2000. External control of 20th century temperature by natural and anthropogenic forcings. *Science* **290**:2133-2137.
- Suggitt, A. J., P. K. Gillingham, J. K. Hill, B. Huntley, W. E. Kunin, D. B. Roy, and C. D. Thomas. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120**:1-8.
- Thomas, C. D. 2010. Climate, climate change and range boundaries. *Diversity and Distributions* **16**:488-495.
- Thomas, C. D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution* **26**:216-221.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**:577-581.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld,

- G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145-148.
- Thomas, C. D. and I. Hanski. 1997. Butterfly Metapopulations. Pages xiii, 512 p. *in* I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego; London.
- Thomas, C. D., J. K. Hill, B. J. Anderson, S. Bailey, C. M. Beale, R. B. Bradbury, C. R. Bulman, H. Q. P. Crick, F. Eigenbrod, H. M. Griffiths, W. E. Kunin, T. H. Oliver, C. A. Walmsley, K. Watts, N. T. Worsfold, and T. Yardley. 2010. A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution*.
- Thomas, C. D., J. K. Hill, B. J. Anderson, S. Bailey, C. M. Beale, R. B. Bradbury, C. R. Bulman, H. Q. P. Crick, F. Eigenbrod, H. M. Griffiths, W. E. Kunin, T. H. Oliver, C. A. Walmsley, K. Watts, N. T. Worsfold, and T. Yardley. 2011. A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution* **2**:125-142.
- Thomas, C. D. and T. M. Jones. 1993. Partial recovery of a Skipper Butterfly (*Hesperia comma*) from Population Refuges: Lessons for Conservation in a Fragmented Landscape. *Journal of Animal Ecology* **62**:472-481.
- Thomas, J. and R. Lewington. 2010. *The butterflies of Britain & Ireland*. Dorling Kindersley, London.
- Thomas, J. A., C. D. Thomas, D. J. Simcox, and R. T. Clarke. 1986. Ecology and Declining Status of the Silver-Spotted Skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology* **23**:365-380.
- Thuiller, W. 2003. BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* **9**:1353-1362.

- Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* **18**:3279–3290.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**:467-473.
- VanDerWal, J., H. T. Murphy, A. S. Kutt, G. C. Perkins, B. L. Bateman, J. J. Perry, and A. E. Reside. 2012. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*: advance online publication.
- Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences* **275**:649-659.
- Von Humboldt, A. 1808. *Ansichten der Natur mit wissenschaftlichen Erläuterungen*. J.G. Cotta, Tübingen, Germany.
- Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**:65-69.
- Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, Slope and Butterflies - Topographic Determinants of Habitat Quality for *Euphydryas editha* *Ecology* **69**:1486-1496.
- Wells, K. and R. B. O'Hara. 2012. Species interactions: estimating per-individual interaction strength and covariates before simplifying data into per-species ecological networks. *Methods in Ecology and Evolution* **4**:1–8.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.

- Wiens, J. A. and D. Bachelet. 2010. Matching the Multiple Scales of Conservation with the Multiple Scales of Climate Change. *Conservation Biology* **24**:51-62.
- Willis, K. and G. MacDonald. 2011. Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annual Review of Ecology, Evolution, and Systematics* **42**:267-287.
- Wilson, R. J., Z. G. Davies, and C. D. Thomas. 2007. Insects and Climate Change: Processes, Patterns and Implications for Conservation. Pages 245-279 *in* A. J. A. Stewart, T. R. New, and O. T. Lewis, editors. *Insect conservation biology*. CABI, Wallingford.
- Wilson, R. J., Z. G. Davies, and C. D. Thomas. 2010. Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. *Ecography* **33**:73-82.
- Wilson, R. J., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* **8**:1138-1146.

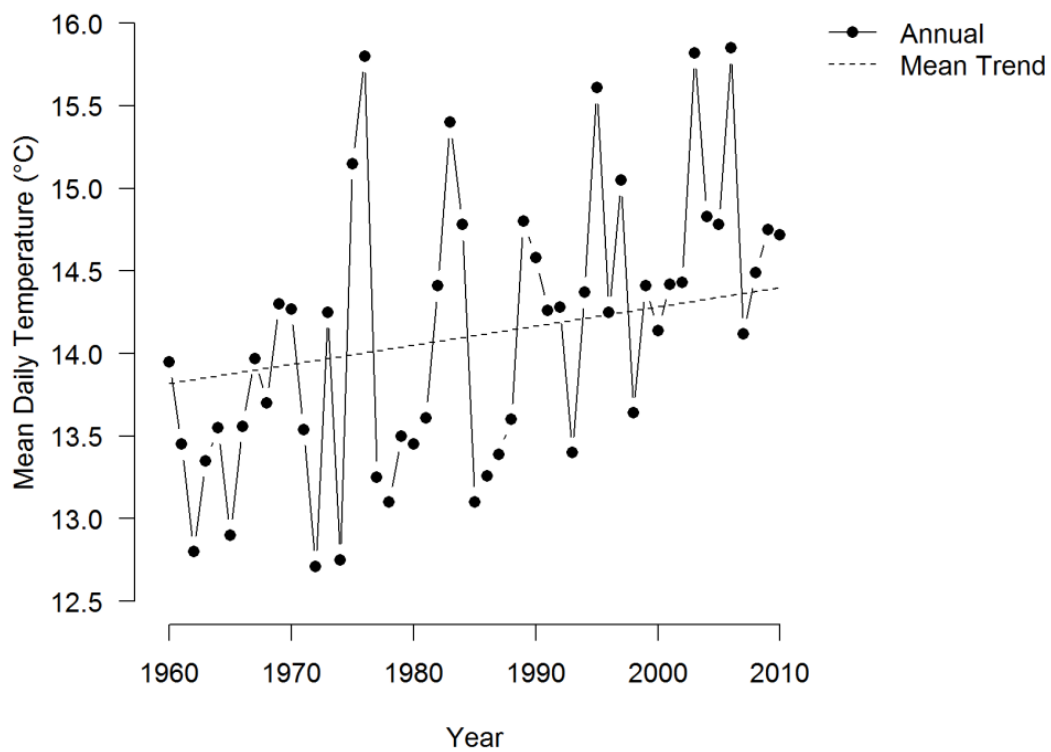


Figure 1.1: Mean daily summer temperatures in Britain from 1960 to 2010 (Perry and Hollis 2005). Over the past 50 years, average summer temperatures have risen by approximately 0.58°C (dashed line). However, the magnitude of the long-term warming trend is dwarfed by inter-annual variation in temperature (filled circles, solid line).



Figure 1.2: *The silver spotted skipper, Hesperia comma. Photo credit: Zoe Davies.*

Chapter 2: Local and Landscape Management of an Expanding Range Margin under Climate Change

2.1. Summary

There is a pressing need to understand how to facilitate species' range shifts under climate change. However, few empirical studies are available to inform decision-making, particularly at fine spatial and temporal resolutions. We present a case study of a thermally-constrained habitat specialist, the silver-spotted skipper butterfly *Hesperia comma*, at its expanding range margin in south-eastern Britain. Using data from 724 habitat patches over a 9-year interval (2000-2009), we examined local and landscape determinants of colonisation, survival, and population density. We then predicted probabilities of colonisation and survival for habitat patches under the observed 1982 and 2009 distributions to investigate how the factors limiting range expansions change through space and time. Between 2000 and 2009, *H. comma* continued to expand its range in Britain, but the 67 recorded colonisation events were offset by 48 local extinctions. Extinctions were strongly linked to climate, occurring predominantly in cooler regions and on shaded north-facing slopes. Population density and probability of survival were closely related to conditions within a site, whereas probability of colonisation was largely determined by functional connectivity. Survival probability was also influenced by connectivity, suggesting that immigration helped to support extinction-prone populations (a "rescue effect"). Patch occupancy beyond the range margin was primarily constrained by colonisation, but close to the expanding front, population survival became the key limiting factor. This pattern was conserved during range expansion, altering management priorities at individual sites. Previous studies on facilitating range shifts have stressed the need to increase landscape-scale connectivity to remove constraints on colonisation, and our data substantiate this advice. However, we show that enhancing population survival can also help to facilitate range expansions, because

populations at leading range edges face high extinction risk. Population survival can be directly improved through local management actions, such as enlarging patch size and increasing habitat quality, or indirectly by improving connectivity. Thus, local management can secure vulnerable populations at the range edge and provide larger and more stable migrant sources for future expansion, and deserves consideration when facilitating range shifts under climate change.

2.2. Introduction

Climate is one of the primary determinants of species' distributions, both directly through impacts on physiology and indirectly through its influence on interacting organisms (Parmesan & Yohe 2003; Hickling *et al.* 2006; Thomas 2010). As climates advance polewards and uphill under global warming (Loarie *et al.* 2009), the suitability of species' current habitats will change (Thomas *et al.* 2004; Araujo, Thuiller & Pearson 2006). This presents potential risks for species at their upper thermal limits, and potential benefits for species at their lower thermal limits, generating needs and opportunities for conservation (Hulme 2005; Thomas *et al.* 2010). Consequently, adapting management to climate change has become a priority (Hulme 2005; Mitchell *et al.* 2007).

Broadly, there are two potential courses of action for conserving climate-sensitive species: improve species' abilities to cope with climate change in habitats within the existing range that are becoming less climatically favourable, and shepherd species toward uncolonised habitats that are becoming climatically suitable (Heller & Zavaleta 2009; Lawler 2009; Thomas *et al.* 2010). As global temperatures continue to rise (Brohan *et al.* 2006) there will be a shift in emphasis from preserving species' current distributions toward the need to facilitate range shifts (Galatowitsch, Frelich & Phillips-Mao 2009). However, since other factors aside from climate constrain species occurrence, the fragmented distribution of suitable habitats can impair range shifts, particularly for species with highly specialised habitat requirements (Warren *et al.* 2001).

In fragmented habitats, the dual issues are how species survive as existing local populations within fragments (or “habitat patches”), and how they spread (colonise) from patch to patch across the landscape, as they expand their distributions (Hanski 1999). Current thinking on managing range expansions centres on increasing the number of colonisation events by boosting dispersal among habitat fragments (i.e. increasing connectivity or, more controversially, assisted colonisation; Heller & Zavaleta 2009, McLachlan, Hellmann & Schwartz 2007; Hoegh-Guldberg et al. 2008; Richardson et al. 2009). Commonly, coordinated landscape-scale schemes are proposed in which *per capita* dispersal success is enhanced through increased habitat aggregation, corridor creation or improved matrix permeability (Lovejoy & Hannah 2005; Manning, Gibbons & Lindenmayer 2009; Krosby *et al.* 2010). However, connectivity may also be improved by augmenting the *number* of dispersing individuals through measures that increase the number or size of extant populations (Hodgson *et al.* 2009).

Despite the potential benefits of region-wide conservation planning, in reality much of landscape structure emerges from the semi-independent actions of many different practitioners and landowners in separate habitat patches (Heller & Zavaleta 2009). Such site-specific or local management is thought to increase population size by improving the areal extent or quality (maximum population density) of a given habitat patch (Hodgson *et al.* 2009). Since larger populations are known to be more resistant to extinction (Hanski 1999), local management is often prescribed to build resistance to climate change at trailing range margins to preserve species’ current distributions (Pearce-Higgins *et al.* 2011). In contrast, local management is rarely considered in discussions on facilitating range shifts, perhaps because many species distribution models assume that only dispersal limitation prevents species from occupying habitats that are predicted to become climatically suitable (Huntley *et al.* 2010). However, on short timescales, inter-annual fluctuations in

climate dwarf the long term trend (Opdam & Wascher 2004), such that newly founded populations at the range edge may require protection.

In practical terms, the key issue is which management strategies to employ under different circumstances (Hoegh-Guldberg *et al.* 2008). Unfortunately, the existing literature on facilitating range shifts remains largely theoretical, with few empirical studies to guide management, especially at a spatial resolution fine enough to examine local-level impacts (Heller & Zavaleta 2009). This has left current advice lacking specificity (Heller & Zavaleta 2009), making it difficult for practitioners to determine the most appropriate actions for particular species or landscapes. Studies on species with specialised habitat requirements are particularly important in this context, since specialist species are likely to have greater difficulty tracking climate change due to the comparative scarcity of habitable land area (Warren *et al.* 2001; Wilson, Davies & Thomas 2010).

Here, we present a case study of a temperature-sensitive species (the silver-spotted skipper butterfly, *Hesperia comma*) with specialised habitat requirements, at its leading range margin in south-eastern Britain. Using data collected across 724 patches at a nine-year interval, we identify local and landscape determinants of population establishment, density, and survival. This empirical evidence is used to draw inferences about the following questions:

1. Does local management (increasing the *areal extent* or *quality* of occupied habitat) have a role to play at expanding margins?
2. Does landscape management (increasing the *connectivity* of habitat patches) help to facilitate range expansions?
3. How do the chances of colonisation and survival, and hence local management priorities, change in space across an expanding range margin and in time as a species expands?

Our results confirm the importance of landscape-scale connectivity in managing range shifts, but additionally show that improving survival through local management represents a key strategy at expanding range margins.

2.3. Methods

2.3.1. Study system

The silver-spotted skipper butterfly *Hesperia comma* is a habitat specialist: in Britain, it is confined to calcareous grassland, laying eggs on a single host plant species, sheep's fescue grass *Festuca ovina* (Thomas *et al.* 1986). Only short tufts (<10 cm) of *F. ovina* are selected for oviposition, restricting the butterfly to sites with intermediate to high levels of grazing (Thomas *et al.* 1986). In *H. comma*, both fecundity and egg-laying microhabitat availability are temperature-dependent: females show increased egg-laying rates at higher temperatures, and select warm microclimates, next to patches of bare ground, for oviposition (Davies *et al.* 2006).

H. comma reaches its northern range limit in Britain, where historically, populations have been confined to hotter south-facing slopes (Thomas *et al.* 1986). However, over the past 30 years, warming summer temperatures have broadened the range of microhabitats suitable for egg-laying (Davies *et al.* 2006) and permitted the colonisation of cooler north-facing habitats (Thomas *et al.* 2001). This, together with more widespread grazing from rabbits and livestock (Thomas & Jones 1993), has increased the availability of suitable breeding habitat, catalysing a range expansion from fewer than 70 populations in 1982 to over 250 by 2000 (Davies *et al.* 2005; Wilson, Davies & Thomas 2010). However, the fragmented distribution of these habitat patches and the species' limited dispersal abilities (Hill, Thomas & Lewis 1996) have constrained the rate of this expansion (Wilson, Davies & Thomas 2009, 2010).

2.3.2. Survey methods

In 2009, we conducted the fourth UK national survey of *H. comma*'s distribution (for previous surveys in 1982, 1991 and 2000 see Thomas *et al.* 1986; Thomas & Jones 1993; Davies *et al.* 2005). Since *H. comma* is univoltine, this represents nine generations since the previous survey (Davies *et al.* 2005). The search was restricted to five main habitat networks in south-east England (in the counties of Kent, Sussex, Surrey, Hampshire, and the Chiltern hills), which encompass the majority of *H. comma* populations in Britain (Davies *et al.* 2005). As in previous surveys, suitable habitat patches were defined as any unimproved chalk grassland containing more than an estimated 5% cover of *F. ovina* plants less than 10 cm tall, and neighbouring patches were defined as separate if their nearest perimeter points were divided by at least 25 m of unsuitable grassland, or a woodland or scrub barrier. All habitat patches meeting these criteria within a 30 km radius of known populations were surveyed; this radius is considered sufficient to detect all new populations since it exceeds the maximum recorded colonisation distance over an 18 year period (1982-2000; Davies *et al.* 2005), and because the species was not recorded between 2001 and 2008 more than 13 km from populations known in 2000 by the British "Butterflies for the New Millennium" recording scheme (R. Fox, pers. comm.).

Once located, the perimeter of each patch was mapped using a handheld Global Positioning System (GPS; accuracy $<\pm 10$ m), and later digitised using ArcMap software (ESRI 2009). Habitat characteristics that could affect *H. comma* occupancy were recorded, including the total area of the patch in hectares, the percentage cover of bare ground and vegetation <10 cm tall, and proportional host plant cover in vegetation <10 cm (Table 2.1). Patches were then searched for the presence of *H. comma*, based either on observation of adults or timed egg searches.

For patches visited in favourable weather during the flight period, adult densities were estimated using transect walks (Pollard & Yates 1993). Using weekly *H. comma* counts from UK Butterfly Monitoring Scheme (BMS) transects, we calculated the proportion of peak abundance on the day each transect was walked. We then divided observed abundance on survey transects by proportion of regional peak to estimate peak density at each site, setting a minimum proportion of 20% to avoid excessively large density adjustments.

2.3.3. Variable collation

The area of each patch (ha) was calculated using digitised patch perimeters in ArcGIS. By multiplying patch area by proportion of the patch with vegetation <10 cm tall, an estimate of effective breeding area was obtained (Table 2.1).

To assess landscape-scale gradients in macroclimate during the adult flight season, we calculated the mean August daily maximum temperature for each site for two separate periods (1982-1991 and 2000-2009), using the UKCP09 5 km resolution gridded observation data set from the UK Meteorological Office (Perry & Hollis 2005). To assess patch-scale differences in microclimate, we calculated incoming solar radiation as a function of aspect and slope: we applied the “hillshade” function to a 5 m resolution digital terrain model in ArcMap (Intermap Technologies 2007; vertical accuracy ±60 cm), using solar azimuth of 180° and altitude 60° (equivalent to the maximum solar radiation in South-eastern UK during mid-August), and extracted the median solar index for each patch using the spatial analyst tool (ESRI 2009).

As a measure of potential immigration into each patch, we calculated functional connectivity using Hanski’s connectivity index:

$$S_i = \sum p_j \exp(-\alpha d_{ij}) A_j^b$$

Where i is the focal patch and j all other patches, which have area A_j and are separated from i by distance d_{ij} (Hanski 1999). Here, A_j is effective area <10cm (ha) of patch j , and d_{ij} edge-to-edge distances between patches i and j (km), both based on 2009 data. α (a negative exponential dispersal kernel) and b (a scaling function for patch emigration) are estimated from a previous study (Wilson, Davies & Thomas 2010). In the original formulation, p_j denotes the presence or absence of the butterfly at site j , and is here used in two different ways. “Direct connectivity” calculates connectivity to occupied patches ($p_j=1$), discounting unoccupied patches ($p_j=0$). “Indirect connectivity” calculates connectivity to *unoccupied* patches, weighting those patches by their direct connectivity scores (i.e. taking area of patch j as $A_j S_j$). Therefore while direct connectivity is a measure of the probability of colonisation in a single dispersal event from currently occupied patches, indirect connectivity is a measure of the probability of colonisation in two dispersal events using currently unoccupied habitat as a “stepping stone”. Both connectivity measures were calculated for occupancy patterns in three years: 1982, 2000, and 2009.

2.3.4. Analyses

Analyses were conducted in two stages. First, we examined whether establishment, survival and density of *H. comma* populations from 2000-2009 could be explained by local and regional factors (Table 2.1). Second, we used the best models to predict the probabilities of survival and colonisation across all patches for two time periods (1982-1991 and 2000-2009). All models were fitted using generalised linear modelling (Crawley 2007) in R 2.12.2 (R Development Core Team 2011).

Survival models considered existing populations in 2000, with a binary response of “survival” or “extinction” by 2009; colonisation models considered unoccupied patches in 2000, with the response as “colonised” or “uncolonised”. In addition to presence information from the 2009 survey, colonisation analyses included temporary colonisations based on additional information from

surveys conducted by the authors in 2001 and 2002, and records from 2001-2008 from Butterfly Conservation, the organisation which coordinates the UK butterfly distribution monitoring scheme. We considered the butterfly as absent from any site not surveyed in 2000 that was more than 5 km from an occupied patch. Population density analyses focussed on density data from the 2009 survey. We assumed a binomial error distribution for survival and colonisation models. Population density models assumed a Tweedie error distribution, a compound poisson-gamma distribution family suited to analysing positive continuous data with exact zeroes; parameters were estimated using the “tweedie” package (Dunn 2010).

Explanatory factors included local and landscape variables (Table 2.1). Local variables comprised solar index and habitat characteristics (Table 2.1; see also *Survey methods*). A squared bare ground term was included since intermediate levels of bare ground are likely to be optimal for this species. We used habitat data gathered in 2000 in survival analyses, but since these data were not available for all unoccupied patches in 2000, we used 2009 habitat data in colonisation analyses. Landscape variables included macroclimate, and direct and indirect connectivity (Table 2.1).

Population density analyses considered only local variables from 2009 and macroclimate (Table 2.1). Density analyses used proportion of turf <10 cm instead of effective area <10cm, because the former investigates how density increases with breeding habitat independently of patch size. An additional variable, “age”, was also included, which indicated whether a population was present in 2000 (“old”), or had been founded after 2000 (“young”).

Data were checked for spatial autocorrelation (Beale *et al.* 2010) using Mantel tests with the “vegan” package (Oksanen *et al.* 2011). There was no evidence that population density estimates were spatially correlated ($r=-0.043$, $P>0.05$). We expected some spatial autocorrelation in survival and colonisation data due to dispersal between neighbouring patches, as explicitly modelled by

connectivity terms. Therefore, to test for autocorrelation over and above that accounted for by these covariates, we conducted mantel tests of the residuals from models including solely the two connectivity measures. Although there was no significant autocorrelation in colonisation model residuals ($r=-0.0080$, $P>0.05$), there was some sign of autocorrelation remaining in survival residuals ($r=0.24$, $P<0.01$). Consequently, we fitted mixed models including a random effect of “grid square”, classifying patches into spatial blocks of (a) 5 km and (b) 10 km squares, using the “lme4” package (Bates & Maechler 2010). However, top model sets were similar and effect sizes were within standard error bounds of those in the original models, indicating that spatial autocorrelation was not seriously affecting model parameters.

For each response variable, we fitted all possible combinations of linear terms, with no interactions, and used the Akaike Information Criterion, adjusted for small sample size (AICc; Burnham & Anderson 2002) to rank models. To obtain our best model sets, we selected models that were within six AICc units of the top-ranked model (Richards 2005), excluding models with simpler, higher-ranking nested variants (Richards 2008). This procedure guards against the selection of over-parameterised models whilst maintaining a high probability of selecting the true best model (Richards 2008).

To further explore which variables best explained survival and colonisation, and to examine how variance was partitioned among them, we conducted hierarchical partitioning (Mac Nally 2002), implemented with the “hier.part” package (Mac Nally & Walsh 2004). Hierarchical partitioning investigates the average change in fit (here, log-likelihood) between equivalent models with and without a given variable X , to assess the explanatory power of X independently of other terms (I_x). By randomising the dataset 1000 times and recalculating I_x , we estimated the probability of obtaining a value of I_x equal to or greater than that observed by chance, allowing us to assign statistical significance to the explanatory power of each variable (Mac Nally 2002). In addition, the average

effect of other variables on the explanatory power of X (“joint” effects, J_X) can be calculated; their direction indicates whether other variables are acting additively (positive), increasing the variation explained by X , or suppressively (negative), sharing variation with X (Mac Nally & Walsh 2004).

Following model selection, we applied our best model sets to predict the probabilities of colonisation and survival across the metapopulations. Predictions were based on distribution data from either 1982 or 2009; in both cases, local variables (Table 2.1) were based on 2009 data since habitat information was not available for all patches in 1982. We used model-averaging (Burnham & Anderson 2002) implemented by the “AICcmodavg” package (Mazerolle 2010) to obtain a single predicted survival and colonisation probability for each patch. Doing so incorporates model selection uncertainty whilst weighting the influence of each model by the strength of its supporting evidence (Burnham & Anderson 2002).

To identify how survival and colonisation limitations varied across the British distribution of *H. comma*, we classified each patch into one of four categories, based on whether they were primarily limited by survival, colonisation, both (“marginal” habitat), or neither (“supported” habitat).

2.4. Results

Between 2000 and 2009, 67 new patches were colonised, 168 populations survived, whilst 48 populations suffered local extinctions (Fig. 2.1). In addition, records from the intervening years detected 29 temporary colonisations that subsequently became extinct before 2009, giving a minimum of 96 colonisations and 77 local extinction events (Fig. 2.1).

Population survival was closely associated with climatic factors, being more likely in warmer regions and on south-facing slopes (macroclimate: $Z=5.03$, $P<0.0001$; solar index: $Z=3.13$, $P<0.0001$; Fig. 2.2a; Table 2.2a). Solar index did not influence chances of colonisation ($Z=-0.26$, $P>0.05$; Fig. 2.2b).

The relationship between macroclimate and colonisation was equivocal: although hierarchical partitioning indicated a significant relationship ($Z=2.75$, $P<0.01$; Fig. 2.2b), the direction of this effect varied, much of its explanatory power was shared with other variables (large “joint” effect, Fig. 2.2b), and macroclimate did not appear in any of the top-fitting colonisation models (Table 2.2b).

Survival was also closely linked to local management variables (Fig. 2.2a; Table 2.2a). There was strong evidence for an effect of patch area ($Z=3.81$, $P<0.001$), with populations in larger patches more likely to survive (Table 2.2a). Survival was also more likely in higher quality patches with increased host plant availability ($Z=2.31$, $P<0.05$). The top-ranked survival models supported a squared relationship with bare ground (Table 2.2a), indicating highest survival at sites with intermediate (around 15%) bare ground cover.

Colonisation was also more likely for patches with greater host plant cover and an intermediate proportion of bare ground (Host plant cover: $Z= 8.65$, $P<0.0001$; Bare ground: $Z=1.80$, $P<0.05$; Fig. 2.2b, Table 2.2b), with around 22% bare ground as the predicted optimum. However, the areal extent of a patch did not affect its chance of colonisation ($Z=-0.38$, $P>0.05$; Fig. 2.2b).

Survival and colonisation increased with direct connectivity to occupied sites (Survival: $Z=16.05$, $P<0.0001$; Colonisation: $Z=26.75$, $P<0.0001$; Fig. 2.2). Indirect connectivity improved colonisation chances ($Z=55.14$, $P<0.0001$; Table 2.2b), but had little impact on survival of pre-existing populations ($Z=0.17$, $P>0.05$; Fig. 2.2a). The high correlation between direct and indirect connectivity means that they share explanatory power (large “joint” effect, Fig. 2.2b).

We obtained density estimates for 142 populations. Population density models corresponded well with survival analyses: density was highest at south-facing sites with high proportions of short vegetation (<10 cm), *F. ovina*, and bare ground (Table 2.2c). Density was lower in more recently established populations (Table 2.2c).

To illustrate spatial and temporal variation in factors limiting the persistence and expansion of *H. comma*, Fig. 2.3b displays model predictions for (a) 1982-1991 and (b) 2000-2009 for the Sussex network. Close to the expanding front are clusters of “*survival-limited*” sites which have a high chance of colonisation, but a low probability of supporting a population in the long term. Further beyond the leading edge, there are scattered “*colonisation-limited*” patches, which are relatively unlikely to be colonised over a nine-year period, but, if colonised, have a high chance of supporting *H. comma* populations due to their large size and/or high quality. With the expansion of *H. comma*, many formerly isolated patches now have closer sources of migrants available and hence improved chances of colonisation and/or survival (“*supported*” patches, Fig. 2.3).

2.5. Discussion

The empirical evidence base to inform management of species’ range shifts is currently lacking (Heller & Zavaleta 2009). Here we present a case study of a thermally constrained habitat specialist, the silver-spotted skipper butterfly *Hesperia comma*, which is expanding its northern range limit in Britain under rising temperatures (Brohan *et al.* 2006). The results allow us to draw conclusions regarding the roles of local- and landscape-scale processes in adapting conservation management to climate change.

2.5.1. Determinants of extinction and colonisation

Although *H. comma* continued to expand its distribution in Britain between 2000 and 2009, there were also a number of setbacks, with 48 local extinctions offsetting the 67 recorded colonisation events. Populations in habitats of lower climatic suitability – in cooler regions and on north-facing slopes - were most likely to suffer extinction. Two non-mutually exclusive explanations are that (a) populations in less suitable climates were smaller (Hanski 1999) or (b) the dynamics of populations at the range edge showed greater fluctuations with weather (Thomas, Moss & Pollard 1994; Opdam

& Wascher 2004). Although we cannot examine inter-annual variability in population size based on the data presented here, we found that population densities were smaller in both cooler microclimates and in more recently founded populations. Thus, although warming temperatures permitted expansion into habitat that was previously too cool (Thomas *et al.* 2001) the vulnerability of these new populations remained higher than those in core habitats.

Several previous studies have suggested that range edge populations may face heightened extinction risk in comparison with those in core habitats. Indirect evidence is provided by analyses of population density across species' ranges: in many but not all cases it has been shown that population densities decline towards range margins (Sagarin & Gaines 2002). A few studies have also gathered direct evidence that extinction risk increases in climatically marginal habitats at leading margins. For example, a study on ringlet butterflies *Aphantopus hyperantus* indicated a retraction to core (partially shaded) habitats following a period of drought (Sutcliffe *et al.* 1997), whilst Mehlman (1997) found that populations of three North American passerine bird species were more likely to go extinct at sites which experienced more severe winters or were closer to the range edge. Our study shows that populations in marginal habitats remain vulnerable when a species is expanding its distribution under increasingly favourable climates.

Since population survival, and not just establishment, limits range expansions under climate change, species' range shifts could be enhanced through management to improve population persistence. Local measures such as increasing patch area have been proposed as an option for building resistance to climate change at contracting margins (Pearce-Higgins *et al.* 2011), but are rarely considered in the context of expanding margins. We found that site-scale factors promoted the survival of populations at the expanding front. Survival was higher in larger patches, either because larger patches support larger populations (Hanski 1999), or perhaps because larger patches capture greater environmental heterogeneity which buffers populations against climatic variability (Opdam

& Wascher 2004; Oliver *et al.* 2010). Moreover, survival was also improved in higher quality patches (those with higher host plant availability and optimal bare ground cover). These results indicate that local management can be important for securing species' footholds in habitats at the range edge, and thus to help facilitate range expansions.

In contrast to population survival, the chance of a patch being colonised was not strongly related to local management, although we did find evidence that higher host plant availability increased colonisation chances. Instead, there was an overriding positive effect on colonisation probability of direct and indirect connectivity. The latter indicates that well-connected networks of habitat, even if initially unoccupied, can facilitate "stepping stone" colonisations, either within generations (connected habitat patches are used as migration routes), or between generations (unoccupied patches are colonised and serve as migrant sources in subsequent years), or both (Lawler 2009). This provides empirical evidence, in the context of an expanding range margin, that beliefs about connectivity enhancing range expansions are well-founded (see also Melles *et al.* 2011).

Population survival was also improved by increased connectivity, indicating a possible role for rescue effects (Hanski 1999), or re-colonisations within the 9 year survey interval. We found little evidence that indirect connectivity influenced survival, perhaps because most patches colonised between 2000 and 2009 were too remote from most pre-existing populations to provide rescue effects. Few discussions on managing range shifts have explicitly considered how increasing connectivity could improve persistence of populations at the expanding front. Our data, using a fine enough spatial resolution to identify individual patches and populations, and a temporal resolution of nine generations, show that increased connectivity enhances both colonisation and survival.

Since both patch area and proximity are incorporated in our connectivity terms, the results do not allow us to differentiate among measures that increase per capita dispersal success (e.g. corridors or

matrix management; Lovejoy & Hannah 2005; Krosby *et al.* 2010) and measures that augment the number of migrants by increasing the number or size of extant populations (Hodgson *et al.* 2009). However, since our results show that both population density and persistence, and hence migrant numbers, increased with patch size and quality (Table 2.2a and c), it follows - assuming a causal relationship between these variables - that local management also increases landscape-scale connectivity. Thus, management to improve patch size or quality brings both direct local and indirect regional benefits (Hodgson *et al.* 2009).

2.5.2. Implications for managing a range expansion

Current management recommendations for *H. comma* focus on local management, with measures increasing the effective size of habitat patches through scrub removal, and grazing to control sward height and bare ground availability (Barnett & Warren 1995; Davies *et al.* 2005). Landscape-scale management of connectivity is less straightforward to achieve, potentially involving coordinated management among several landowners, although voluntary agri-environment schemes such as Environmental Stewardship have successfully improved connectivity for some taxa (Donald & Evans 2006). Local prioritisation of management strategies will depend on the current chances of colonisation by and survival of *H. comma* (Table 2.3).

Applying our models to predict colonisation and survival across the British distribution of *H. comma* for 2009-2018 showed that colonisation and survival are differentially limiting across the species' range margin, due to among-patch differences in size and quality (influenced by local management) and connectivity to existing populations (influenced by landscape management and the species' current distribution; Fig. 2.3b). Because connectivity (direct and indirect) is the primary determinant of colonisation probability, colonisation becomes increasingly limiting as distance beyond the expanding front increases (Davies *et al.* 2005), whereas survival is strongly influenced by local factors

and is therefore less constrained by proximity to *H. comma*'s current distribution. Practically, this means that whilst survival limitation can be remedied through site-specific actions (Table 2.3; survival-limited and marginal patches, Fig. 2.3b), there is less that local management can do to directly encourage colonisation of a patch. Nonetheless, knowing the chance of colonisation can usefully inform site-scale management decisions (Table 2.3). For large, south-facing, but isolated patches (colonisation-limited patches, Fig. 2.3) artificial introductions might be considered, since their success rate is likely to be high (McLachlan, Hellmann & Schwartz 2007; Hoegh-Guldberg *et al.* 2008; Richardson *et al.* 2009). Alternatively, since managers must balance decisions for many species with different requirements and distributions, local management for species that are currently unlikely to reach a site may represent a low priority.

However, as species expand their distributions, connectivity to extant populations, and hence local management priorities, can change rapidly. With the proliferation of *H. comma* across Sussex, owners of previously isolated sites may consider management for *H. comma* of higher importance now that colonisation chances have improved, whilst formerly survival-limited patches on the periphery of the *H. comma* distribution are now well-supported by rescue effects, making local management to improve population survival less of a necessity (Fig. 2.3). This rapid and widespread shift in priorities suggests that, if management is to be conducted on an independent, site-by-site basis, regular monitoring of species shifting distributions (Lepetz *et al.* 2009) and flexible decision-making (Lovejoy & Hannah 2005) will be required to maximise efficiency. However, there are two reasons why coordinated landscape-scale management might prove preferable to independent local management. First, retrospective adjustments of policy might be too slow for species with particularly dynamic patterns of population turnover or rapid rates of spread. If so, predictive modelling (Hannah *et al.* 2007, Huntley *et al.* 2010) could help management to keep pace with species' shifting distributions. Second, connectivity will only increase if habitat availability provides

the opportunity to expand, such as in the Sussex network here. Where habitat patches are more isolated, such as in Hampshire (Fig. 2.1), colonisation may remain limiting pending increased habitat connectivity, artificial introductions, or rare long-distance colonisation events (McLachlan, Hellmann & Schwartz 2007).

The simple models employed here are not intended to provide an exact blueprint for management, since they assume that correlations observed between environmental variables and population survival or colonisation are causal, and assess limiting factors for each site based on a single point in time, ignoring the complex interplay among changes in management practices, occupancy patterns, and connectivity. Nonetheless, Figure 3 demonstrates how, for *H. comma* at least, survival is the primary limiting factor close to the leading edge, and remains so as the distribution shifts, potentially slowing the rate of expansion. Our results provide encouragement that local management can help to alleviate survival limitation at an expanding front and provide larger and more stable platforms for future expansion.

2.6. Conclusion

Range shifts under climate change are not a continuous march toward pastures new, but a dynamic process resulting from an imbalance in extinction and colonisation events. Consequently, founding new populations at the leading edge is only the first step towards a range expansion, because populations at the range edge face heightened extinction risk. Since colonisation rates may be high close to species' current distributions, survival can become the primary factor limiting expansion at the range edge. There are thus two complementary strategies for facilitating species' range shifts: encourage colonisation of unoccupied habitat through landscape management for connectivity and/or assisted colonisation; and support populations by increasing patch size or quality, or providing nearby migrant sources, wherever new footholds are established. Since local management

can increase both population persistence and connectivity, it represents an important strategy for facilitating range shifts under climate change.

2.7. References

- Araujo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712-1728.
- Barnett, L.K. & Warren, M.S. (1995) *Species Action Plan - Silver-spotted skipper, Hesperia comma*. Butterfly Conservation, Wareham, Dorset.
- Bates, D. & Maechler, M. (2010) lme4: Linear mixed-effects models using S4 classes.
<http://CRAN.R-project.org/package=lme4>.
- Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D.A. (2010) Regression analysis of spatial data. *Ecology Letters*, **13**, 246-264.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference : a practical information-theoretic approach*, 2nd edn. Springer, New York, London.
- Brohan, P., Kennedy, J.J., Harris, I., Tett, S. F. B. & Jones, P.D. (2006) Uncertainty estimates in regional and global observed temperature changes: a new dataset from 1850. *Journal of Geophysical Research*, **111**, D12106
- Crawley, M.J. (2007) *The R book*. Wiley, Chichester; Hoboken, N.J.
- Davies, Z.G., Wilson, R.J., Brereton, T.M. & Thomas, C.D. (2005) The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, **124**, 189-198.

- Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**, 247-256.
- Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, **43**, 209-218.
- Dunn, P.K. (2010) tweedie: Tweedie exponential family models.
- <http://cran.r-project.org/web/packages/tweedie/index.html>.
- ESRI (2009) ArcMap 9.3.1. ESRI, Redlands, CA, USA.
- Galatowitsch, S., Frelich, L. & Phillips-Mao, L. (2009) Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. *Biological Conservation*, **142**, 2012-2022.
- Hannah, L., Midgley, G., Anelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. & Williams, P. (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**, 131-138.
- Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.
- Heller, N. & Zavaleta, E. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, **142**, 14-32.
- 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., Thomas, C.D. & Lewis, O.T. (1996) Effects of Habitat Patch Size and Isolation on Dispersal by *Hesperia comma* Butterflies: Implications for Metapopulation Structure. *Journal of Animal Ecology*, **65**, 725-735.
- Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, **46**, 964-969.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008) Assisted colonization and rapid climate change. *Science*, **321**, 345-346.
- Hulme, P.E. (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, **42**, 784-794.
- Huntley, B., Barnard, P., Altwegg, R., Chambers, L., Coetsee, B.W.T., Gibson, L., Hockey, P.A.R., Hole, D.G., Midgley, G.F., Underhill, L.G. & Willis, S.G. (2010) Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography*, **33**, 621-626.
- Intermap Technologies (2007) NEXTMap Britain: Digital terrain mapping of the UK. NERC Earth Observation Data Centre.
- Krosby, M., Tewksbury, J., Haddad, N.M. & Hoekstra, J. (2010) Ecological Connectivity for a Changing Climate. *Conservation Biology*, **24**, 1686-1689.
- Lawler, J.J. (2009) Climate Change Adaptation Strategies for Resource Management and Conservation Planning. *Annals of the New York Academy of Sciences*, **1162**, 79-98.
- Lepetz, V., Massot, M., Schmeller, D.S. & Clobert, J. (2009) Biodiversity monitoring: some proposals to adequately study species' responses to climate change. *Biodiversity and Conservation*, **18**, 3185-3203.

- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052-1055.
- Lovejoy, T.E. & Hannah, L.J. (2005) *Climate change and biodiversity*. Yale University Press, Michigan.
- Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation*, **11**, 1397-1401.
- Mac Nally, R. & Walsh, C. (2004) Hierarchical Partitioning Public-domain Software. *Biodiversity and Conservation*, **13**, 659-660.
- Manning, A.D., Gibbons, P. & Lindenmayer, D.B. (2009) Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology*, **46**, 915-919.
- Mazerolle, M.J. (2010) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).
- McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A Framework for Debate of Assisted Migration in an Era of Climate Change. *Conservation Biology*, **21**, 297-302.
- Mehlman, D.W. (1997) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614-624.
- Melles, S.J., Fortin, M.J., Lindsay, K. & Badzinski, D. (2011) Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Global Change Biology*, **17**, 17-31.
- Mitchell, R.J., Morecroft, M.D., Acreman, M., Crick, H.Q.P., Frost, M., M.Harley, Maclean, I.M.D., Mountford, O., Piper, J., Pontier, H., Rehfisch, M.M., Ross, L.C., Smithers, R.J., Stott, A.,

- Walmsley, C., Watts, O. & Wilson, E. (2007) England Biodiversity Strategy - towards adaptation to climate change. Final report to Defra for contract CRO327. *Defra*, 177pp. (Contract CRO327). (Unpublished).
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2011) vegan: Community Ecology Package.
- <http://CRAN.R-project.org/package=vegan>.
- Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, **13**, 473-484.
- Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Pearce-Higgins, J.W., Bradbury, R.B., Chamberlain, D.E., Drewitt, A., Langston, R.H.W. & Willis, S.G. (2011) Targeting research to underpin climate change adaptation for birds. *Ibis*, **153**, 207-211.
- Perry, M. & Hollis, D. (2005) The development of a new set of long-term climate averages for the UK. *International Journal of Climatology*, **25**, 1023-1039.
- Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme*. Chapman & Hall, London.

- R Development Core Team (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richards, S.A. (2005) Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology*, **86**, 2805-2814.
- Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, **45**, 218-227.
- Richardson, D.M., Hellmann, J.J., McLachlan, J.S., Sax, D.F., Schwartz, M.W., Gonzalez, P., Brennan, E.J., Camacho, A., Root, T.L., Sala, O.E., Schneider, S.H., Ashe, D.M., Clark, J.R., Early, R., Etterson, J.R., Fielder, E.D., Gill, J.L., Minter, B.A., Polasky, S., Safford, H.D., Thompson, A.R. & Vellend, M. (2009) Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences*, **106**, 9721-9724.
- Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137-147.
- Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davies, J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109**, 235-241.
- Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488-495.
- 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., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.
- Thomas, C.D., Hill, J.K., Anderson, B.J., Bailey, S., Beale, C.M., Bradbury, R.B., Bulman, C.R., Crick, H.Q.P., Eigenbrod, F., Griffiths, H.M., Kunin, W.E., Oliver, T.H., Walmsley, C.A., Watts, K., Worsfold, N.T. & Yardley, T. (2010) A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution*, **2**, 125-142.
- Thomas, C.D. & Jones, T.M. (1993) Partial recovery of a Skipper Butterfly (*Hesperia comma*) from Population Refuges: Lessons for Conservation in a Fragmented Landscape. *Journal of Animal Ecology*, **62**, 472-481.
- Thomas, J.A., Moss, D. & Pollard, E. (1994) Increased Fluctuations of Butterfly Populations towards the Northern Edges of Species' Ranges. *Ecography*, **17**, 215-220.
- Thomas, J.A., Thomas, C.D., Simcox, D.J. & Clarke, R.T. (1986) Ecology and Declining Status of the Silver-Spotted Skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology*, **23**, 365-380.
- 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.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65-69.

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: Biological Sciences*, **276**, 1421-1427.

Wilson, R.J., Davies, Z.G. & Thomas, C.D. (2010) Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. *Ecography*, **33**, 73-82.

Variable name	Symbol	Description	Spatial Scale	Analyses
Area <10cm	AR	Effective area (ha) of turf <10 cm tall	Local	S, C
Host plant cover	HO	Proportional coverage (%) of <i>Festuca ovina</i> in turf <10 cm	Local	S, C, P
Bare ground cover	BG	Proportional coverage (%) of bare ground in patch	Local	S, C, P
Solar index	IN	Incident solar radiation at midday in mid-August	Local	S, C, P
Macroclimate	MC	Mean August maximum temperature over nine-year period	Local	S, C, P
Direct connectivity	CD	Connectivity to occupied sites	Landscape	S, C
Indirect connectivity	CI	Connectivity to initially unoccupied sites, weighted by connectivity to occupied sites	Landscape	S, C
<10cm cover	TE	Proportional coverage (%) of turf <10 cm tall in patch	Local	P
Population age	AGE	Categorical variable indicating whether population was founded after 2000 (“young”) or prior to 2000 (“old”)	Local	P

Table 2.1: Explanatory variables and the analyses they are used in (S=Survival, C=Colonisation, P=Population density)

Rank	K	$\Delta AICc$	%LL	Formula
(a) Survival (n=214)				
1	7	0.00	0.25	+ AR + IN + CD + MC + BG - BG ²
2	7	2.84	0.24	+ AR + IN + CD + BG - BG ² - CI
3	6	2.92	0.23	+ AR + IN + CD + BG - BG ²
4	6	3.20	0.23	+ AR + IN + CD + MC + HO
5	5	4.26	0.21	+ AR + IN + CD + MC
(b) Colonisation (n=510)				
1	4	0.00	0.27	+ CD + CI + HO
2	5	2.72	0.27	+ CD + CI + BG - BG ²
3	3	3.94	0.26	+ CD + CI
(c) Population Density (n=142)				
1	6	0.00	0.04	+ AGE + IN + TE + HO
2	5	0.35	0.04	+ AGE + IN + TE
3	5	1.05	0.03	+ AGE + IN + HO
4	4	1.59	0.03	+ AGE + TE
5	5	2.02	0.03	+ AGE + IN + BG
6	4	2.83	0.03	+ AGE + IN
7	4	3.20	0.03	+ AGE + HO
8	4	3.84	0.03	+ AGE + BG
9	3	4.53	0.02	+ AGE

Table 2.2: Top-ranking models for (a) survival, (b) colonisation and (c) population density analyses.

K=number of parameters; $\Delta AICc$ =difference in AICc between current and best model; %LL = Percent change in log-likelihood from null model; Formula indicates which terms were included in the model (Table 2.1) and the direction of their coefficients (+/-).

Category	Colonisation Probability	Survival Probability	Recommended management actions
Supported	High (>50%)	High (>50%)	<ul style="list-style-type: none"> • Continue existing management • Monitor for changes and adapt management if necessary
Colonisation-limited	Low (<50%)	High (>50%)	<ul style="list-style-type: none"> • Increase connectivity of surrounding habitat through matrix softening or creation of corridors / stepping stones • Increase patch quality through grazing management • Assisted colonisations where viable • Await further spread
Survival-limited	High (>50%)	Low (<50%)	<ul style="list-style-type: none"> • Increase patch size through habitat restoration (e.g. scrub removal) • Increase patch quality through grazing
Marginal	Low (<50%)	Low (<50%)	<ul style="list-style-type: none"> • Low priority • May become more important as species spreads

Table 2.3: Site classification scheme and management recommendations

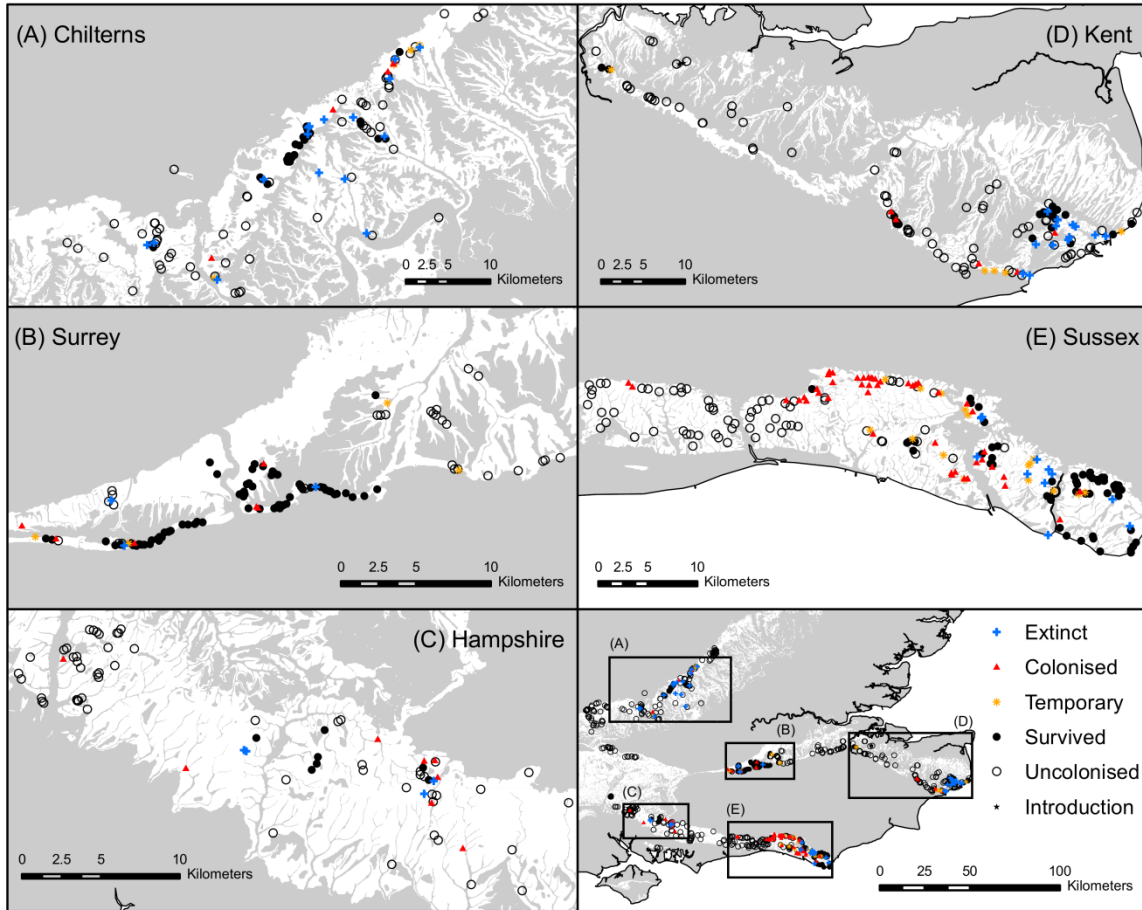


Figure 2.1: Maps of recorded changes in *H. comma* site occupancy between 2000 and 2009 across south-eastern Britain, with chalk geology shown in white.

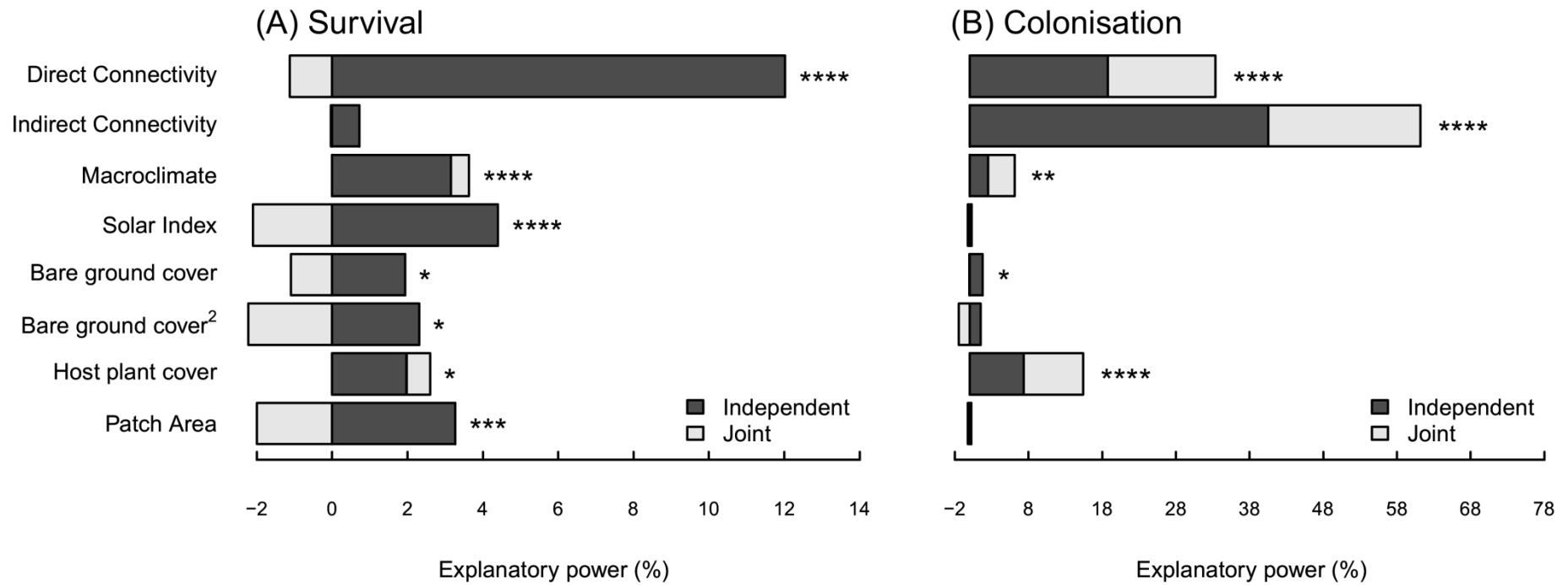


Figure 2.2: Independent (black) and joint (grey) contributions of explanatory variables (Table 2.1) in (a) survival and (b) colonisation models, based on hierarchical partitioning analyses and expressed as mean percent change in log-likelihood. Asterisks indicate significance of independent effects ($P < 0.05$, 0.01, 0.001 and 0.0001 denoted by one, two, three and four asterisks respectively).

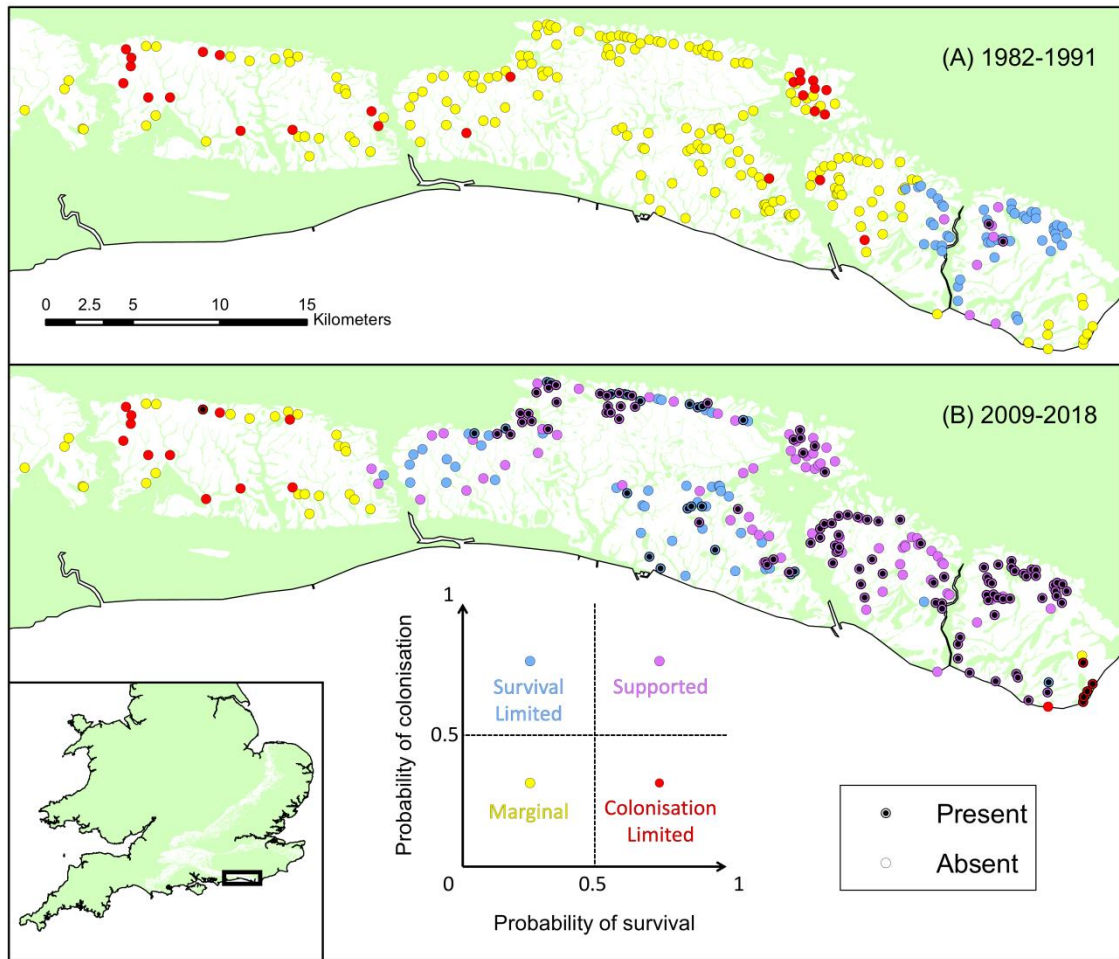


Figure 2.3: Map of patches in Sussex network, classified according to predicted probabilities of colonisation and survival for (a) 1982-1991 and (b) 2000-2009. *H. comma* occupancy in the first year is indicated by filled (present) and open (absent) circles.

Chapter 3: Active conservation enhances metapopulation expansion under climate change

3.1. Summary

There is a need to adapt biodiversity conservation to climate change, but little empirical evidence for how to do so. Existing networks of protected areas (PAs) have been preferentially colonised during species' range expansions, but this could be due to their original habitat quality and/or to ongoing management activity. Here, we examine how PA status and active conservation management have influenced the range expansion of a butterfly *Hesperia comma* through fragmented landscapes. PAs under active conservation management were over three times more likely to be colonised than unprotected, unmanaged sites of the same basic vegetation type. Conservation action increased the survival rate of existing populations inside or outside of PAs. We conclude that PAs facilitate range expansions by preventing habitat degradation and encouraging active conservation that improves habitat quality, and that conservation interventions on non-designated sites also have a role to play in adapting conservation to climate change.

3.2. Introduction

Species are responding to climate change by shifting their geographic distributions (Chen et al. 2011), but range expansions may be retarded or prevented by a lack of habitats available to colonise (Warren et al. 2001, Hill et al. 2002). Conservation strategies to preserve biodiversity in the face of global warming may aim to secure the survival of extant populations whilst helping species to colonise new habitats and expand their distributions (Lawler 2009; Chapter 2). Existing conservation programs could assist species' range shifts through a combination of statutory protection to prevent damage to habitats, and active conservation to enhance habitat quality and encourage colonisation

(Warren 1993, Nicholson et al. 2012). However, a key question is whether static networks of protected areas (PAs), established to safeguard ecological assemblages *in situ*, offer sufficient protection for range-shifting species, or whether more flexible, reactive approaches to conservation must be adopted (Gaston et al. 2006, Hannah et al. 2007, Thomas et al. 2012).

The evidence base for PA effectiveness under climate change comes largely from theoretical studies (Gaston et al. 2008, Thomas et al. 2012). Typically, range shift forecasts derived from species distribution models are coupled with maps of existing PA networks to assess which species will be protected under future climates (Hannah et al. 2007, Hole et al. 2009). These studies have generally predicted that climate change will drive species outside of their protected habitats, suggesting that failure to modify existing conservation measures will result in widespread biodiversity loss (Hannah et al. 2007, Coetzee et al. 2009, Araújo et al. 2011, D'Amen et al. 2011, Zimbres et al. 2012; but see Hole et al. 2009). However, this conclusion rests on several assumptions. First, predictive approaches implicitly rely on accurate forecasts of species' range shifts, which cannot be verified without empirical data (Pearce and Ferrier 2000). Second, populations inside PAs are assumed to survive, but PA designation may be ineffective without management to maintain or improve habitat quality (Gaston et al. 2008, Nicholson et al. 2012). Third, populations outside of PAs are assumed to suffer extinction, ignoring the role of conservation actions in habitats lacking statutory protection (Araújo et al. 2011). There is thus a need for empirical research that assesses the extent to which (a) PA designation and (b) active conservation can facilitate range shifts.

Recent empirical work (Thomas et al. 2012) suggests that PAs are preferentially colonised during species' range expansions. However, this study did not dissect the relative roles of PAs and active conservation (Thomas et al. 2012). The increased colonisation of PAs could thus reflect (a) direct benefits of reduced habitat destruction, (b) indirect benefits, if PA designation encourages conservation interventions which maintain or improve habitat quality, and/or (c) that PAs act as a

label for “high quality” sites that would have been colonised anyway, in which case further legislation will be of limited effect. Examining the relative contributions of PAs and active conservation would help to explain *why* PAs are colonised more frequently than non-PAs, and assess the extent to which conservation actions outside of PAs can facilitate range expansions.

Here, we analyse the impacts of existing conservation approaches on the dynamics of an exemplar species, the silver-spotted skipper butterfly *Hesperia comma*, during a period of climate-driven range expansion. We quantify the effects of PAs and active conservation on the colonisation and survival of *H. comma* populations at a nine-year interval, across a network of 615 habitat patches. The results show that PAs facilitate range shifts both by preventing habitat destruction and by promoting conservation interventions that improve habitat quality, and that conservation interventions on non-designated sites also have a role to play in adapting conservation to climate change.

3.3. Methods

Our study species, *Hesperia comma*, has specialised habitat requirements: eggs are laid exclusively on sheep’s fescue grass *Festuca ovina*, limiting populations to heavily-grazed patches of unimproved calcareous grassland in which the host plant grows (Chapter 2). The distribution of habitats available to this species is patchy across the landscape: first because of the locations of chalk geology, second because of widespread agricultural improvement and abandonment, and third because of heterogeneous grazing pressure (Warren 1993). At its northern range limit in Britain, thermal constraints on egg-laying and activity restrict *H. comma* to sites with sufficiently warm ground surface temperatures (Davies et al. 2006). In recent decades, rising summer temperatures in Britain have allowed *H. comma* to occupy cooler north-facing slopes, catalysing a range expansion (Thomas et al. 2001a; Chapter 2).

We comprehensively surveyed the distribution of *H. comma* in Britain in two years: 2000 and 2009. Habitat patches were defined as calcareous grassland with short (<10cm) sward containing *F. ovina*. Surveys encompassed the vast majority (c. 95%) of *H. comma* populations in Britain, mapped using handheld Global Positioning Systems (accuracy $<\pm 10\text{m}$). In each patch, we used timed searches for adults and/or eggs to establish presence of *H. comma* (Chapter 2).

We classified each patch according to its protection status and its ongoing management. In the UK, protection of habitat against damaging activities is largely realised through designating Sites of Special Scientific interest (SSSIs). SSSIs represent the basic level of site-based nature conservation legislation in the UK, and require the owners and occupiers of designated land to consult the official conservation body and obtain consent to carry out certain potentially damaging activities (Gaston et al. 2006). We classified patches that overlapped with SSSIs as *protected*, and those that did not as *unprotected*.

Conservation management of chalk grassland in the UK is realised through appropriate levels of grazing by livestock, which increases species richness by reducing competitive exclusion (Maalouf et al. 2012). We classified the management of habitat patches into three categories. Patches in which the primary purpose of the land was to promote biodiversity were classified as under *primary management*, which included land owned by: Natural England, the official nature conservation body in England; local authorities; or non-governmental conservation organisations (e.g. the National Trust, County Wildlife Trusts). Patches managed by private landowners as part of voluntary “agri-environment schemes” (AES), in which payments are offered for management that benefits nature conservation, were classified as under *voluntary management*. Two such schemes, Environmentally Sensitive Areas (ESA) and Countryside Stewardship Schemes (CSS) ran during the majority of the period of this study. We defined *unmanaged areas* as habitats which fell outside either of the two previous categories but which nevertheless fulfil the habitat requirements of our focal species (chalk

grassland containing Sheep's fescue grass *Festuca ovina* growing in short turf). We calculated SSSI, CSA, and ESA status using the *rgeos* library in *R* (R Development Core Team 2011, Bivand and Rundel 2012) and shapefiles available from Natural England (2010).

We tested the effects of management on (a) colonisation, by 2009, of patches that were not occupied by *H. comma* in 2000 and (b) population survival, in 2009, of patches that were occupied in 2000. Colonisation and survival probabilities were modelled using generalised linear models in *R* (R Development Core Team 2011), assuming a Bernoulli error structure. To assess the effects of PAs and conservation interventions whilst controlling for other determinants of colonisation and survival, we used the top-fitting models from a previous analysis (Chapter 2) as null models, to which terms were subsequently added (the previous analysis included patch area, connectivity, vegetation characteristics and climate variables; see Appendix 3A.1). *Protection* was modelled as a factor with two levels: *protected* and *unprotected*. *Management* was modelled as a factor with up to three levels (Table 3.1). Models were compared based on the corrected version of Akaike's information criterion (AICc; Richards 2008) using the *AICcmodavg* *R* package (Mazerolle 2012), and excluding models that ranked below their simpler nested variants (Richards 2008). We also fitted mixed models with spatial autocorrelation effects, but this did not change any of the important conclusions, so is only reported in the Appendix (methods: 3A.2; results: 3A.4).

3.4. Results

Of the 510 habitat patches that were unoccupied by *H. comma* in 2000, 105 were colonised between 2000 and 2009. Of the 214 *H. comma* pre-existing populations recorded in 2000, 168 remained in 2009 (46 habitat patches no longer held populations, despite generally suitable habitats remaining). Across all sites, habitat patches in PAs were more likely to be part of primary conservation schemes

than patches outside of PAs (Fig. 3.1; chi-squared test of association: $\chi^2=139.6$, $p<0.00001$), suggesting that PA designation encouraged active conservation management.

Patches under primary management were more likely to be colonised than voluntarily managed or unmanaged sites (Fig. 3.1a; all top-ranked colonisation models included a positive effect of primary management, Table 3.2a). Moreover, protection status interacted with primary management, such that primary management produced a greater increase in colonisation probability in PAs than in unprotected sites (*primary * protection* model ranks 5.8 AICc units above next best model, Table 3.2a). Overall, PAs under primary management were over three times more likely to be colonised than unmanaged, unprotected sites (Table 3.2a; Fig. 3.1a).

The best colonisation models did not distinguish between voluntary and unmanaged sites (Table 3.2a), even though the raw data indicate that a higher proportion of sites in voluntary management were colonised (Fig. 3.1a). Examination of habitat variables (Appendix 3A.5) showed that voluntarily managed sites tended to be situated in higher-connectivity landscapes compared to unmanaged sites, suggesting that the more frequent colonisation of voluntarily managed sites can be explained by their location rather than direct benefits of management.

We found reasonable evidence that primary management improved the survival of *H. comma* populations (Fig. 3.1b; *primary + protection* model ranks 2.3 AICc units above *protection* model, and *primary* model ranks 5.1 units above *null* model, Table 3.2b). The raw data indicated that population survival was more likely on voluntarily managed sites than unmanaged sites (Fig. 3.1b), but this difference was not statistically meaningful once other determinants of patch occupancy were controlled for (Table 3.2b). As in the colonisation analyses, the higher survival of populations in voluntarily managed sites (Fig. 3.1b) could be explained by their location and habitat attributes, rather than management effects: sites under voluntary management were larger than unmanaged

sites, and tended to be found in more well-connected habitat networks (Appendix 3A.5). Similarly, the higher survival of populations in PAs than in non-PAs (Fig. 3.1b) appears to be a byproduct of landscape context and climate (Table 3.2b; Appendix 3A.5), and may be exaggerated by spatial autocorrelation effects (Appendix 3A.4).

3.5. Discussion

Our analysis of the metapopulation dynamics of *H. comma* provides empirical evidence that pre-existing conservation measures can provide effective means to facilitate range expansions, even when not specifically established to deal with climate change impacts. The results show that PA designation greatly increased colonisation rates of unoccupied habitat, despite being designed to protect species over pre-existing, implicitly static distributions (Gaston et al. 2006, Thomas et al. 2012). By examining the range expansion of *H. comma* at the level of individual populations, we also demonstrated *why* PAs increased colonisation chances: first, because PAs directly protected key habitat patches from destruction, and second, because their designation encouraged active conservation actions (in our system, realised through management, e.g. appropriate grazing levels; Warren 1993, Maalouf et al. 2012) that promoted habitat quality (Fig. 3.1). Thus, our findings encourage the idea that existing PAs can continue to form an important component of biodiversity conservation under climate change.

The ability of PAs to protect biodiversity may be critically dependent on how they are managed (Gaston et al. 2008, Nicholson et al. 2012). In our study, conservation interventions were integral to the success with which PAs facilitated the range expansion of *H. comma*; the combination of statutory protection and active conservation generated a three-fold increase in colonisation rates, but the benefits of protection and primary conservation were diminished when employed in isolation (Fig. 3.1a). Moreover, our analysis of the survival of *H. comma* populations indicates that

active conservation interventions can help to preserve vulnerable range-edge populations outside of PAs, consolidating gains made during periods of expansion (Fig. 3.1b). Complementing PA designation with appropriate habitat management activities both inside and outside of reserves is thus likely to be key to efficient range shift management.

Analysing the establishment and survival of populations in individual habitat patches provided a level of control not achievable in previous assessments of PA effectiveness under climate change (Araújo et al. 2011, Thomas et al. 2012). We only studied potentially suitable *H. comma* habitats of the same vegetation and geology type, such that our analyses did not represent unfair comparisons between PAs and elements of the wider landscape which could not have been colonised. Moreover, the impacts of conservation actions could be quantified whilst controlling for the effects of other environmental variables influencing habitat patch occupancy, which allows two strong conclusions. First, PAs and “primary” management (where conservation is the primary aim) have positive effects over and above the habitat quality attributes influencing site designation. Second, voluntary agri-environmental conservation schemes have at best weak effects on the range expansion rates of *H. comma*; raw colonisation and population survival rates suggest apparent benefits of voluntary management (Fig. 3.1), but detailed examination shows that these benefits are likely to be a byproduct of the high quality and connectivity of sites selected for management (Table 3.2, Appendix 3A.5). We therefore remain cautious about the success with which voluntary agri-environment schemes can facilitate range shifts.

Modelling studies have predicted that climate change will force many species to shift their distributions outside of PA networks (Coetzee et al. 2009, Araújo et al. 2011, D’Amen et al. 2011, Zimbres et al. 2012), suggesting a need to adopt more dynamic designation approaches (Hannah et al. 2007). Methods to plan PA networks that will enable range shifting have been proposed (Phillips et al. 2008, Hodgson et al. 2011), but these have yet to be tested empirically. Changing ownership or

legal status, changing habitat (e.g. restoring from agricultural land) and changing management regimes all have associated costs and uncertainties. Although all of these will probably be needed to some extent under climate change, it is vital to have empirical indications of what can be achieved with existing measures. For *H. comma* we have shown that existing PAs can facilitate species' range expansions if habitat quality is maintained through conservation interventions, and that traditional management practices can protect populations established outside of PAs. If these results hold true for other species, we would expect current conservation measures to be an integral and cost-efficient part of any strategy to preserve biodiversity under climate change.

3.6. References

- Araújo, M. B., D. Alagador, M. Cabeza, D. Nogués-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. *Ecology Letters* **14**:484-492.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. <http://CRAN.R-project.org/package=lme4>.
- Bivand, R. and C. Rundel. 2012. rgeos: Interface to Geometry Engine - Open Source (GEOS). <http://CRAN.R-project.org/package=rgeos>.
- Chen, I., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**:1024-1026.
- Coetzee, B. W. T., M. P. Robertson, B. F. N. Erasmus, B. J. Van Rensburg, and W. Thuiller. 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography* **18**:701-710.

- D'Amen, M., P. Bombi, P. B. Pearman, D. R. Schmatz, N. E. Zimmermann, and M. A. Bologna. 2011. Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? *Biological Conservation* **144**:989-997.
- Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**:247-256.
- Gaston, K. J., K. Charman, S. F. Jackson, P. R. Armsworth, A. Bonn, R. A. Briers, C. S. Q. Callaghan, R. Catchpole, J. Hopkins, and W. E. Kunin. 2006. The ecological effectiveness of protected areas: the United Kingdom. *Biological Conservation* **132**:76-87.
- Gaston, K. J., S. F. Jackson, L. Cantú-Salazar, and G. Cruz-Piñón. 2008. The Ecological Performance of Protected Areas. *Annual Review of Ecology, Evolution, and Systematics* **39**:93-113.
- Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5**:131-138.
- Hill, J., C. Thomas, R. Fox, M. Telfer, S. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**:2163-2171.
- Hodgson, J. A., C. D. Thomas, S. Cinderby, H. Cambridge, P. Evans, and J. K. Hill. 2011. Habitat re-creation strategies for promoting adaptation of species to climate change. *Conservation Letters* **4**:289-297.

- Hole, D. G., S. G. Willis, D. J. Pain, L. D. Fishpool, S. H. M. Butchart, Y. C. Collingham, C. Rahbek, and B. Huntley. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* **12**:420-431.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* **1162**:79-98.
- Maalouf, J. P., L. Bagousse-Pinguet, L. Marchand, E. Bâchelier, B. Touzard, and R. Michalet. 2012. Integrating climate change into calcareous grassland management. *Journal of Applied Ecology* **49**:795–802.
- Mazerolle, M. J. 2012. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). <http://CRAN.R-project.org/package=AICcmodavg>.
- Natural England. 2012. The Natural England Data portal. <http://www.naturalengland.org.uk/publications/data/default.aspx>.
- Nicholson, E., B. Collen, A. Barausse, J. L. Blanchard, B. T. Costelloe, K. M. E. Sullivan, F. M. Underwood, R. W. Burn, S. Fritz, and J. P. G. Jones. 2012. Making Robust Policy Decisions Using Global Biodiversity Indicators. *PloS one* **7**:e41128.
- Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**:225-245.
- Phillips, S. J., P. Williams, G. Midgley, and A. Archer. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications* **18**:1200-1211.
- R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* **45**:218-227.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conratt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**:577-581.
- Thomas, C. D., P. K. Gillingham, R. B. Bradbury, D. B. Roy, B. J. Anderson, J. M. Baxter, N. A. D. Bourn, H. Q. P. Crick, R. A. Findon, R. Fox, J. A. Hodgson, A. R. Holt, M. D. Morecroft, N. J. O'Hanlon, T. H. Oliver, J. W. Pearce-Higgins, D. A. Procter, J. A. Thomas, K. J. Walker, C. A. Walmsley, R. J. Wilson, and J. K. Hill. 2012. Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences* **109**:14063-14068.
- Warren, M. 1993. A review of butterfly conservation in central southern Britain: I. Protection, evaluation and extinction on prime sites. *Biological Conservation* **64**:25-35.
- Warren, M., J. Hill, J. Thomas, J. Asher, R. Fox, B. Huntley, D. Roy, M. Telfer, S. Jeffcoate, and P. Harding. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**:65-69.
- Zimbres, B. Q. C., P. D. P. U. de Aquino, R. B. Machado, L. Silveira, A. T. A. Jácomo, R. Sollmann, N. M. Tôrres, M. M. Furtado, and J. Marinho-Filho. 2012. Range shifts under climate change and the role of protected areas for armadillos and anteaters. *Biological Conservation* **152**:53-61.

Variable name	Management category		
	primary	voluntary	unmanaged
primary	1	2	2
voluntary	2	1	2
unmanaged	2	2	1
management	1	2	3

Table 3.1: Management groupings used in statistical models. Factors with different codings were generated, comprising either: two levels, in which one management category was distinguished from the others (primary, voluntary or unmanaged groupings); or three levels, one for each management type (the management grouping).

Variables in model	K	$\delta AICc$	LL	Predicted colonisation or survival probability (%)					
				protected			unprotected		
				primary	voluntary	unmanaged	primary	voluntary	unmanaged
<i>(a) colonisation</i>									
primary * protection	7	0.0	-172.2	28.2	5.1	5.1	9.3	8.3	8.3
primary	5	5.8	-177.2	23.2	7.5	7.5	23.2	7.5	7.5
<i>(b) survival</i>									
primary + protection	9	0.0	-78.7	91.7	81.8	81.8	83.2	67.0	67.0
primary	8	0.6	-80.1	90.7	77.2	77.2	90.7	77.2	77.2
protection	8	2.3	-80.9	88.7	88.7	88.7	73.7	73.7	73.7
voluntary	8	4.7	-82.1	88.2	75.9	88.2	88.2	75.9	88.2
unmanaged	8	4.8	-82.2	87.8	87.8	78.1	87.8	87.8	78.1
null	7	5.1	-83.4	86.1	86.1	86.1	86.1	86.1	86.1

Table 3.2: Top-ranking models for colonisation (a) and population survival (b) in H. comma habitat patches. K=number of parameters; $\delta AICc$ = difference in $AICc$ between model and top model; LL=log-likelihood. Only models with $\delta AICc \leq 6$ are shown. The (*) symbol indicates a statistical interaction. Note that all models, including the "null" model, include patch attributes found to be statistically important in a previous study (Appendix 3A.1). The six right-hand columns show predicted probabilities of colonisation (a) or survival (b) for a habitat patch with average attributes (Appendix 3A.3).

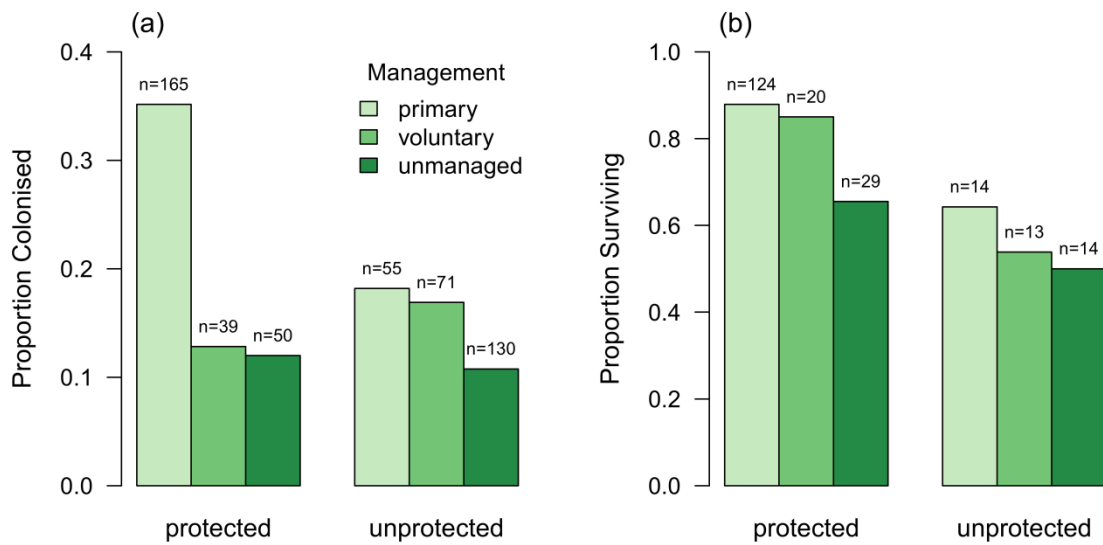


Figure 3.1: Effects of protection status and management on (a) the proportion of empty patches which were colonised and (b) the proportion of populations to survive between 2000 and 2009. Bars indicate raw proportions unadjusted for other habitat patch attributes. “n” indicates the sample size for each category.

Appendix to Chapter 3

3A.1. Null model structure

We used the top-fitting models from a previous study (Chapter 2) as “null models” for the colonisation and survival of *Hesperia comma* populations in this study. Terms indicating management and protection status were subsequently added to assess their effects over and above those explained by other variables. The structures of the null models are given below; further explanation of variables can be found in Chapter 2.

3A.1.1. Colonisation

$$\text{logit}(c_i) = \alpha + \beta_1 CD_i + \beta_2 CI_i + \beta_3 HO_i$$

$$y_i \sim \text{Bernoulli}(c_i)$$

Where c_i indicates the probability of colonising patch i , CD_i indicates the “direct connectivity” of patch i to patches that were occupied in 2000, and CI_i indicates the “indirect connectivity” of patch i , reflecting the availability of suitable but uncolonised habitat surrounding the patch (see Chapter 2), and HO indicates the proportion of the patch that was covered by the host plant *Festuca ovina*. y_i is a binary variable indicating whether patch i was colonised between 2000 and 2009.

3A.1.2. Survival

$$\text{logit}(s_j) = \alpha + \beta_1 CD_j + \beta_2 AR_j + \beta_3 IN_j + \beta_4 MC_j + \beta_5 BG_j + \beta_6 BG_j^2$$

$$z_j \sim \text{Bernoulli}(s_j)$$

Where s_j indicates the probability of survival in patch j , CD indicates the “direct connectivity” of patch j to patches that were occupied in 2000, AR indicates the areal extent of the patch, IN indicates the solar index of the patch (a combination of aspect and slope), MC indicates the “macroclimate” of the patch (mean daily August maximum temperature from 2000-2009), and BG

indicates the proportion of the patch that was bare ground. z_j is a binary variable indicating whether the population in patch j remained present in 2009.

3A.2. Mixed models to test for spatial autocorrelation effects

To assess the extent to which our results were robust to spatial autocorrelation effects, we repeated our analyses using generalised linear mixed models. Instead of a single intercept for all sites (α in the equations above), we fitted a random intercept which grouped patches within (a) 5 km and (b) 10 km squares, using the *lme4* package in *R* (Bates et al. 2011, R Development Core Team 2011). To calculate patch groups, we constructed *R* code (R Development Core Team 2011) which superimposed a grid of either 5 km or 10 km resolution across the British Isles, with the origin (southwest corner with spatial coordinates [0,0]) taken to be the origin of the UK Ordnance Survey National Grid. We then classified patches into grid square groups based on whether they were within the same grid square. As such, the fixed intercept α was replaced with a random intercept:

$$\alpha_k \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

Where α_k is the intercept for patches in grid cell group k , μ_α is the mean probability of colonisation or survival across all patches, and σ_α^2 represents the variance in the probability of colonisation or survival among grid cells. Results for mixed model analyses are compared with the main analyses in Appendix 3A.4.

3A.3. Detail on method for predicting colonisation and survival probabilities

Table 3.2 (main text) displays predicted colonisation and survival probabilities for a patch in each of the management categories. Because our models also incorporated effects of other patch attributes (e.g. patch size and connectivity; Chapter 2), we needed to choose values for these variables to produce colonisation and survival predictions for an “average” patch. We chose to use the mean values based on all patches used in each analysis (colonisation and survival). The values of these

variables are given in Tables 3A.1 and 3A.2. Note that only variables which entered models (see section 3A.1) are given.

3A.4. Comparison of original and mixed model results

3A.4.1. Colonisation

Table 3A.3 displays model selection tables for colonisation models with and without spatial autocorrelation effects. The rank order of the best models and the direction of predictions remain consistent whether or not a random intercept is used, indicating that the findings of this analysis are robust to spatial autocorrelation.

3A.4.2. Survival

Table 3A.4 displays model selection tables for colonisation models with and without spatial autocorrelation effects. The finding that primary management improves the probability of survival remains consistent whether or not the effects of spatial autocorrelation are considered (Table 3A.4). However, the evidence that populations were more likely to survive in protected patches weakens once spatial autocorrelation is accounted for, such that the effects of protection status on survival may have been exaggerated by spatial autocorrelation effects.

3A.5. Relationships between management categories and variables in null models

Some management categories were associated with improvements in colonisation and survival probabilities (Fig. 3.1, main text), but had apparently little benefit once important environmental variables were controlled for (Table 3.1, main text; see section S1 of this supplementary material for environmental variables included in models). To further explore why this might be, we investigated whether management or protection designation was associated with the environmental variables included in our null models. In Figures 3A.1 and 3A.2, we plot the distributions of environmental variables for patches used in (a) the colonisation analysis (3A.1) and (b) the survival analysis (3A.2). In the following paragraphs, we briefly discuss differences in environmental variables among protection and management categories.

3A.5.1. Colonisation data

Amongst sites that were unoccupied by *H. comma* in 2000, patches that were close to existing *H. comma* populations (*i.e.* patches that had higher direct connectivity) and were in more well-connected networks of habitat (*i.e.* had higher indirect connectivity; see Chapter 2) tended to be under primary management by conservation bodies, rather than voluntarily managed under agri-environment schemes or unmanaged. Our models therefore suggest that primary management greatly improved colonisation chances of patches over and above the benefits of their higher connectivity (Table 3.1a, main text).

Voluntarily managed sites tended to have higher indirect connectivity than unmanaged sites, which might explain why we found little evidence for positive effects of voluntary management on colonisation once the effects of connectivity had been accounted for.

There was no overall tendency for protected sites to have higher connectivity (direct or indirect) or host plant cover than unprotected sites, supporting our conclusion that protected areas improved colonisation independently of these variables (Table 3.1a, main text).

3A.5.2. Survival data

Amongst habitat patches occupied by *H. comma* in 2000, voluntarily managed sites tended to be larger and in more well-connected habitat networks (higher indirect connectivity) than either managed or unmanaged sites. Thus, patch size and connectivity variables may have played a role in influencing land managers' decisions to "opt-in" to agri-environment schemes (AES), and could explain why we found no positive effect of AES once these variables had been accounted for (Table 3.1b, main text).

On average, sites with higher direct connectivity were more likely to be protected as Sites of Special Scientific Interest (SSSIs). This reflects the fact that the 2000 distribution of *H. comma* was concentrated around protected areas. Protected sites also tended to be found in warmer regions of Britain (*i.e.* with higher mean August maximum temperatures). Both of these variables may have exaggerated the impacts of protected areas on population survival between 2000 and 2009 (Fig. 3.1b, main text), explaining why we found only relatively weak evidence that protection enhanced population survival (Table 3.1b, main text) despite survival in protected areas being higher than in unprotected areas (Fig. 3.1b, main text).

Appendix 3 Tables

Variable	Value
Direct connectivity	2.0
Indirect connectivity	4.9
Host plant cover (%)	16

Table 3A.1: values of other environmental variables in colonisation models that were used to predict colonisation probabilities for habitat patches in different management and protection categories.

Variable	Value
Direct connectivity	12
Areal extent of patch (ha)	2.3
Solar index	230
Macroclimate (mean daily maximum temperature during August)	22
Bare ground cover (%)	9.4

Table 3A.2: values of other environmental variables in survival models that were used to predict survival probabilities for habitat patches in different management and protection categories.

Variables in model	K	$\delta AICc$	LL	Predicted colonisation probability (%)					
				protected			unprotected		
				primary	voluntary	unmanaged	primary	voluntary	unmanaged
<i>(a) fixed intercept</i>									
primary * protection	7	0.0	-172.2	28.2	5.1	5.1	9.3	8.3	8.3
primary	5	5.8	-177.2	23.2	7.5	7.5	23.2	7.5	7.5
<i>(b) 5km</i>									
primary * protection	8	0.0	-159.4	20.5	2.5	2.5	5.3	4.0	4.0
primary	6	2.9	-162.9	15.9	3.5	3.5	15.9	3.5	3.5
<i>(c) 10km</i>									
primary * protection	8	0.0	-158.1	23.0	2.6	2.6	7.1	5.4	5.4
primary	6	4.6	-162.4	18.5	4.5	4.5	18.5	4.5	4.5

Table 3A.3: Comparison of colonisation models with (a) fixed intercept, (b) a random intercept among 5km squares, and (c) a random intercept among 10km squares. K =number of parameters; $\delta AICc$ = difference in $AICc$ between model and top model; LL =log-likelihood. The six right-hand columns show the predicted probabilities of colonisation for an “average” patch in each of the different management categories, assuming mean values for other patch attributes. Only models with $\delta AICc \leq 6$ are shown; models with $AICc$ scores lower than the $AICc$ scores of simpler (nested) models have been excluded.

Variables in model	K	$\delta AICc$	LL	Predicted survival probability (%)					
				protected			unprotected		
				primary	voluntary	unmanaged	primary	voluntary	unmanaged
<i>(a) fixed intercept</i>									
primary + protection	9	0.0	-78.7	91.7	81.8	81.8	83.2	67.0	67.0
primary	8	0.6	-80.1	90.7	77.2	77.2	90.7	77.2	77.2
protection	8	2.3	-80.9	88.7	88.7	88.7	73.7	73.7	73.7
voluntary	8	4.7	-82.1	88.2	75.9	88.2	88.2	75.9	88.2
management	8	4.8	-82.2	87.8	87.8	78.1	87.8	87.8	78.1
null	7	5.1	-83.4	86.1	86.1	86.1	86.1	86.1	86.1
<i>(b) 5km</i>									
primary	9	0.0	-77.7	94.3	81.3	81.3	94.3	81.3	81.3
voluntary	9	4.2	-79.8	92.1	79.5	92.1	92.1	79.5	92.1
protection	9	4.4	-79.8	90.9	90.9	90.9	80.0	80.0	80.0
management	9	4.7	-80.0	91.4	91.4	82.4	91.4	91.4	82.4
null	8	4.8	-81.1	90.1	90.1	90.1	90.1	90.1	90.1
<i>(c) 10km</i>									
primary	9	0.0	-78.8	92.9	80.5	80.5	92.9	80.5	80.5
management	9	3.9	-80.7	90.5	90.5	81.7	90.5	90.5	81.7
null	8	4.0	-81.9	88.9	88.9	88.9	88.9	88.9	88.9

Table 3A.4: Comparison of survival models with (a) fixed intercept, (b) a random intercept among 5km squares, and (c) a random intercept among 10km squares. K =number of parameters; $\delta AICc$ = difference in $AICc$ between model and top model; LL =log-likelihood. The six right-hand columns show the predicted probabilities of survival for an “average” patch in each of the different management categories, assuming mean values for other patch attributes. Only models with $\delta AICc \leq 6$ are shown; models with $AICc$ scores lower than the $AICc$ scores of simpler (nested) models have been excluded.

Appendix 3 Figures

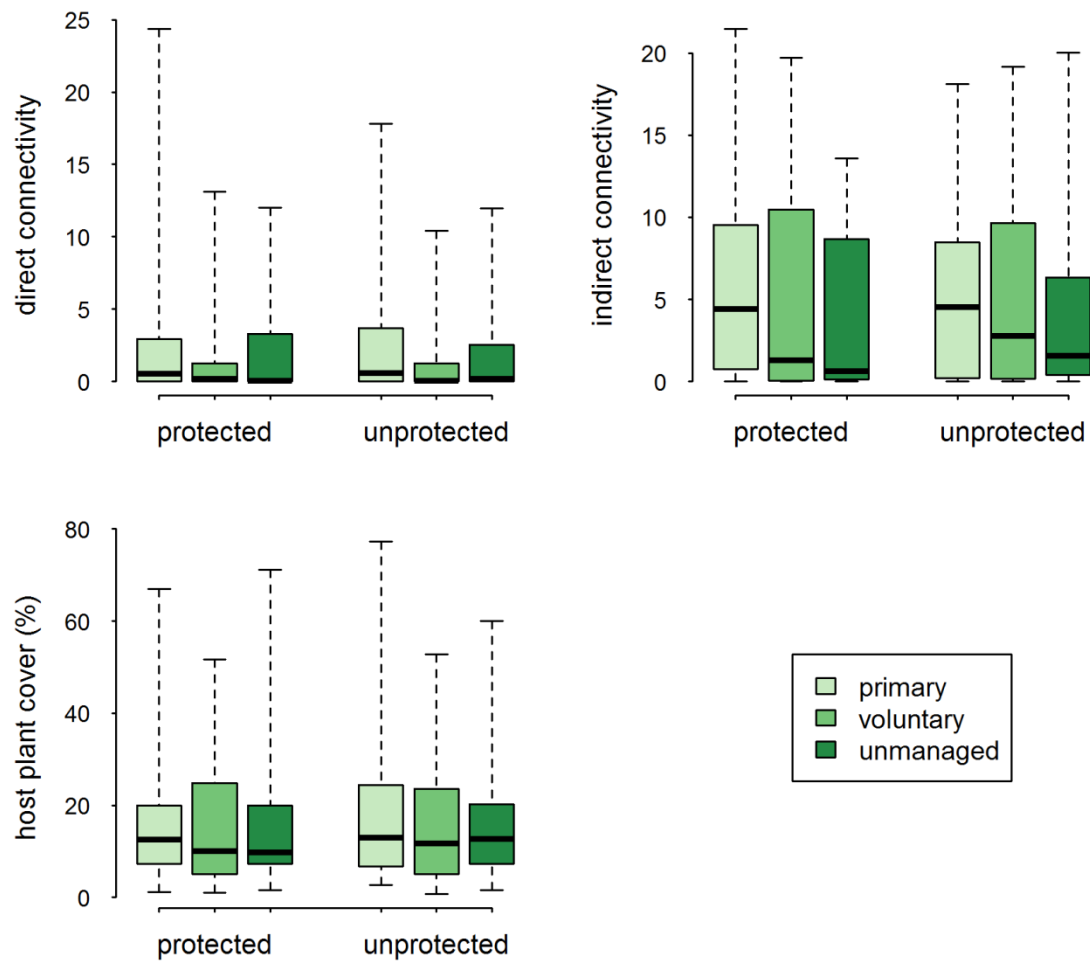


Figure 3A.1: Boxplots showing values of environmental variables for sites in colonisation analyses (i.e. for patches that were unoccupied in 2000) in each of the different protection and management categories.

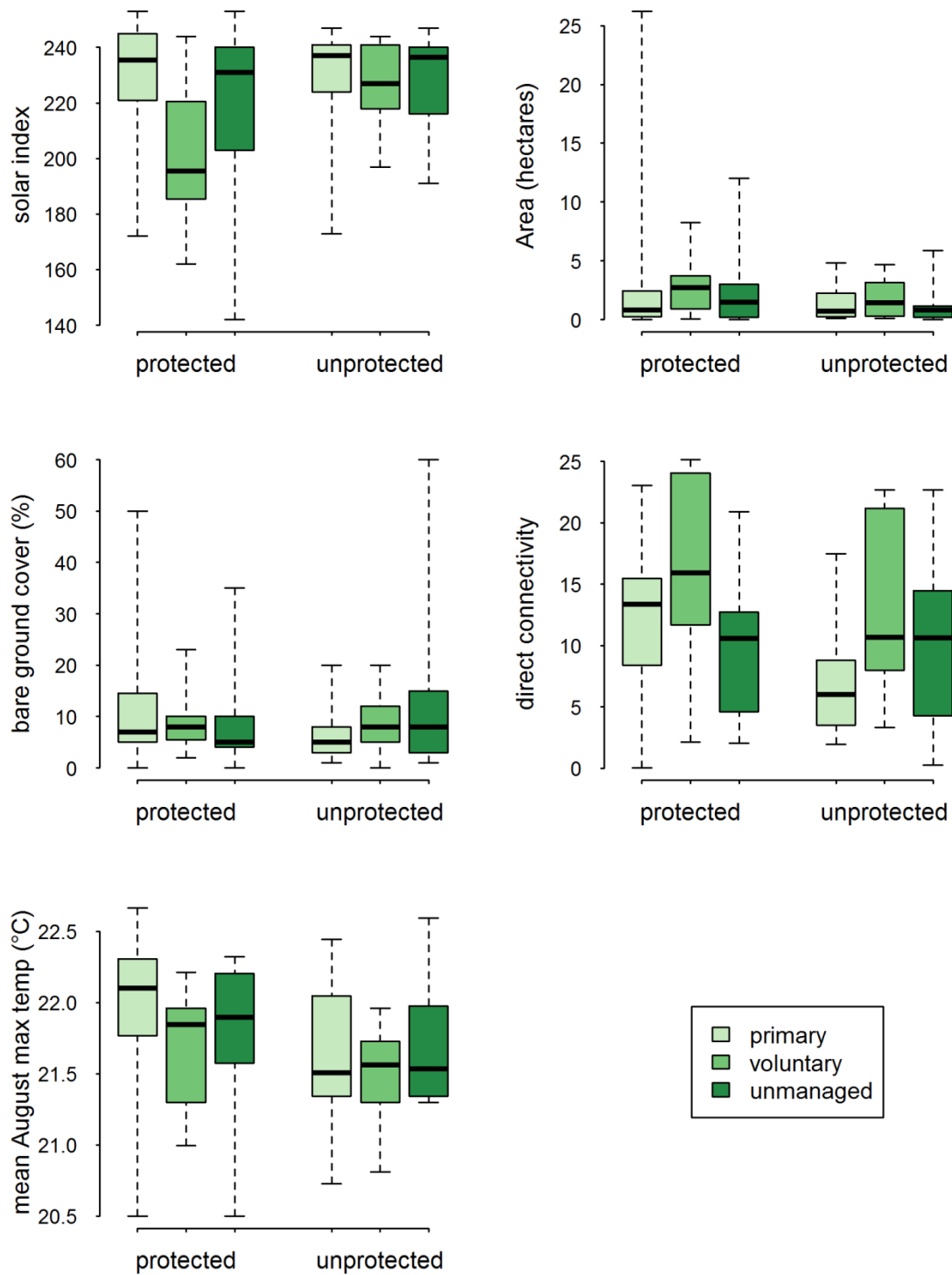


Figure 3A.2: Boxplots showing values of environmental variables for sites in survival analyses (i.e. for patches that were occupied in 2000) in each of the different protection and management categories.

Chapter 4: Climate drives changing microhabitat associations in a butterfly

4.1. Summary

The concept of habitat is central to our understanding of species' ecology. Ecological studies at broad spatial scales typically assume that responses to environmental variables remain constant within a species, but behavioural studies suggest that species' habitat use could change with both habitat availability and with background environmental conditions such as climate. We examined the selection of egg-laying microhabitats by populations of a thermally-constrained butterfly, the skipper *Hesperia comma*, across 16 different sites and at a single site in 5 different years. We combined resource selection and microclimate modelling to quantify functional responses to temperature and habitat availability. At sites with higher estimated vegetation surface temperatures, *H. comma* showed reduced association with the warm microhabitats generated by bare ground, demonstrating a temperature-driven functional response in habitat associations. Furthermore, association with bare ground and the host plant *Festuca ovina* weakened in sites with higher bare ground and host plant availability. Changes in microhabitat association in time were consistent with those in space, but only when both temperature and habitat availability effects were considered simultaneously. These results highlight the importance of interactions between climate and habitat in resource selection, and demonstrate the need to integrate dynamic habitat requirements into projections of species' responses to climate change.

4.2. Introduction

The concept of "habitat" underpins our understanding of species' ecological requirements and our capacity to predict their responses to climate and habitat change (Johnson 1980, Beyer et al. 2010). However, ecologists working at different spatial scales often view habitat in different ways. In

biogeographical studies and conservation biology, habitat requirements are typically viewed as species-level attributes, implicitly assuming that habitat associations will remain constant within species (Oliver et al. 2009, Peterson et al. 2011). In behavioural ecology, in contrast, habitat associations are viewed as a consequence of individual-level decisions, the outcome of which may vary with both the internal state of the animal and external conditions (Myserud and Ims 1998, McLoughlin et al. 2010). Under this more dynamic view of habitat, expectations derived from patterns of habitat association observed in one context may not predict habitat associations in other places or times (McLoughlin et al. 2010, Matthiopoulos et al. 2011).

In practice, species' habitat associations are generally assessed by comparing the environmental conditions in locations at which the species is present to those at which it is absent, parameterising a model which predicts a probability of presence under a range of possible environments (Johnson 1980, Beyer et al. 2010, McLoughlin et al. 2010). When adopting a species-level approach to habitat characterisation, each species' association with a particular habitat or climate variable is often described independently of other variables (McLoughlin et al. 2010, Matthiopoulos et al. 2011). However, there are important reasons why the relationship between habitat and probability of presence may change under new scenarios.

First, observed patterns of habitat use depend not only on an animal's preference for a given habitat type, but also on the alternative choices it has available (Singer 2000, Beyer et al. 2010). For example, a species may be strongly associated with a particular resource when it is rare, but show apparently reduced "selection" for the resource when it is common, even if the underlying behavioural processes remain the same (Myserud and Ims 1998, Godvik et al. 2009, Moreau et al. 2012). This results in a non-linear change in resource association with resource availability known as a functional response in habitat selection (Myserud and Ims 1998, Matthiopoulos et al. 2011).

Second, habitat preference itself may change as external conditions alter an individual's requirements or change the perceived value of a given habitat (Johnson 1980). For example,

preference for a certain habitat type may change with habitat configuration (Gillies and St Clair 2010) and disturbance levels (Hebblewhite and Merrill 2008, DeCesare et al. 2012, Moreau et al. 2012). Furthermore, it is thought that climate may alter habitat preferences (Singer and Thomas 1996, Morris and Dupuch 2012). Vegetation structure and topography create local microclimates (Suggitt et al. 2011), the thermal suitability of which may vary according to the prevailing climate of the time or region. Behavioural studies on single populations have shown that microclimates may influence the distribution of individuals (Shreeve 1986, Prinzing 2005), and have linked changes in weather to changes in habitat selection choices (Davies et al. 2006, Dubois et al. 2009, Schofield et al. 2009). Studies on population-level habitat associations have demonstrated shifts into cooler microhabitats at hotter times (Roy and Thomas 2003, Davies et al. 2006) or places (Adolph 1990, Burton 2006, Merrill et al. 2008, Ashton et al. 2009; but see Navas 1996). At a larger scale, Oliver et al. (2009) found that species' habitat requirements became narrower towards their climatic range boundaries. As such, species may show climate-driven functional responses in habitat selection, generating an interaction between climate and habitat requirements.

There has been a growing appreciation of the importance of functional responses in habitat selection (McLoughlin et al. 2010), with developments in mixed effects modelling providing the necessary tools to integrate changing habitat associations with resource availability (Hebblewhite and Merrill 2008, Duchesne et al. 2010, Matthiopoulos et al. 2011). However, due to constraints on data collection time or resources, studying habitat associations at fine spatial resolutions usually entails restricting the spatial extent of a study. Consequently, evidence for climate-driven habitat selection generally comes either from behavioural studies of individuals within a single population (e.g. Dubois et al. 2009, Schofield et al. 2009), or comparisons of habitat associations between a pair of populations or time points (Roy and Thomas 2003, Davies et al. 2006). Although valuable, the habitat associations observed in these studies are conditional on the specific populations and environments studied (Beyer et al. 2010, Matthiopoulos et al. 2011), limiting inference to a narrow range of scenarios. Moreover, because effects of habitat availability are rarely accounted for, it is

difficult to separate effects of climate and habitat availability on resource selection. Consequently, whilst the potential importance of climate-driven functional responses in habitat selection has been widely acknowledged (McLoughlin et al. 2010), few convincing, empirically-quantified examples exist.

Here, we quantify the egg-laying microhabitat associations of a thermally-constrained butterfly, the skipper *Hesperia comma* (Hesperiidae), under changing conditions of climate and habitat availability. Using data collected from 16 different sites and at a single site in 5 different years, we investigate changes in population-level egg-laying site selection. We find that microhabitat associations change with both climate and microhabitat availability, emphasising the need to consider functional responses in the prediction and management of species' responses to climate change.

4.3. Methods

4.3.1. Study species

Our study took place in Britain, where *H. comma* reaches the northern limit of its range. The British distribution of *H. comma* is strongly constrained by both habitat and temperature. Female *H. comma* adults lay eggs on a single host plant species, sheep's fescue grass *Festuca ovina*, which is found in heavily-grazed fragments of calcareous grassland (Thomas et al. 1986). In adult *H. comma*, both activity levels and egg-laying rates increase with ambient temperature (Davies et al. 2006). Because of the thermal requirements for egg-laying and/or thermal impacts on egg development, eggs are generally laid on host plants next to patches of bare ground, which heat up more than the surrounding vegetation in direct sunlight (Thomas et al. 1986, Davies et al. 2006).

Between 1982 and 2009, warming summer temperatures and increased availability of short-sward grassland have facilitated a range expansion of *H. comma* in Britain, from fewer than 70 populations in 1982 to over 300 populations by 2009 (Thomas et al. 1986; Chapter 2). The dynamics of range expansion have been linked to microclimates generated by topography, with warmer south-facing

slopes more likely to be colonised (Thomas et al. 2001) and populations on cooler north-facing slopes more likely to suffer extinction (Chapter 2). Furthermore, within a single site, a comparison of the microhabitats selected for egg-laying between two time periods (1982 and 2001/2002) indicated that *H. comma* showed a weakened association with bare ground cover in the second (warmer) period (Davies et al. 2006), consistent with a climate-driven functional response in habitat selection. However, Davies et al. (2006) only tested habitat associations in two years at a single site, without accounting for changes in habitat availability.

4.3.2. Sampling design

We sampled the selection of sites for egg-laying by *H. comma* through both space and time. For the spatial analysis, sampling was conducted across 16 sites at which *H. comma* was known to be present (Fig. 4.1a and b) in 2010. Sites were chosen to represent a range of aspects across a geographical extent that encompassed most of the existing *H. comma* populations in Britain (Fig. 4.1a and b; Chapter 2). For the temporal analysis, one of the sites (Old Plantation Banks in Surrey: black square symbol, Fig. 4.1b) was sampled in five separate years (1982, 2001, 2002, 2009 and 2010); we hereafter refer to this site as “the temporal site”. The data from the first three of these years were taken from previous studies on *H. comma* (Thomas et al. 1986, Davies et al. 2006). All sampling took place between 26 August and 30 September at the end of the *H. comma* flight season, at which point the vast majority of eggs for that year would have been laid (*H. comma* is univoltine in the UK, and overwinters as an egg; Thomas et al. 1986).

At each site, we sampled 25 × 25cm quadrats for the presence of *H. comma* eggs (Fig. 4.1c and d). Because egg densities were low, we combined presence-only and random sampling, necessary to reduce the sample size needed to obtain a sufficient number of presences for model-fitting (i.e. we adopted a case-control design in which controls were sampled for presences or absences; Manly et al. 2002). In presence-only sampling, we ran transects in which we searched for eggs across a 1m search zone, and took quadrats wherever eggs were found. On “random” transects, we took

stratified samples of five quadrats, each 1m apart, at regular intervals (usually 20m; Fig 1d). At the temporal site, only random quadrats were taken to maintain consistency with previous work (Thomas et al. 1986a, Davies et al. 2006b). All presence-only quadrats contained eggs, but some quadrats on random quadrats also contained eggs, and were counted as presences. Therefore, we have two types of quadrat at each site: with and without eggs (present and absent). The number of presence-only and random quadrats taken varied among sites: the mean numbers of presences and absences sampled at each site were 26 (standard deviation=13) and 79 (standard deviation=51), respectively.

4.3.3. Variables

In each quadrat, we recorded: (1) whether or not eggs were present; (2) the percentage cover of bare ground; and (3) the percentage cover of the host plant, *F. ovina* (Table 4.1). We also calculated three “site-level” variables: vegetation surface temperature, which was calculated using a microclimate model (see below); and two habitat availability variables, mean percentage bare ground cover and mean percentage host plant cover across each site, calculated based on data from random quadrats (following Matthiopoulos et al. 2011). Each of these site-level variables was calculated separately for each year studied, so that changes in climate and habitat availability through time were incorporated into the analyses (Table 4.1).

Site-level temperatures were modelled using an empirically validated 5 × 5m resolution model of grassland surface microclimate (Bennie et al. 2008). The model combines information on topography, radiation balance, and wind speed to estimate the number of hours in which sward temperatures exceed 25°C (the thermal threshold for egg-laying; Davies et al. 2006b). Modelled temperatures therefore reflect the combined effects of regional climate (Fig. 4.1b) and microclimates generated by topography, with south-facing slopes being warmer than north-facing slopes (Fig. 4.1c). We digitised the sampled sites as polygons in ArcMap 9.3 (ESRI 2009; Fig. 1c) and, using hourly climate data from the UK MET office (Perry and Hollis 2005) and a 5 x 5m resolution

Digital Elevation Model (Intermap Technologies 2011) as inputs, calculated the mean hours exceeding 25°C for each polygon in 2010, and additionally for the temporal site polygon in 1982, 2001, 2002, and 2009. Therefore, although we modelled thermal microclimate at a 5 × 5m resolution, the temperature values used in the analysis were spatially averaged across each habitat patch to give a measure of site-level temperature.

4.3.4. Model-fitting

We modelled egg-laying (probability of presence of an egg in a quadrat) using logistic generalised linear mixed models (Manly et al. 2002, Bolker 2008, Matthiopoulos 2011). The full model consisted of the following processes:

- A site-specific intercept, modelled as a random factor, which allowed us to account for variability in the proportion of presences sampled among different sites.
- Quadrat-level main effects of percent bare ground and percent host plant cover.
- Site-level main effects of temperature (hours >25°C) and habitat availability (mean bare ground and mean host plant cover).
- Interactions between quadrat-level variables and site-level habitat availability (mean bare ground and mean host plant cover), allowing us to investigate whether amount of bare ground and/or host plant cover selected depended on the availability of bare ground or host plant across the whole site.
- An interaction between bare ground and temperature, allowing us to investigate whether amount of bare ground selected depended on the temperature of the site. We had no *a priori* reason for expecting an interaction between host plant cover and temperature, and consequently we do not include this interaction in the models presented here. However, Appendix 4A.1 presents additional results demonstrating that there was no statistical support for this interaction.

The full model was therefore:

$$\begin{aligned}
 \text{logit}(p_{ij}) = & \alpha_j + \beta_1 b_{ij} + \beta_2 h_{ij} \\
 & + \beta_3 \bar{b}_j + \beta_4 \bar{h}_j + \beta_5 T_j \\
 & + \beta_6 b_{ij} \bar{b}_j + \beta_7 b_{ij} \bar{h}_j \\
 & + \beta_8 h_{ij} \bar{b}_j + \beta_9 h_{ij} \bar{h}_j \\
 & + \beta_{10} b_{ij} T_j
 \end{aligned}$$

$$\alpha_j \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

$$y_{ij} \sim \text{Bernoulli}(p_{ij})$$

Where y is a binary variable indicating the presence or absence of an egg, p indicates the probability of presence, i indexes the quadrat, j indexes the site, b is the percent bare ground in quadrat i , and h is the percent *F. ovina* in quadrat i (Table 4.1). T_j is the modelled vegetation surface temperature for site j , \bar{b}_j is the mean bare ground cover across the whole of site j , and \bar{h}_j is the mean host plant cover across the whole of site j (Table 4.1). We therefore modelled egg-laying site selection at the population level, assuming that all sampled locations within a site are equally accessible to individuals (Hill et al. 1996).

Note that the proportion of quadrats that contained presences at each site was determined by the number of presence-only and random quadrats taken at each site; consequently, as in the majority of studies on resource selection functions, our models estimate relative rather than absolute probabilities of presence (Manly et al. 2002). This means that the site-level main effects of climate and habitat availability (coefficients β_{3-5}) are not meaningful in themselves; their purpose is to allow their interaction with bare ground and host plant associations to be quantified.

Models were fitted to three datasets. We began by analysing spatial and temporal trends in egg-laying separately: we fitted models to (1) the *spatial* dataset, which comprised of all sites in 2010, and to (2) the *temporal* dataset, which incorporated data from the temporal site from five different

years, excluding other sites. Then, to assess the combined evidence for habitat availability and temperature effects on egg-laying, we fitted the same models to (3) the *combined* dataset, which included all sites in 2010 and all five years from the temporal site. Where temporal data was included, each site/year combination was in effect treated as a separate site within the model, so that j indexed each site/year combination. Since in the combined dataset we fit the same coefficients to describe variation in egg-laying in both space and time, we make the assumption that egg-laying changes in a similar way through space and time.

4.3.5. Statistical tests

To test hypotheses about egg associations, models were fitted using the *lmer* function in the *lme4* package (Bates et al. 2011), assuming a binomial error structure. We assessed the empirical support for each model using Akaike's Information Criterion (AIC; Burnham and Anderson 2002b). Using each of the three datasets (see Model-fitting), we compared seven different models, representing seven different hypotheses about the processes driving egg-laying locations. The models were as follows: *full* included all terms specified above; *inhabitat* included interactions between habitat availability and both bare ground and host plant cover, but no interaction with temperature; *intbare* included only interactions between habitat availability and bare ground cover; *inthost* included only interactions between habitat availability and host plant cover; *temp* included an interaction between site-level temperature and bare ground cover, but no interactions with habitat availability; *main* modelled a constant response to bare ground and host plant cover across all sites, with no interactions; and *null* included only a random intercept, with no response to bare ground or host plant cover. Full model specifications are illustrated in Table 4.2.

4.3.6. Model predictions

Following model selection, we parameterised the best model using a Bayesian approach in the software WinBUGS, via the *R2WinBUGS* package (Sturtz et al. 2005). This allowed us to better

incorporate uncertainty in our predictions, estimating credible intervals without making assumptions such as asymptotically large sample size (Clark 2007, Kery and Schaub 2011). We ran 3 chains of 50000 draws, with a thinning rate of 25 and a burn-in of 10000 (Kery and Schaub 2011).

4.4. Results

We sampled 2093 quadrats in total, of which 516 contained eggs (presences) and 1577 represented absences. The spatial analysis incorporated 1317 quadrats (338 presences and 979 absences), while the temporal analysis incorporated 988 quadrats (195 presences and 793 absences). Note that the quadrats from the temporal site in 2010 were used in both spatial and temporal analyses.

The spatial dataset offered strong support for the full model (Table 4.2a; δ AIC between full model and next best model = 7.31). The coefficients of this full model (Fig. 4A.1) corroborate several hypotheses about egg locations. First, the positive main effects of bare ground and host plant cover confirm that egg locations were positively associated with high bare ground and host plant cover (Thomas et al. 1986a). Second, the negative interaction between bare ground cover and site-level temperature demonstrates that eggs were most strongly associated with bare ground in relatively cool sites (Fig. 4.2a). Third, the interactions of quadrat-level effects of bare ground cover and host plant cover with site-level habitat variables show that habitat associations depended on habitat availability. The effect of bare ground decreased as the availability of bare ground increased, such that butterflies disproportionately selected quadrats with high levels of bare ground only in sites where bare ground was relatively rare (Fig 2b). There was also an indication that the effect of bare ground increased in sites with increased host plant availability, but there was very high uncertainty associated with this conclusion (Fig 2c). The effect of host plant cover on egg presence weakened with increasing availability of both bare ground and host plants across the site (Fig 2d-e). Thus, in general, the apparent association between eggs and high bare ground or host plant cover was reduced as these resources became more common across the site.

The results from the temporal analysis were less clear-cut (Table 4.2b): differences in fit between models based on the temporal data were difficult to resolve, perhaps because only 5 scenarios (years) were sampled in comparison with the 16 scenarios (sites) for the spatial analysis. Though there was an indication of an interaction between bare ground association and site-level temperature (Table 4.2b), this interaction appeared much weaker than the interaction between bare ground association and temperature evident from the spatial data (Fig. 4.2a, triangle symbols; Fig. 4A.1). The most probable reason for this discrepancy is that the amount of bare ground at the temporal study site was the highest out of all our study sites (Fig. 4.2b), meaning that the association with bare ground appeared weaker due to its wider availability (Mysterud and Ims 1998, Godvik et al. 2009).

Nonetheless, the direction and magnitude of the model coefficients in the temporal analysis were consistent with those derived from the spatial dataset (Fig. 4A.1), and when both the spatial and temporal datasets were combined and analysed together, we found very strong support for the full model (Table 4.2c; δ AIC between full model and next best model = 33.85). Posterior distributions for coefficients for the full model, based on the combined dataset, are given in Fig. 4A.2, whilst predictions and data for each site-year combination are shown in Fig. 4A.3. The fact that spatial and temporal datasets may be accommodated within the same model does not imply that egg associations vary in identical ways through time and space, but suggests that habitat associations may at least be determined by the same processes.

4.5. Discussion

Our ability to assess species' habitat requirements underlies both our understanding of their ecology and our capacity to predict their responses to climate and habitat change (Beyer et al. 2010). Typically, patterns of habitat association are assumed to be conserved in other places or times, but recent work has demonstrated that habitat associations may change non-linearly with variables such

as resource availability (Mysterud and Ims 1998, Godvik et al. 2009) and disturbance levels (Hebblewhite and Merrill 2008, DeCesare et al. 2012, Moreau et al. 2012), producing a functional response in habitat associations. Here, using the skipper butterfly *Hesperia comma* as a case study, we examined changes in population-level habitat associations with both climate and habitat availability. We found that *H. comma* populations in hotter regions and slopes were less likely to lay eggs next to warm microhabitats provided by bare ground (Fig. 4.2a). Furthermore, we found that *H. comma* eggs were less likely to be associated with microsites of high bare ground (Fig. 4.2b-c), or with high host plant cover (Fig 2d-e), in sites with increased availability of these resources. These results quantify a climate-driven functional response in habitat association, showing that habitat associations may change with temperature through both space and time. They also demonstrate that climate and habitat availability may act simultaneously to drive changes in habitat associations (Fig. 4.2).

Relatively few studies have investigated the effects of climate on habitat associations (Oliver et al. 2009, Suggitt et al. 2012). Nonetheless, behavioural studies on individuals have shown that temperature can influence microhabitat selection decisions (Davies et al. 2006, Dubois et al. 2009, Schofield et al. 2009), whilst population-level habitat associations have been found to differ between times or places with different climates (Adolph 1990, Roy and Thomas 2003, Davies et al. 2006, Ashton et al. 2009, Oliver et al. 2009, Suggitt et al. 2012). However, behavioural studies are generally restricted to a single population, limiting their generality to other places or times (Beyer et al. 2010, Matthiopoulos et al. 2011), whilst in population-level studies, usually only a pair of times or locations are compared (e.g. Roy and Thomas 2003, Davies et al. 2006, Oliver et al. 2009). Consequently, quantified functional responses to climate have remained elusive. Our approach draws on recent developments in resource selection modelling (Hebblewhite and Merrill 2008, Matthiopoulos et al. 2011), adopting a mechanistic, predictive approach to model dynamic habitat associations based on 16 different sites with a range of climates.

The changing habitat associations of *H. comma* populations under different temperatures (Fig. 4.2) reflect the variable importance of microclimates created by bare ground (Suggitt et al. 2011). In *H. comma*, the preference for a certain temperature may remain unchanged, but the preference for the hotter microhabitats decreases as ambient temperatures rise (Davies et al. 2006). In the coolest habitats experienced at the range margin, the realised distribution of *H. comma* eggs is most strongly associated with the hot microhabitats provided by bare ground, but becomes less strongly associated with bare ground in warmer sites and years. As a result, the range of habitats available for egg-laying would be expected to broaden towards the centre of *H. comma*'s range and as summer temperatures rise due to global warming (Davies et al. 2006, Oliver et al. 2009), potentially enhancing population survival or accelerating range expansion rates (Thomas et al. 2001, Wilson et al. 2010, Pateman et al. 2012).

Fine-scale and short-term variation in temperature are increasingly being recognised as important determinants of species' distributions (Gillingham et al. 2012; Chapter 2), but need to be incorporated explicitly into population-level habitat association models (Thomas et al. 1999, Kearney et al. 2009, 2010). Our study employed fine-scale (5m resolution) models of grassland surface temperature that included thermal effects of topography, such that modelled temperatures closely matched those actually experienced by *H. comma* populations (Fig. 4.1c). In our study system, the variation in temperature among slopes and between years is considerably greater than the yearly warming trend (J. Bennie, unpublished data). Thus, our results indicate that temperature may drive considerable differences in habitat associations among neighbouring populations, and in the same population among different years, requiring highly plastic habitat definitions to be adopted.

The decreased association with both bare ground and the host plant *F. ovina* with increasing availability (Fig. 4.2b-e) is consistent with previous habitat association studies (Mysterud and Ims 1998, Godvik et al. 2009). This supports the idea that selection of a given habitat rarely occurs independently from the alternative habitat choices available, despite the fact that the probability of

presence is often modelled independently in each cell or event (Beyer et al. 2010, Matthiopoulos et al. 2011). For example, each *H. comma* female lays a limited number of eggs during her lifetime, which means that rather than judging each microsite independently, she might be expected to assess a range of microhabitats and lay in the “best” microhabitats she finds (either by active choice or through varying motivation during sequential encounters; Courtney and Forsberg 1988, Mackay and Singer 2008). Consequently, a given microsite with high bare ground may be more attractive when bare ground is limited than when it is widely available, and its probability of containing an egg will decrease with increasing bare ground availability. This effect is analogous to the increased likelihood that an isolated host plant individual may receive more eggs (Courtney and Forsberg 1988, Mackay and Singer 2008), or that an isolated individual animal may experience a higher risk of predation than one within a herd (Connell 2003).

If too few scenarios (sites and/or years) are studied, the effects of habitat availability and climate on habitat selection cannot be separated, potentially masking or yielding spurious responses to climate. Similarly, changes in habitat associations due to unmeasured variables may be attributed to climate effects. A case in point is provided by the temporal analysis in this study. Taken in isolation, the temporal data revealed an apparently weak functional response to climate that was difficult to separate from changes in habitat amongst years (Fig. 4.2a). However, once combined with inference from the spatial dataset, the relatively weak response to climate could be explained by habitat availability effects: specifically, the high bare ground availability at the temporal study site (Fig. 4.2b). This demonstrates that studying multiple populations and habitat availability scenarios, as here, is a crucial step towards general conclusions about habitat associations (Beyer et al. 2010).

Climate-driven functional responses in habitat selection could have important practical implications for both conservation management and prediction of species’ responses to climate change. If species’ microhabitat requirements change with climate, region-specific management schemes and adaptable long-term plans will form important components of management policy (Lawler 2009).

However, given the short-term and fine-scale changes in habitat association highlighted in this study, providing microclimatic heterogeneity is likely to be a key step towards maximising species' persistence and expansion opportunities under climate change (Opdam and Wascher 2004, Oliver et al. 2009). For *H. comma*, grazing to maintain patches of bare ground at each site will ensure that suitable microhabitats remain available in cool years, which is of particular importance at the edge of the range and on cooler north-facing slopes. Conversely, failure to provide sufficiently cool microhabitats produced by a longer sward height could be detrimental in hot years and on south-facing slopes, especially as August temperatures rise. In short, dynamic and flexible management plans will support species' shifting habitat requirements under climate change.

Integrating functional responses in habitat selection with species distribution models could provide new insights and improved predictions of species' responses to both climate and habitat change. At present, most studies assume that species' requirements can be characterised by a single model that applies to all places and times (Oliver et al. 2009, Peterson et al. 2011). However, our study has shown that species' habitat relationships may change when models are extrapolated to new conditions. Although this cautions against over-reliance on "single-response" projections, quantitative and predictive approaches such as that taken here could be incorporated into current modelling approaches and anticipate changes in habitat selection. Thus, this simple step of including interactions between climate and habitat variables (Mysterud and Ims 1998, Oliver et al. 2009, Matthiopoulos et al. 2011) could help to reconcile the different views of habitat and enhance our understanding of species' responses to climate change.

4.6. References

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* **71**:315-327.

- Ashton, S., D. Gutiérrez, and R. J. Wilson. 2009. Effects of temperature and elevation on habitat use by a rare mountain butterfly: implications for species responses to climate change. *Ecological entomology* **34**:437-446.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using Eigen and Eigen. <http://CRAN.R-project.org/package=lme4>.
- Bennie, J., B. Huntley, A. Wiltshire, M. O. Hill, and R. Baxter. 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling* **216**:47-59.
- Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use–availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:2245-2254.
- Bolker, B. M. 2008. *Ecological models and data in R*. Princeton University Press, Princeton, N.J.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer, London.
- Burton, N. H. K. 2006. Nest orientation and hatching success in the tree pipit *Anthus trivialis*. *Journal of Avian Biology* **37**:312-317.
- Clark, J. S. 2007. *Models for ecological data: an introduction*. Princeton University Press, Oxford.
- Connell, S. D. 2003. Is there safety-in-numbers for prey? *Oikos* **88**:527-532.
- Courtney, S. and J. Forsberg. 1988. Host use by two pierid butterflies varies with host density. *Functional ecology* **2**:67-75.

- Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**:247-256.
- DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, and L. E. Morgantini. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications* **22**:1068-1083.
- Dubois, Y., G. Blouin-Demers, B. Shipley, and D. Thomas. 2009. Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. *Journal of Animal Ecology* **78**:1023-1032.
- Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* **79**:548-555.
- ESRI. 2009. ArcMap 9.3.1. ESRI, Redlands, CA, USA.
- Gillies, C. S. and C. C. St Clair. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology* **47**:182-190.
- Gillingham, P. K., S. C. F. Palmer, B. Huntley, W. E. Kunin, J. D. Chipperfield, and C. D. Thomas. 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**:831–838.
- Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Ø. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* **90**:699-710.

- Hebblewhite, M. and E. Merrill. 2008. Modelling wildlife–human relationships for social species with mixed effects resource selection models. *Journal of Applied Ecology* **45**:834-844.
- Hill, J., C. Thomas, and O. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology* **65**:725-735.
- Intermap Technologies. 2011. NEXTMap Britain: Digital terrain mapping of the UK. NERC Earth Observation Data Centre. Available from http://badc.nerc.ac.uk/view/neodc.nerc.ac.uk_ATOM_dataent_11658383444211836 (accessed 2011).
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65-71.
- Kearney, M., W. P. Porter, C. Williams, S. Ritchie, and A. A. Hoffmann. 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Functional ecology* **23**:528-538.
- Kearney, M., S. J. Simpson, D. Raubenheimer, and B. Helmuth. 2010. Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**:3469-3483.
- Kery, M. and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Oxford.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* **1162**:79-98.
- Mackay, D. A. and M. C. Singer. 2008. The basis of an apparent preference for isolated host plants by ovipositing *Euptychia libye* butterflies. *Ecological entomology* **7**:299-303.

- Manly, B. F. J., D. L. Thomas, and L. L. McDonald. 2002. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.
- Matthiopoulos, J. 2011. How to be a quantitative ecologist: the 'A to R' of mathematics and statistics. Wiley-Blackwell, Oxford.
- Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalised functional responses for species distributions. *Ecology* **92**:583-589.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology* **79**:4-12.
- Merrill, R. M., D. Gutiérrez, O. T. Lewis, J. Gutiérrez, S. B. Díez, and R. J. Wilson. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* **77**:145-155.
- Moreau, G., D. Fortin, S. Couturier, and T. Duchesne. 2012. Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. *Journal of Applied Ecology* **49**:611-620.
- Morris, D. W. and A. Dupuch. 2012. Habitat change and the scale of habitat selection: shifting gradients used by coexisting Arctic rodents. *Oikos* **121**:975-984.
- Mysterud, A. and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* **79**:1435-1441.
- Navas, C. A. 1996. Implications of microhabitat selection and patterns of activity on the thermal ecology of high elevation neotropical anurans. *Oecologia* **108**:617-626.
- Oliver, T., J. K. Hill, C. D. Thomas, T. Brereton, and D. B. Roy. 2009. Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters* **12**:1091-1102.

- Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117**:285-297.
- Pateman, R. M., J. K. Hill, D. B. Roy, R. Fox, and C. D. Thomas. 2012. Temperature-Dependent Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science* **336**:1028-1030.
- Perry, M. and D. Hollis. 2005. The development of a new set of long-term climate averages for the UK. *International Journal of Climatology* **25**:1023-1039.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. *Ecological niches and geographic distributions*. Princeton University Press, Oxford.
- Prinzing, A. 2005. Corticolous arthropods under climatic fluctuations: compensation is more important than migration. *Ecography* **28**:17-28.
- Roy, D. and J. Thomas. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia* **134**:439-444.
- Schofield, G., C. M. Bishop, K. A. Katselidis, P. Dimopoulos, J. D. Pantis, and G. C. Hays. 2009. Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology* **78**:14-21.
- Shreeve, T. 1986. Egg-laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behaviour, host plant abundance and temperature. *Ecological entomology* **11**:229-236.
- Singer, M. C. 2000. Reducing ambiguity in describing plant-insect interactions: "preference", "acceptability" and "electivity". *Ecology Letters* **3**:159-162.

- Singer, M. C. and C. D. Thomas. 1996. Evolutionary responses of a butterfly metapopulation to human-and climate-caused environmental variation. *American Naturalist* **148**:9-39.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of Statistical Software* **12**:1-16.
- Suggitt, A. J., P. K. Gillingham, J. K. Hill, B. Huntley, W. E. Kunin, D. B. Roy, and C. D. Thomas. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120**:1-8.
- Suggitt, A. J., C. Stefanescu, F. Páramo, T. Oliver, B. J. Anderson, J. K. Hill, D. B. Roy, T. Brereton, and C. D. Thomas. 2012. Habitat associations of species show consistent but weak responses to climate. *Biology Letters* **8**:590-593.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**:577-581.
- Thomas, J., C. Thomas, D. Simcox, and R. Clarke. 1986. Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology* **23**:365-380.
- Thomas, J. A., R. J. Rose, R. T. Clarke, C. D. Thomas, and N. R. Webb. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional ecology* **13**:55-64.
- Wilson, R. J., Z. G. Davies, and C. D. Thomas. 2010. Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. *Ecography* **33**:73-82.

Name	Symbol	Description
Bare ground cover	b_{ij}	Percentage bare ground cover in quadrat i at site j
Host plant cover	h_{ij}	Percentage cover of host plant <i>Festuca ovina</i> in quadrat i at site j
Temperature	T_j	Mean hours above 25°C in site j
Bare ground availability	\bar{b}_j	Mean percentage cover of bare ground at site j
Host plant availability	\bar{h}_j	Mean percentage cover of host plant <i>Festuca ovina</i> at site j

Table 4.1: Glossary of variables used in the study.

Dataset	Model	Terms										K	AIC	δ AIC	AICWt
		main effects					interactions								
		quadrat		site-level			bare ground		host plant		temperature				
b_{ij}	h_{ij}	\bar{b}_j	\bar{h}_j	T_j	$b_{ij}\bar{b}_j$	$b_{ij}\bar{h}_j$	$h_{ij}\bar{b}_j$	$h_{ij}\bar{h}_j$	$b_{ij}T_j$						
(a) Spatial	full	+	+	+	+	+	+	+	+	+	+	12	1178.90	0.00	0.97
	inhabitat	+	+	+	+		+	+	+	+		10	1186.21	7.31	0.03
	intbare	+	+	+			+	+				8	1205.83	26.93	0.00
	inhost	+	+		+				+	+		8	1226.81	47.92	0.00
	temp	+	+			+					+	6	1269.12	90.23	0.00
	main	+	+									4	1278.87	99.97	0.00
	null											2	1463.40	284.50	0.00
(b) Temporal*	temp	+	+	+	+	+					+	6	947.16	0.00	0.43
	main	+	+									4	948.04	0.88	0.28
	inhost	+	+		+				+	+		8	949.57	2.42	0.13
	inhabitat	+	+	+	+		+	+	+	+		10	950.53	3.37	0.08
	intbare	+	+	+			+	+				8	950.82	3.66	0.07
	full	+	+	+	+	+	+	+	+	+	+	12	954.01	6.85	0.01
	null											2	956.16	9.00	0.00
(c) Combined*	full	+	+	+	+	+	+	+	+	+	+	12	2002.30	0.00	1.00
	inhabitat	+	+	+	+		+	+	+	+		10	2036.15	33.85	0.00
	inhost	+	+		+				+	+		8	2075.20	72.90	0.00
	intbare	+	+	+			+	+				8	2104.12	101.81	0.00
	temp	+	+			+					+	6	2143.24	140.94	0.00
	main	+	+									4	2155.00	152.69	0.00
	null											2	2292.76	290.46	0.00

Table 4.2: Empirical support for different models based on (a) the spatial dataset, sampled in 2010; (b) the temporal dataset, sampled at a single site in five different years; and (c) the combined evidence from both spatial and temporal datasets (assuming responses in space are equivalent to those in time). All fitted models are shown, with names matching descriptions in the Methods section. Constituent terms are indicated by filled circles (●), with empty circles (○) indicating terms that were not included; see Table 4.1 for term descriptions. K=number of parameters; AIC=Akaike's Information Criteria Score; δ AIC=difference in AIC between current and highest-ranked model; AICWt =AIC weights. *Year is modelled as equivalent to site in the temporal and combined models.

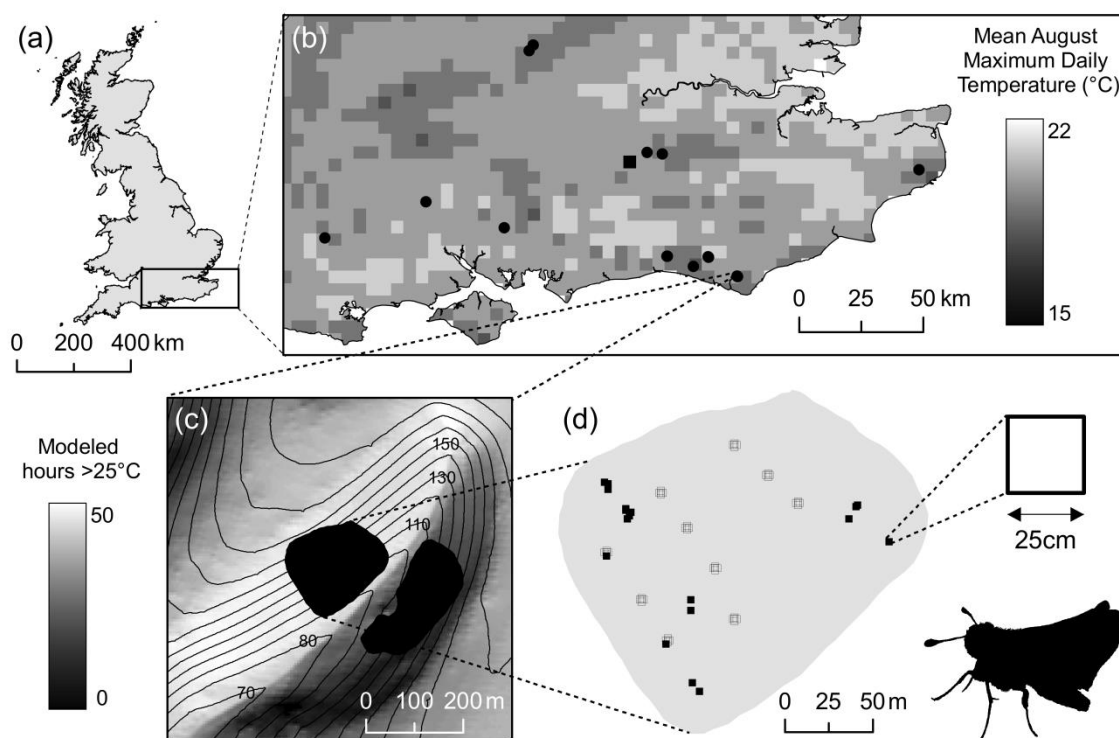


Figure 4.1: Study sampling design. Sites were chosen to span the extent of *H. comma*'s distribution in Britain (a). We surveyed populations from a range of large-scale climates (b; black circles indicate surveyed areas; black square indicates “temporal” site at which sampling took place in five different years) with mean August maximum daily temperatures generally cooler in the north-western and coastal areas (lighter grid squares indicate warmer temperatures, based on mean daily maximum temperature in 2010 for each 5km square). We also chose populations from a range of aspects, to include topographic variation in temperature; panel c shows two populations sampled from a warm south-easterly facing slope and a cooler north-westerly facing slope (lighter greys indicate warmer microclimates). These topography-generated microclimate effects were incorporated in our models of vegetation surface temperatures (see Methods). Within each site (d), we sampled quadrats containing *H. comma* eggs using a transect-based search method (solid squares), and randomly across the site using stratified sampling (open squares; see Methods). Within each quadrat, we recorded the percentage cover of bare ground and the host plant *F. ovina*.

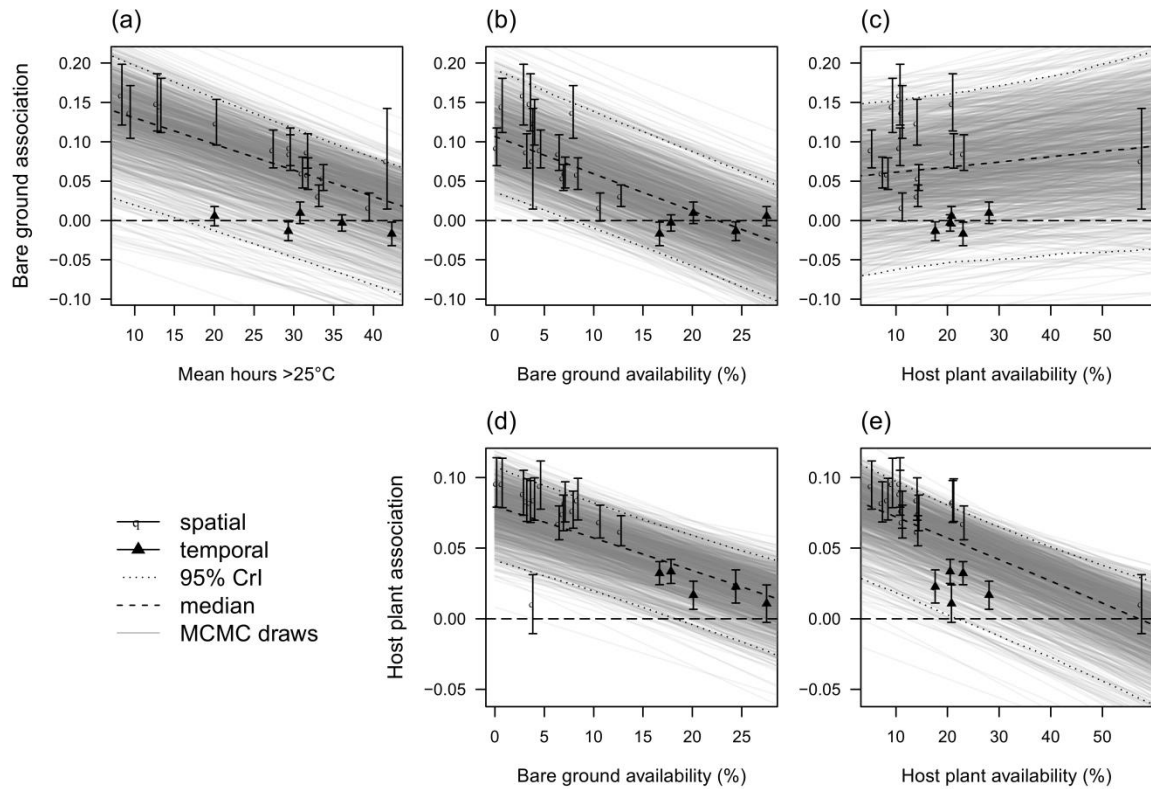


Figure 4.2: Coefficients indicating the association of *H. comma* eggs with bare ground (a-c) and the host plant *F. ovina* (d-e), in sites with different temperatures (a), bare ground availability (b,d) and host plant availability (c,e). Coefficients are based on the full model parameterised on the combined dataset. The median (marginal) prediction across all sites is shown as a dashed line, 95% credible intervals are shown as dots, whilst grey lines show random draws from the joint posterior distribution. Site-specific (conditional) predictions are shown as for the spatial dataset, sampled in 2010 (circles) and the temporal dataset, sampled at a single site in five separate years (triangles), along with 95% credible intervals (error bars). Note that the temporal site features in both spatial and temporal datasets (joint circle and triangle symbol).

Appendix to Chapter 4

4A.1. Model selection tables including host plant-temperature interaction

We used the *combined* dataset to test whether host plant cover had different effects on egg-laying at different temperatures. We fitted two models additional to those in the main text:

- *hfull* contained all terms present in the *full* model, plus an interaction between host plant cover and temperature. This tests the hypothesis that the strength of association with host plant cover changes with site-level temperature.
- *htemp* is the equivalent of the *temp* model, except with an interaction between host plant cover and temperature instead of the interaction between bare ground cover and temperature. This tests the hypothesis that the effect of host plant cover varies with temperature but there are no other interactions with habitat availability or temperature.

We compared these models to the other models given in the main text, based on AIC. The results are shown on the following page, with the additional models highlighted in red:

Dataset	Model	Terms											K	AIC	δ AIC	AICWt
		main effects						interactions								
		quadrat		site-level		T_j	bare ground		host plant		temperature					
		b_{ij}	h_{ij}	\bar{b}_j	\bar{h}_j		$b_{ij}\bar{b}_j$	$b_{ij}\bar{h}_j$	$h_{ij}\bar{b}_j$	$h_{ij}\bar{h}_j$	$b_{ij}T_j$	$h_{ij}T_j$				
Combined	full	+	+	+	+	+	+	+	+	+	+	+	12	2002.30	0.00	1.00
	hfull	+	+	+	+	+	+	+	+	+	+	+	13	2003.83	1.53	0.32
	intboth	+	+	+	+		+	+	+	+			10	2036.15	33.85	0.00
	inthost	+	+		+				+	+			8	2075.20	72.90	0.00
	intbare	+	+	+			+	+					8	2104.12	101.81	0.00
	temp	+	+			+					+		6	2143.24	140.94	0.00
	htemp	+	+			+						+	6	2146.71	144.41	0.00
	main	+	+										4	2155.00	152.69	0.00
	null												2	2292.76	290.46	0.00

Table 4A.1: Model selection table for oviposition analysis including interactions between host plant cover in the quadrat and the temperature (modelled microclimate) of the site.

Including the interaction between temperature and host plant cover worsened the fit of the full model. Moreover, the model containing only an interaction between host plant cover and temperature ranked below all other models except the null and the main effects only model. Thus, there was little support for the hypothesis that the effects of host plant cover on egg-laying differed at different temperatures.

Appendix 4 Figures

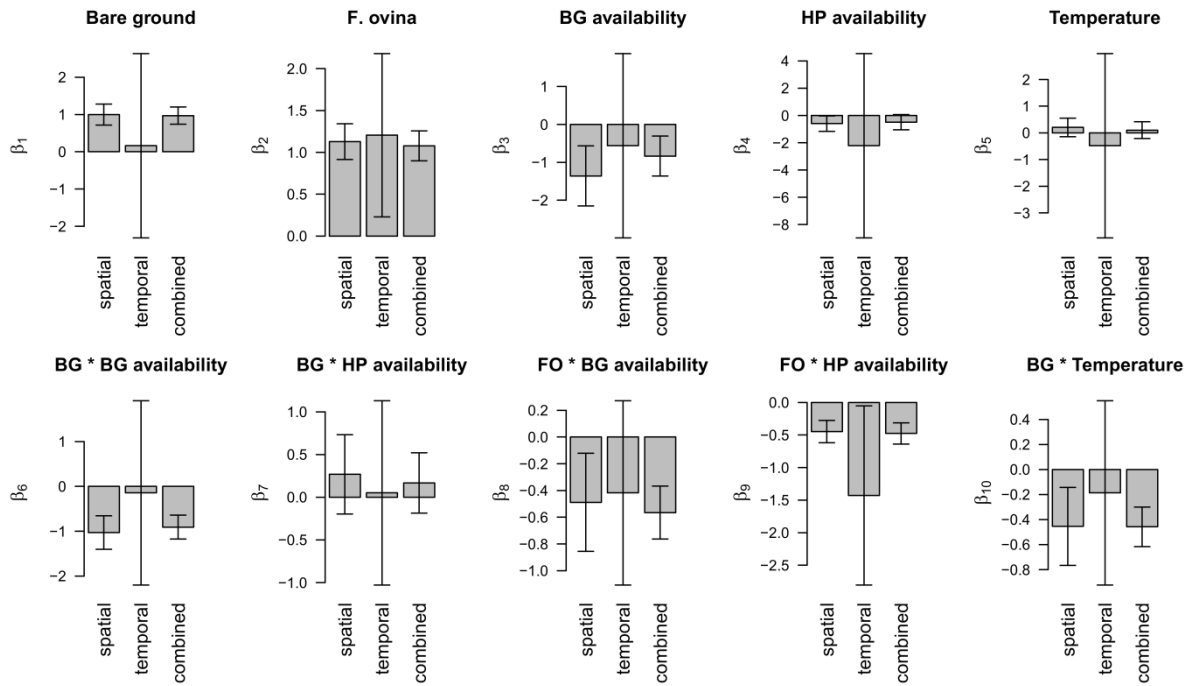


Figure 4A.1: Comparison of parameter estimates from the full model based on the spatial, temporal, and combined datasets. Bars show maximum likelihood estimates, whilst error bars show 95% confidence intervals.

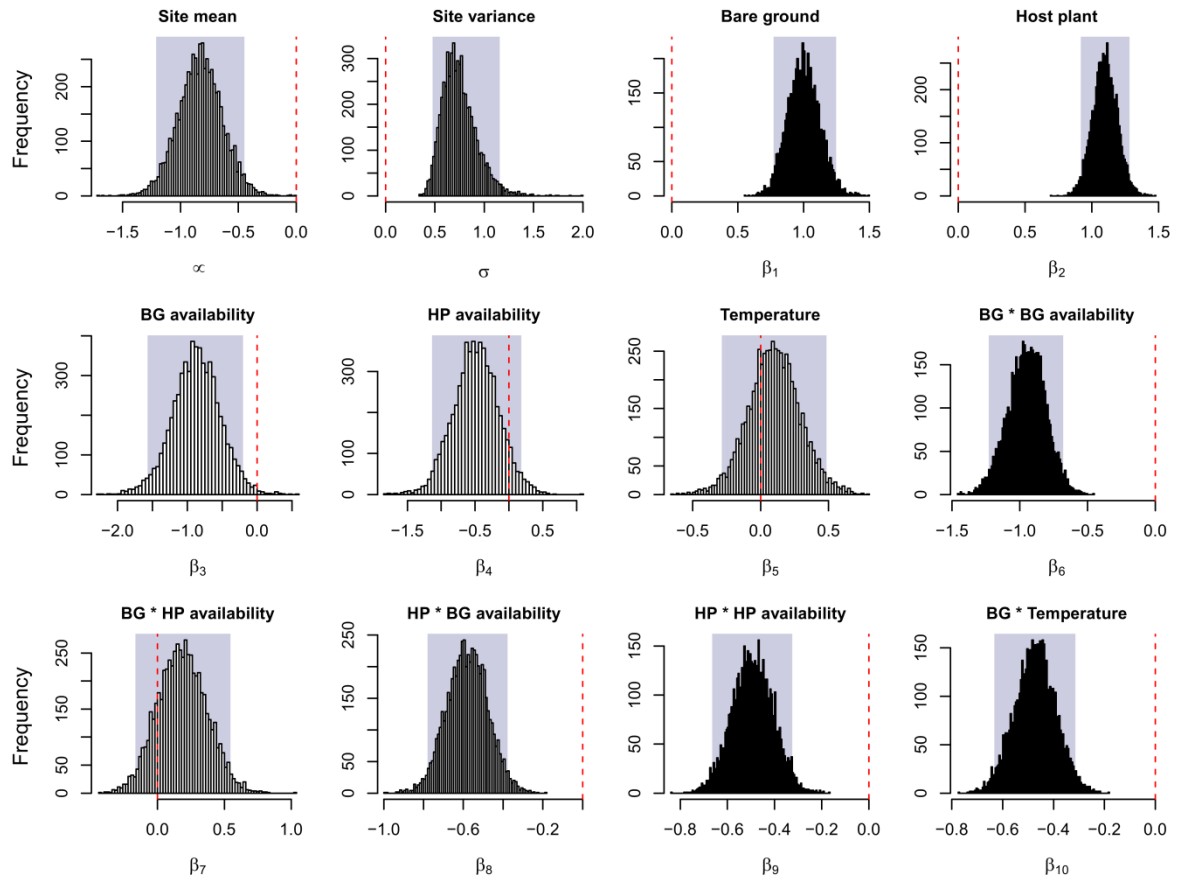


Figure 4A.2: Histograms showing posterior distributions of parameters from MCMC draws. The red line highlights the parameter value of zero, whilst the blue box shows the 95% credible interval for each parameter

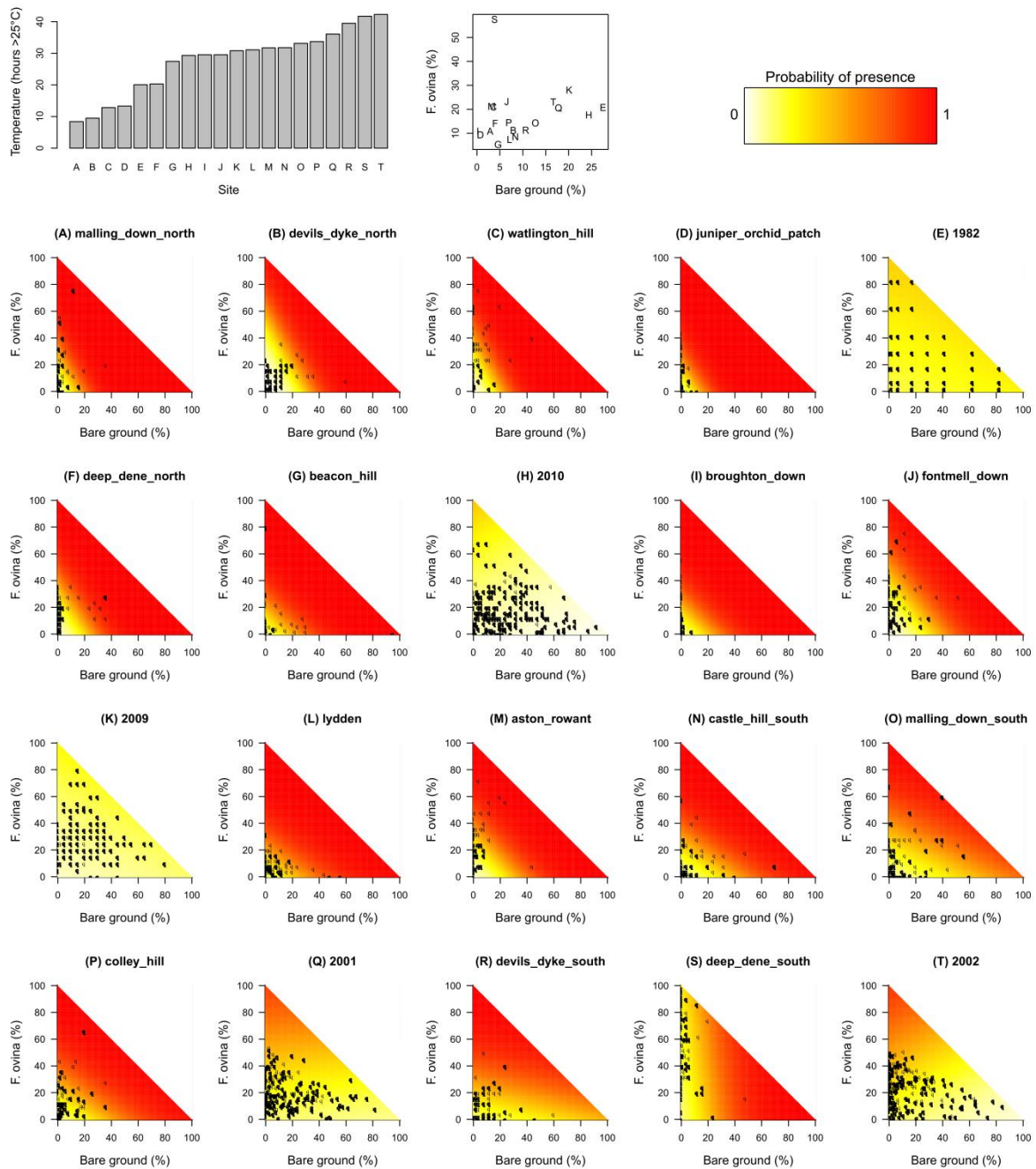


Figure 4A.3: Predictions and data for each of the 20 site/year combinations in the study (labelled A-T), from the full model based on the combined dataset. Surveys at the temporal site are indicated by years instead of site names. Sites/years are ordered by temperature, from the least to the most hours above 25°C; the temperatures for each site are shown in the barplot at the top of the figure. The mean percentage cover of bare ground and mean percentage host plant cover at each site is shown in the letters scatterplot. Probability of presence predictions range from 0 (white) to 1 (red). Quadrats

in which eggs were present are shown with filled circles, and quadrats in which no eggs were present are shown as open circles. The axes on the individual plots indicate quadrat-level bare ground and host plant cover.

Chapter 5: Prevalence, thresholds, and the performance of presence-absence models

5.1. Summary

The use of species distribution models (SDMs) to understand and predict species' distributions necessitates tests of fit to empirical data. General guidelines for measuring SDM performance remain limited, but there is wide agreement that the values of performance metrics should be independent of the proportion of locations that were occupied (known as prevalence), and that continuous predictions can be transformed into binary predictions for "threshold-dependent" performance assessment. We developed a conceptual framework for classifying SDM performance metrics, based on (a) whether the metric measured the numerical accuracy of predictions (calibration), or only their ability to separate presences from absences (discrimination), and (b) whether binary or continuous predictions were involved in the calculation of the metric. Using this framework, we reviewed 100 SDM studies to assess current trends in performance assessment. We then used a combination of analytical approaches and illustrative examples to investigate (a) the effects of factoring out prevalence from performance metrics, and (b) the effects of using binary metrics to evaluate SDM performance. Factoring out prevalence from performance metrics prevents assessment of model calibration, meaning that only the discrimination ability of predictions can be assessed. This result applies to both continuous and binary predictions. Probabilistic predictions can be assessed using binary ("threshold-dependent") performance metrics without applying thresholds to transform the predictions. However, binary metrics reward binary predictions more highly than probabilistic predictions, often favouring models with reduced discriminatory power, poorly calibrated expectations, and misleading uncertainty. Prevalence-independent metrics can be used to measure qualitative ranking ability, but their inability to measure calibration makes them unsuitable for measuring performance when the numerical values of predictions are important. The use of

binary (“threshold-dependent”) metrics to assess SDM performance can lead to misleading conclusions and predictions, and continuous metrics should be used instead wherever possible. We recommend likelihood-based metrics such as Akaike’s information criterion (AIC) for assessing model calibration.

5.2. Introduction

Species distribution models (SDMs) are useful tools for understanding species’ habitat requirements and for predicting their distributions in different places or times (Peterson et al. 2011). Measuring how well model predictions reproduce observed species distributions is integral to inferences derived from SDMs. Predictive performance may be assessed to (a) test which environmental variables have an important influence on the distribution of a species; (b) find the model (parameter set or modelling method) that best predicts a species’ distribution; (c) assess the reliability of predictions; or (d) suggest areas for model improvement (model criticism; Guisan and Zimmermann 2000, Bolker 2008, Peterson et al. 2011). Typically, performance is summarised into a single number which scores how well predictions from the model match an observed dataset of occupied (presences) and unoccupied (absences) locations. However, the definition of a “good match” between model and data depends on the objectives of the study, and there are a wealth of SDM performance metrics available (Liu et al. 2011).

With SDMs increasingly applied to predict ecological and evolutionary responses to climate and habitat change (Peterson et al. 2011), there has been an accompanying rise in empirical and theoretical studies investigating the strengths and weaknesses of different performance metrics (e.g. McPherson et al. 2004, Allouche et al. 2006, Lobo et al. 2008, Foody 2011). However, following two important reviews of SDM performance measures (Pearce and Ferrier 2000, Vaughan and Ormerod 2005), research has largely focussed on the merits of individual metrics, with less emphasis on developing a conceptual underpinning for their classification. Consequently, there are few general

concepts for measuring SDM performance, with much uncertainty over which metrics are best for a given application (Elith and Leathwick 2009, Peterson et al. 2011).

Two general practices in SDM performance assessment are examined in this study. First, there have been concerns that the proportion of presences in a dataset, known as *prevalence* (Royle et al. 2012), alters the values of performance metrics (McPherson et al. 2004, Allouche et al. 2006, Foody 2011). Prevalence differs among datasets due to differences in rarity among species, and because species occupy a smaller proportion of locations when surveyed at higher spatial resolutions (Kunin 1998). Prevalence has been shown to affect the scores of many performance metrics, an effect viewed as a statistical artefact (Pearce and Ferrier 2000, Vaughan and Ormerod 2005, Allouche et al. 2006, Lobo et al. 2008). Consequently, the application of performance metrics that eliminate the effects of prevalence has been widely advocated (Allouche et al. 2006, Lobo et al. 2008).

Second, the application of “threshold-dependent” performance metrics has been encouraged (Liu et al. 2005, Lobo et al. 2008, Bean et al. 2011). Threshold-dependent metrics require binary rather than continuous predictions. Model predictions are often probabilistic (non-binary), and are converted into binary predictions by selecting a threshold value above which predictions are classed as present, and below which predictions are classified as absent (Liu et al. 2005). Threshold selection complicates SDM performance measurement, because changing the threshold value changes predicted presences into absences or vice-versa (Bean et al. 2011), potentially altering performance scores and conclusions (e.g. Nenzén and Araújo 2011). As such, there exists a substantial literature on threshold selection methods (Liu et al. 2005, Lobo et al. 2008). The necessity of threshold-dependent metrics has been questioned in some quarters (Vaughan and Ormerod 2005), but the additional step of threshold selection makes threshold-dependent and threshold-independent metrics difficult to compare (Liu et al. 2011).

In this study, we aim to refine both the theoretical underpinning and practical guidelines for SDM performance assessment. We develop a conceptual framework for SDM performance metrics, and

apply this framework to review their applications in 100 recent studies. We then show that (a) prevalence forms a necessary component of performance assessment in quantitative applications of SDMs, and (b) that “threshold-dependent” metrics can be used to assess probabilistic predictions without applying thresholds, but that using threshold-dependent metrics can lead to misleading conclusions and predictions. We address situations where absence data are available; presence-only evaluation methods are discussed elsewhere (Hirzel et al. 2006, Phillips and Elith 2010). We focus on SDM evaluation, but our conclusions apply to binary modelling in general.

5.3. Conceptual framework and literature review

5.3.1. Conceptual framework

We begin by developing a conceptual framework for classifying SDM performance metrics, drawing on work from Murphy and Winkler (1987, introduced to ecology by Pearce and Ferrier 2000). Presence-absence models are based on observations of species presence or absence ($y \in \{1,0\}$) at spatial locations (grid cells, study sites, etc.; hereafter “cells”) $i = 1, \dots, n$. Each presence-absence observation y_i is associated with environmental conditions x_i . SDMs use species’ associations with environmental variables (the relationship between y and x) to parameterise a function $f(x)$ which describes the predicted probability of an individual of the species being present in each cell $\mathbf{p} = p_1, \dots, p_n$ (Fig. 5.1a; notation summarised in Table 5.1).

SDM performance is assessed by measuring the extent to which the predictions \mathbf{p} provide information about the data \mathbf{y} , using the prediction-observation pairs or joint distribution (\mathbf{p}, \mathbf{y}) (Fig. 5.1b,c; Murphy and Winkler 1987). Different components of SDM performance can be extracted from the joint distribution. The number of presences and absences over the dataset as a whole defines the *marginal* distribution $\Pr(\mathbf{y})$, which indicates the prevalence or spatially-averaged probability of occurrence $\bar{y} = \Pr(y = 1)$ (Fig. 5.1d; Royle et al. 2012). The marginal distribution $\Pr(\mathbf{p})$ reveals how often each prediction was made (Fig. 5.1e,f; Murphy and Winkler 1987). The

conditional distributions ($\mathbf{p}|\mathbf{y}$) indicate the predictions for occupied cells $\Pr(\mathbf{p}|\mathbf{y} = 1)$ and the predictions for unoccupied cells $\Pr(\mathbf{p}|\mathbf{y} = 0)$ (Fig. 5.1g,f); comparing these distributions allows the *discrimination ability* of the predictions to be assessed (Pearce and Ferrier 2000, Vaughan and Ormerod 2005, Wilks 2011). Discrimination measures the ability to tell presences and absences apart based on model predictions. In a discriminating model, higher prediction values are associated with presences, and lower values with absences: the distributions of $\Pr(\mathbf{p}|\mathbf{y} = 1)$ and $\Pr(\mathbf{p}|\mathbf{y} = 0)$ are easily separated (Fig. 5.1g,f). Crucially, when assessing discrimination ability, the absolute values of the predictions are unimportant; the model needs only to rank presences higher than absences.

Discrimination can be contrasted with *calibration*, which measures the numerical match between the predicted and observed probabilities of occurrence. For example, if a species is present in 60 out of 100 cells in a given environment, then a perfectly-calibrated model will predict a probability of presence of 60% in that environment (Murphy and Winkler 1987, Vaughan and Ormerod 2005). It follows that a discriminating model is not necessarily well-calibrated, because the value of the predictions may be misleading despite their rank order being largely correct (Pearce and Ferrier 2000). We classify performance metrics by whether they measure calibration or discrimination ability (Fig. 5.1, b,c vs. g,h). We show later that transitioning from a calibration to a discrimination metric involves mathematically factoring out prevalence.

The second axis along which we divide SDM metrics is according to whether they are restricted to binary predictions (Fig. 5.1, b,e,g vs. c,f,h). In practice, binary predictions $\hat{\mathbf{p}}$ are usually obtained by applying a threshold τ to the probabilities of presence \mathbf{p} :

$$\hat{p}_i = \begin{cases} 1, & \text{if } p_i \geq \tau_i \\ 0, & \text{otherwise} \end{cases}$$

...where i indexes the cell. Given binary predictions $\hat{\mathbf{p}}$ and observations \mathbf{y} , a confusion matrix (contingency table) can be assembled (Fig. 5.1c), from which “threshold-dependent” metrics are calculated (Liu et al. 2005, Peterson et al. 2011). We show later that confusion matrices can be

calculated directly from continuous predictions \mathbf{p} without applying a threshold transformation; consequently, we henceforth refer to “threshold-dependent” metrics as *binary* metrics, and “threshold-independent” metrics as *continuous* metrics. In essence, binary metrics incorporate a confusion matrix, whereas continuous metrics do not.

Previous studies have assumed that binary metrics measure discrimination ability (Pearce and Ferrier 2000, Vaughan and Ormerod 2005, Liu et al. 2011) or have found them difficult to reconcile with the concepts of calibration and discrimination (Peterson et al. 2011). However, we show that binary metrics share the same conceptual foundation as continuous metrics, and can measure both calibration and discrimination. The confusion matrix represents the joint distribution of prediction-observations pairs $(\hat{\mathbf{p}}, \mathbf{y})$ (Fig. 5.1c). The prevalence \bar{y} remains the same (the data are unchanged), but the predictions $\hat{\mathbf{p}}$ are now either one or zero. As with continuous predictions, the conditional distributions $\Pr(\hat{\mathbf{p}}|\mathbf{y})$ can be calculated, allowing discrimination ability to be assessed (Fig. 5.1h). For any given observation, a single binary prediction \hat{p}_i will always be perfectly calibrated ($\hat{p}_i = y_i$; cells a and d of the confusion matrix) or entirely mis-calibrated ($|\hat{p}_i - y_i| = 1$; cells b and c of the confusion matrix) (Vaughan and Ormerod 2005). However, the overall calibration of binary predictions may be measured as the match between predicted proportion of occupied cells $\Pr(\hat{\mathbf{p}} = 1)$ and the observed proportion of occupied cells $\Pr(\mathbf{y} = 1)$ (i.e. the prevalence \bar{y}). Consequently, two binary models may be equally effective at separating presences and absences (have equal discrimination ability), yet differ in how well they predict the species’ frequency of occurrence (have different calibration). This distinction between discrimination and calibration in binary metrics is emphasised with an example later in this paper (see “Discrimination and the importance of prevalence”).

5.3.2. Literature review

To assess current trends in SDM performance assessment, we systematically reviewed 100 SDM studies that employed single-number measures of performance (Appendix 5A.1). We classified each

performance metric used into one of the four categories identified by our framework. The most common metrics are categorised in Table 5.2, and definitions and formulae for specific metrics are given in Appendix 5A.2.

Across all studies, continuous discrimination metrics were more widely used than calibration metrics (Fig. 5.2a). Continuous discrimination metrics were by far the most widely-employed type due to the widespread application of the Area Under the Curve (AUC; Appendix 5A.2; see also Yackulic et al. 2012), but continuous calibration metrics were less frequently employed than either type of binary metric (Fig. 5.2a). When we examined whether the type of performance metric employed depended on the purpose of the application, we found the importance of explanatory variables was most commonly assessed using calibration metrics, but that binary and continuous discrimination metrics were most commonly used to select the best models for prediction and quantify predictive performance (Fig. 5.2b). However, in the following sections, we highlight the advantages of using continuous calibration metrics more frequently than at present, in all of the above applications.

5.4. Discrimination and the importance of prevalence

In ecological studies there has been virtually universal agreement that metrics of SDM performance should remain unaffected by changes in prevalence \bar{y} (Pearce and Ferrier 2000, Vaughan and Ormerod 2005, Allouche et al. 2006), and metrics such as AUC, the True Skill Statistic (TSS), Sensitivity and Specificity (Appendix 5A.2) have been recommended because of their insensitivity to prevalence (McPherson et al. 2004, Allouche et al. 2006, Lobo et al. 2008). However, here we show that factoring out prevalence from SDM performance inevitably precludes assessment of model calibration, meaning that only discrimination ability can be measured.

Conceptually, the consequences of mathematically factoring out for prevalence $\Pr(\mathbf{y} = 1)$ can be illustrated using Murphy and Winkler's *likelihood-base rate factorisation* (1987):

$$\Pr(\mathbf{p}, \mathbf{y}) = \Pr(\mathbf{p}|\mathbf{y}) \Pr(\mathbf{y})$$

This equation shows that factoring out prevalence $\Pr(\mathbf{y} = 1)$ from the joint distribution $\Pr(\mathbf{p}, \mathbf{y})$ leaves the conditional distributions $\Pr(\mathbf{p}|\mathbf{y})$. These conditional distributions indicate the predictions given for cells that contained presences $\Pr(\mathbf{p}|\mathbf{y} = 1)$ and for cells that contained absences $\Pr(\mathbf{p}|\mathbf{y} = 0)$, and are used to calculate discrimination ability (Fig. 5.1g; Murphy and Winkler 1987, Pearce and Ferrier 2000, Wilks 2011). However, the likelihood-base rate factorisation also shows that once prevalence is factored out, the joint distribution $\Pr(\mathbf{p}, \mathbf{y})$ cannot be recovered; the data \mathbf{y} no longer indicate absolute occurrence probabilities, but only relative occurrence probabilities, so the numerical match between \mathbf{p} and \mathbf{y} (calibration; Fig. 5.1b) cannot be assessed.

The importance of prevalence in model calibration is illustrated by the following example. Figure 5.3 displays three different predictive models for an observed dataset; each model is described by a logistic equation with a different intercept value, which results in different prevalence predictions (Fig. 5.3a; Royle et al. 2012). The model with intermediate prevalence is the best-calibrated of the three models: predicted and observed occurrence probabilities are tightly aligned (Fig. 5.3b). However, if prevalence is factored out, all models place the data in the same rank order (all the functions are monotonic in x), and have the same discrimination ability (Fig. 5.3c). Consequently, a prevalence-independent metric would assign all three models the same performance value (e.g. here, AUC=0.76), despite evident differences in calibration.

Our conceptual framework can be used to demonstrate the effects of factoring out prevalence from binary performance metrics. The confusion matrix $\Pr(\hat{\mathbf{p}}, \mathbf{y})$ is also subject to the likelihood-base rate factorisation:

$$\Pr(\hat{\mathbf{p}}, \mathbf{y}) = \Pr(\hat{\mathbf{p}}|\mathbf{y}) \Pr(\mathbf{y})$$

The conditional distributions $\Pr(\hat{\mathbf{p}}|\mathbf{y})$ are widely used to assess SDM performance through *sensitivity* $\Pr(\hat{\mathbf{p}} = 1|\mathbf{y} = 1)$, which measures the chance of making a presence prediction given that the species was present (left-most bar, Fig. 5.1h), and *specificity* $\Pr(\hat{\mathbf{p}} = 0|\mathbf{y} = 0)$, which measures the chance of making an absence prediction given that the species was absent (right-most bar, Fig.

5.1h; Appendix 5A.2). Another widely-used binary metric, the True Skill Statistic (TSS), is calculated from sensitivity and specificity (Appendix 5A.2; Allouche et al. 2006). Because sensitivity, specificity, and TSS are all based on $\Pr(\hat{\mathbf{p}}|\mathbf{y})$, they are unaffected by prevalence (the relative frequencies of \mathbf{y} are factored out). Thus, under our conceptual framework, it is expected that prevalence-independent binary metrics assess the same aspects of model performance as continuous prevalence-independent metrics such as AUC; we confirm this expectation by proving that $TSS = 2(AUC - 0.5)$ when predictions are binary (Appendix 5A.3).

We use an example to show that knowledge of prevalence is required to assess calibration using binary metrics. Consider a set of binary predictions $\hat{\mathbf{p}}$ that always correctly predict an absence when the species is absent (specificity=1), but have a 40% chance of mistakenly predicting an absence when the species is present (sensitivity=0.6). The probability of a correct prediction depends on whether the species is present or absent in each cell: if it is absent, a correct prediction is certain, but if it is present, a mistake is likely. Consequently, the more common the species is across the landscape (the higher the prevalence), the higher the probability that any given cell will contain a presence, and the less likely it is that any given prediction will be correct (Fig. 5.4a). Calibration - the match between the predicted and observed proportion of presences in the dataset - decreases with prevalence (Fig. 5.4b), but sensitivity, specificity, and TSS scores remain constant. Failure to consider prevalence in this scenario is an example of a common statistical misconception known as the *base rate fallacy* (Gigerenzer 2003, Bolker 2008).

Previous studies have argued that prevalence-dependent metrics should be avoided because their values vary systematically with prevalence (McPherson et al. 2004, Allouche et al. 2006), making performance difficult to compare across datasets (McPherson et al. 2004, Vaughan and Ormerod 2005). However, in Appendix 5A.4, we show that this conclusion rests on the unjustified assumption that calibration will not change with prevalence, and in our discussion, we argue that performance metrics are not easily comparable among datasets, whether or not they factor out prevalence. Thus,

the key conclusion from this section is that prevalence-independent metrics cannot measure model calibration, meaning that prevalence must be considered when SDMs are used to make quantitative predictions such as occupancy patterns.

5.5. The disadvantages of “threshold-dependent” metrics

Having demonstrated that prevalence distinguishes discrimination and calibration metrics (our first classification axis, moving down Fig. 5.1 and Table 5.2), we now compare continuous and binary performance metrics (our second classification axis, moving across Fig. 5.1 and Table 5.2). The need to select a threshold has meant that binary and continuous metrics have typically been treated as separate and incomparable ways of measuring SDM performance (Liu et al. 2011, Peterson et al. 2011b). Here, we use a new method to show that the confusion matrix can be calculated directly from probabilistic predictions, allowing binary performance metrics to be used without applying a threshold transformation.

The method involves re-writing each cell of the confusion matrix (Table 5.2a) as a probabilistic function of the continuous predictions \mathbf{p} and observations \mathbf{y} (Table 5.2b). This probabilistic confusion matrix can be used to calculate any binary metric for a vector of predictions $0 \leq \mathbf{p} \leq 1$. If predictions are binary ($\mathbf{p} = \hat{\mathbf{p}}$), the usual (whole-number) confusion matrix results; if predictions are probabilistic ($\mathbf{p} \neq \hat{\mathbf{p}}$), each prediction-observation pair is “split” between two cells of the confusion matrix, with a presence predicted with probability p_i , and absence predicted with probability $1 - p_i$.

The probabilistic confusion matrix brings several advantages. First, it makes the threshold selection process redundant. Second, it further strengthens the conceptual unification between binary and continuous metrics developed in this paper. For example, it can be used to show that the mean absolute prediction error (a continuous metric) equals one minus the overall accuracy (a binary calibration metric), despite the fact that these two metrics were previously considered to be distinct

and incomparable measure of performance (Liu et al. 2011; Appendix 5A.3). Third, it enables a direct comparison of binary and continuous metrics, using them to estimate the same parameters.

We use the probabilistic confusion matrix to demonstrate analytically that any metric that can be formulated as a confusion matrix is always maximised by binary (rather than probabilistic) predictions (Appendix 5A.3). This means that even if the true probability of species presence ψ_i is known to be between 0 and 1, binary metrics such as Cohen's Kappa or TSS will be maximised by predictions of 0 or 1, such that it necessary to select the wrong parameters and make false predictions ($p_i \neq \psi_i$) to achieve high performance. In the statistical literature, such measures are known as *improper* scoring rules (Roulston and Smith 2002, Wilks 2011). In short, we have shown that binary metrics can be used to evaluate the performance of probabilistic predictions, but that they always favour binary predictions.

Binary predictions carry two drawbacks. First, binary predictions will have reduced discriminatory ability when there are more than two different underlying probabilities of occurrence, because gradients of suitability cannot be accommodated within two ranks of predictions ($\hat{p} \in 0,1$). Second, binary predictions will be poorly calibrated when underlying occurrence probabilities lie between 0 or 1; as such, the proportion of occupied cells in each environment will be over- or under-estimated, accentuating or masking differences between environments, and predictions will be made with false certainty, because the species will be predicted to be either always present or always absent in each environment (Clark 2007). Thus, models selected using binary performance metrics will often have both reduced discrimination and calibration; and, conversely, poorly discriminating, poorly calibrated models may achieve misleadingly high performance scores.

5.6. Simulated conservation example

We use a simple simulation to illustrate the advantages of continuous calibration metrics over continuous discrimination and binary calibration metrics in an applied context. We imagine a species

whose true probability of presence ψ_i in cell i can be described by a logistic function of a single environmental covariate x :

$$\text{logit}(\psi_i) = \alpha + \beta x_i$$

We chose the “true” parameters $\alpha = 0$ and $\beta = 0.25$, and simulated a training distribution of 100 grid cells based on a landscape with varying values of x (see Appendix 5A.5). We then calculated the performance of different parameter combinations and selected the best model using three different performance metrics: log-likelihood (a continuous calibration metric; hereafter “likelihood”), AUC (a continuous discrimination metric), and kappa (a binary metric; Table 5.2; see Appendix 5A.2 for performance metric formulae).

We used the same values of α and β to simulate a second occupancy distribution in a new geographical area. Predictions from the three best models were then used to design a conservation strategy for this new area, without knowledge of which cells were occupied. Each cell could be either be protected at a cost or left unprotected at no cost. Populations present in protected cells survived, and populations in unprotected cells became extinct. Predictions were used to calculate the optimal conservation strategy under three cost scenarios (Appendix 5A.5). In scenario 1, all cells had equal costs, and conservation resources were available to protect all occupied cells ($n=47$). In scenario 2, all cells had equal costs, but resources were only sufficient to protect a subset of occupied cells ($n=10$). In scenario 3, different cells had different costs, such that the number of cells that could be protected depended on which cells were selected for protection; here, the “conservation value” of each cell was a function of both its predicted probability of containing the species and its protection cost relative to other cells.

Maximum likelihood gave a reasonable estimate of the underlying parameters (Fig. 5.5a). AUC correctly identified a positive relationship between species presence y and the environmental covariate x (models with positive β received higher scores than models with negative β , Fig. 5.5c). However, all models with positive β had the same rank order of predictions and thus the same AUC

score (AUC=0.77; Fig. 5.5c), such that a best parameter set was not identifiable (Fig. 5.5f). Kappa selected incorrect values of α and β , predicting that the species would switch from total absence to constant presence at an x value of around -2 (Fig. 5.5b, e; note that predictions are restricted from being truly binary by the logistic function).

When conservation resources matched the number of occupied cells, the three performance metrics selected models that resulted in equally successful conservation strategies (Fig. 5.5j). AUC correctly ranked sites in terms of suitability (valuing cells with high x above cells with low x), allowing effective prioritisation of cells, but quantitative occupancy predictions could not be made without identifiable parameter estimates, thereby precluding estimation of the number of populations saved (Fig. 5.5j). The Kappa-selected model conserved as many populations as the log-likelihood and AUC models, because resources were sufficient to protect all predicted populations, such that there was no need to discriminate among cells with predicted presences (Fig. 5.5j). However, the poor calibration of the Kappa-selected model resulted in overestimation of expected probabilities of presence, such that the number of populations conserved was overestimated and the uncertainty in the expected number of populations saved was misleadingly low. Under the likelihood-based strategy, in contrast, the expected number of populations saved closely matched the actual number saved, and the actual number saved lay within estimated uncertainty bounds (Fig. 5.5j).

When conservation resources were insufficient to protect all occupied cells, Kappa lacked the ability to correctly prioritise sites, because all presences were ranked equally ($p = 1$) despite differences in suitability. Models selected by maximum likelihood and AUC continued to perform well under this scenario, because the relative suitability of cells remained the same. However, when the cost of protection differed among sites (Fig. 5.5i), the scenario changed from a simple ranking problem to a quantitative task, requiring occupancy predictions to calculate optimal resource allocation efficiency. Because a best parameter set could not be identified using AUC, quantitative predictions could not be supplied, precluding the design of a conservation strategy. In contrast, both likelihood and Kappa

were able to assess model calibration and devise conservation strategies under this quantitative scenario.

Despite its simplicity, this example demonstrates the importance of both discrimination and calibration in SDM assessment. Measuring discrimination ability was sufficient to devise a rank-based conservation strategy, but calibration assessment was necessary for estimates of conservation success. Choosing predictive models using a binary performance metric instead of a continuous metric reduced the number of populations saved (due to poor discrimination ability) and produced conservation success estimates that were misleadingly high and misleadingly certain (due to poor calibration).

5.7. Discussion and recommendations

Assessing model performance is a necessary step towards useful and predictive species distribution models (Guisan and Zimmermann 2000, Peterson et al. 2011). In this paper, we developed a unified conceptual framework for classifying performance metrics and identifying the circumstances under which they should be employed (Elith and Leathwick 2009). We applied this framework to address two core issues relating to measurement of SDM performance.

First, we demonstrated that prevalence constitutes a crucial component of the goodness-of-fit between model and data. This conclusion is contrary to prevailing views in the SDM literature, in which prevalence-independence has been regarded as a desirable property of performance metrics (Vaughan and Ormerod 2005, Allouche et al. 2006, Lobo et al. 2008). However, we showed that factoring out prevalence results in a metric that only measures discrimination (the ability to rank presences above absences), and is unable to measure calibration (the ability to correctly predict the number of occupied cells). Further, we demonstrated that the inability of prevalence-independent metrics to assess calibration applies both to continuous metrics such as AUC and binary metrics such as TSS, sensitivity, and specificity.

Second, we united binary (“threshold-dependent”) and continuous (“threshold-independent”) metrics, showing that binary metrics can be calculated directly from probabilistic predictions, without applying threshold transformations. By removing the need to select a threshold, we showed that binary metrics favour binary predictions ($p = 0,1$) over probabilistic predictions ($0 \leq p \leq 1$), even when the true, underlying probability of occurrence is known to lie between 0 and 1. Consequently, using binary metrics to compare SDMs will often result in predictions with reduced discriminatory power, poorly-calibrated expectations, and misleading uncertainty.

The choice of performance metric can have important practical consequences, as illustrated by our simple simulation in which we showed that using a more appropriate performance metric (specifically, log-likelihood) in SDM model selection ultimately increased the efficiency of a biodiversity conservation application. Combined with a literature review of 100 SDM studies (Fig. 5.2), our findings suggest that overly-frequent use of discrimination and binary performance metrics may be leading to substantial information loss during the evaluation of SDM predictions, reducing both their discrimination and calibration. We therefore suggest two practical steps which would help to improve assessment of SDM performance.

Our first recommendation is that when SDM predictions are applied quantitatively, prevalence-dependent performance metrics should be employed. Predictions of absolute probabilities of occurrence - such as estimates of range size or local extinction risk - should be accompanied by an assessment of numerical accuracy (calibration), but prevalence-independent performance metrics such as AUC are not suitable for this purpose, because they measure only the ability of predictions to rank presences above absences (discrimination ability; Pearce and Ferrier 2000, Vaughan and Ormerod 2005). Nonetheless, our literature review showed that of those SDM studies that employed model predictions quantitatively, 64% assessed solely discrimination ability, without considering calibration. We therefore encourage the wider uptake of calibration performance metrics in SDM.

Our second recommendation is to use continuous (threshold-independent) instead of binary (threshold-dependent) metrics wherever possible. Given the concerted effort to develop sophisticated and predictive SDMs (Elith and Leathwick 2009, Peterson et al. 2011), there seems little reason to assess performance using binary metrics that will frequently reduce the discrimination and calibration of predictions. The principal arguments in favour of binary metrics are that (1) many SDM procedures produce binary predictions, and (2) binary predictions are necessary for conservation planning (Allouche et al. 2006, Lobo et al. 2008). However, of the 100 of the studies we reviewed, only one study was restricted to binary predictions by software, whilst only two studies required binary predictions for use with conservation algorithms. Moreover, probabilistic predictions facilitate more efficient conservation strategies than binary predictions (Moilanen and Cabeza 2005). We thus urge that continuous metrics be used in place of binary metrics wherever possible.

We feel that likelihood functions offer excellent options for assessing the calibration of SDMs, in view of the strong body of statistical theory on their application and their familiarity to ecologists (Clark 2007, Bolker 2008). In Appendix 5A.6, we show that given a set of predictions \mathbf{p} and a test dataset \mathbf{y} , it is straightforward to calculate log-likelihoods, information criteria such as Akaike's information criterion, and likelihood-based R-squared values (see also Nakagawa and Schielzeth 2012). In a recent simulation study (Warren and Seifert 2011), AIC was found to be superior to AUC at uncovering the relationships underlying species distributions - a result we interpret as further evidence for the importance of measuring calibration (AIC measures calibration, but AUC does not).

It is, however, essential to be aware of the limitations of performance metrics, and based on our literature review, two important issues are worthy of note. First, SDM performance is conditional on the test dataset, irrespective of which type of metric (discrimination or calibration) is used (see also Yackulic et al. 2012). Consequently, the absolute values of performance cannot easily be compared among datasets, as occurred in 31% of studies we reviewed. Likelihood metrics such as AIC are

instructive in this regard because only their relative values are compared, based on a single dataset; their absolute values are not meaningful (Bolker 2008, Nakagawa and Schielzeth 2012). The wish to compare model performance among species or regions has fuelled a search for metrics that are independent of data properties; yet, there are often trade-offs between factoring out data properties and preserving the information required to test predictions, as we have shown for prevalence. Performance metrics are thus best employed to compare different predictions based on the same data: there is no universal grading for SDM performance.

Second, graphical methods can convey more information about performance than single numbers (Wilks 2011, Yackulic et al. 2012). For example, calibration plots such as those in Figures 5.1b and 5.3b can indicate overfitting or bias (see Pearce & Ferrier 2000, Wilks 2011), yet were used in just 2% of the studies we surveyed. Moreover, whilst geographical maps of predictions are widely employed (75% of studies), plots of predictions against data in environmental space (Fig. 5.1a, Fig. 5.3a, Fig. 5.5d-f) are rarely included (6% of studies), despite being potentially more informative about both model fit and the biological explanations behind species' responses to environmental variables (Yackulic et al. 2012). Finally, providing confidence intervals on predictions (including on predictive maps) can allow the reliability of predictions to be gauged far more effectively than when only the mean prediction is provided (Clark 2007, Bolker 2008). These techniques, coupled with the wider application of continuous calibration metrics, will lead to improved understanding and prediction from species distribution models.

5.8. References

- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223-1232.
- Beale, C. M. and J. J. Lennon. 2012. Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**:247-258.

Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **105**:14908-14912.

Bean, W. T., R. Stafford, and J. S. Brashares. 2011. The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. *Ecography* **35**:250-258.

Bolker, B. M. 2008. *Ecological models and data in R*. Princeton University Press, Princeton, N.J.

Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer, London.

Clark, J. S. 2007. *Models for ecological data: an introduction*. Princeton University Press, Oxford.

Elith, J. and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677-697.

Foody, G. M. 2011. Impacts of imperfect reference data on the apparent accuracy of species presence–absence models and their predictions. *Global Ecology and Biogeography* **20**:498-508.

Gigerenzer, G. 2003. *Reckoning with risk: learning to live with uncertainty*. Penguin, London.

Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147-186.

Hijmans, R. J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* **93**:679-688.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* **199**:142-152.

Kunin, W. E. 1998. Extrapolating species abundance across spatial scales. *Science* **281**:1513-1515.

Liu, C., M. White, and G. Newell. 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography* **34**:232-243.

Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385-393.

Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* **17**:145-151.

McFadden, D. 1973. Conditional Logit Analysis of Qualitative Choice Behavior. Pages 105-142 in P. Zarembka, editor. *Frontiers in Econometrics*. Academic Press, New York.

McPherson, J., W. Jetz, and D. J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology* **41**:811-823.

Moilanen, A. and M. Cabeza. 2005. Variance and uncertainty in the expected number of occurrences in reserve selection. *Conservation Biology* **19**:1663-1667.

Murphy, A. and R. Winkler. 1987. A general framework for forecast verification. *Monthly Weather Review* **115**:1330-1338.

Nakagawa, S. and H. Schielzeth. 2012. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*: Early View.

Nenzén, H. and M. Araújo. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**:3346-3354.

Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**:225-245.

Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. *Ecological niches and geographic distributions*. Princeton University Press, Oxford.

Phillips, S. J. and J. Elith. 2010. POC plots: calibrating species distribution models with presence-only data. *Ecology* **91**:2476-2484.

R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Roulston, M. S. and L. A. Smith. 2002. Evaluating probabilistic forecasts using information theory. *Monthly Weather Review* **130**:1653-1660.

Royle, J. A., R. B. Chandler, C. Yackulic, and J. D. Nichols. 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution* **3**:545-554.

UCLA. 2012. FAQ: What are pseudo R-squareds?

Vaughan, I. and S. Ormerod. 2005. The continuing challenges of testing species distribution models. *Journal of Applied Ecology* **42**:720-730.

Warren, D. L. and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* **21**:335-342.

Wilks, D. S. 2011. *Statistical methods in the atmospheric sciences*. 3rd edition. Elsevier/Academic Press, London.

Yackulic, C. B., R. Chandler, E. F. Zipkin, J. A. Royle, J. D. Nichols, E. H. Campbell Grant, and S. Veran. 2012. Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution*: Early View.

Symbol	Description
i	Index indicating grid cell (location)
n	Number of cells in dataset
\mathbf{x}	Vector of values of an environmental variable determining species presence
\mathbf{p}	Vector of model-predicted probabilities of presence
\mathbf{y}	Binary vector indicating the observed presence (1) or absence (0) of species
\bar{p}	Mean predicted probability of presence for dataset
\bar{y}	Prevalence (mean probability of presence in dataset)
τ	Threshold for conversion of continuous predictions into binary predictions
$\hat{\mathbf{p}}$	Vector of binary predictions of species presence (1) or absence (0)
a	Number of presences correctly predicted as present
b	Number of absences incorrectly predicted as present
c	Number of presences incorrectly predicted as absent
d	Number of absences correctly predicted as absent
$\boldsymbol{\psi}$	Vector of “true” underlying probability of presence values used to simulate data in the conservation scenario

Table 5.1: Glossary of notation used in this paper.

	Continuous	Binary
Calibration	Mean Squared Error (MSE) Root Mean Squared Error (RMSE) Likelihood or Deviance Akaike's Information Criterion (AIC) Bayesian Information Criterion (BIC) R-squared (standard or likelihood-based)	Overall accuracy Cohen's Kappa
Discrimination	Area Under the Curve (AUC) Pearson's correlation Spearman's correlation	Sensitivity Specificity True Skill Statistic (TSS)

Table 5.2: Classification scheme for performance metrics with examples. See Appendix 5A.2 for definitions of specific performance metrics.

(a) Traditional confusion matrix		Observed (\mathbf{y})		Mean prediction $= \frac{a+b}{n}$ $n = a + b + c + d$
Predicted ($\hat{\mathbf{p}}$)	Present ($\hat{\mathbf{p}} = 1$)	Present ($\mathbf{y} = 1$) True presence (a)	Absent ($\mathbf{y} = 0$) False presence (b)	
		Absent ($\hat{\mathbf{p}} = 0$)	False absence (c)	True absence (d)
		Prevalence = $\frac{a+c}{n}$		

(b) Probabilistic confusion matrix		Observed (\mathbf{y})	
Predicted (\mathbf{p})	Present ($\mathbf{p} = 1$)	Present ($\mathbf{y} = 1$)	Absent ($\mathbf{y} = 0$)
		Absent ($\mathbf{p} = 0$)	$a = \sum_{i=1}^n \Pr(p_i = 1 \cap y_i = 1)$ $= \sum_{i=1}^n p_i y_i$
		$c = \sum_{i=1}^n \Pr(p_i = 0 \cap y_i = 1)$ $= \sum_{i=1}^n (1 - p_i) y_i$	$d = \sum_{i=1}^n \Pr(p_i = 0 \cap y_i = 0)$ $= \sum_{i=1}^n (1 - p_i) (1 - y_i)$

Table 5.3: Traditional (a) and probabilistic (b) confusion matrices. The probabilistic confusion matrix allows “threshold-dependent” metrics to be used with probabilistic predictions (\mathbf{p}), and reverts to the traditional confusion matrix when binary predictions ($\hat{\mathbf{p}}$) are used. The probabilistic confusion matrix removes the need to select thresholds and unifies continuous and binary performance metrics.

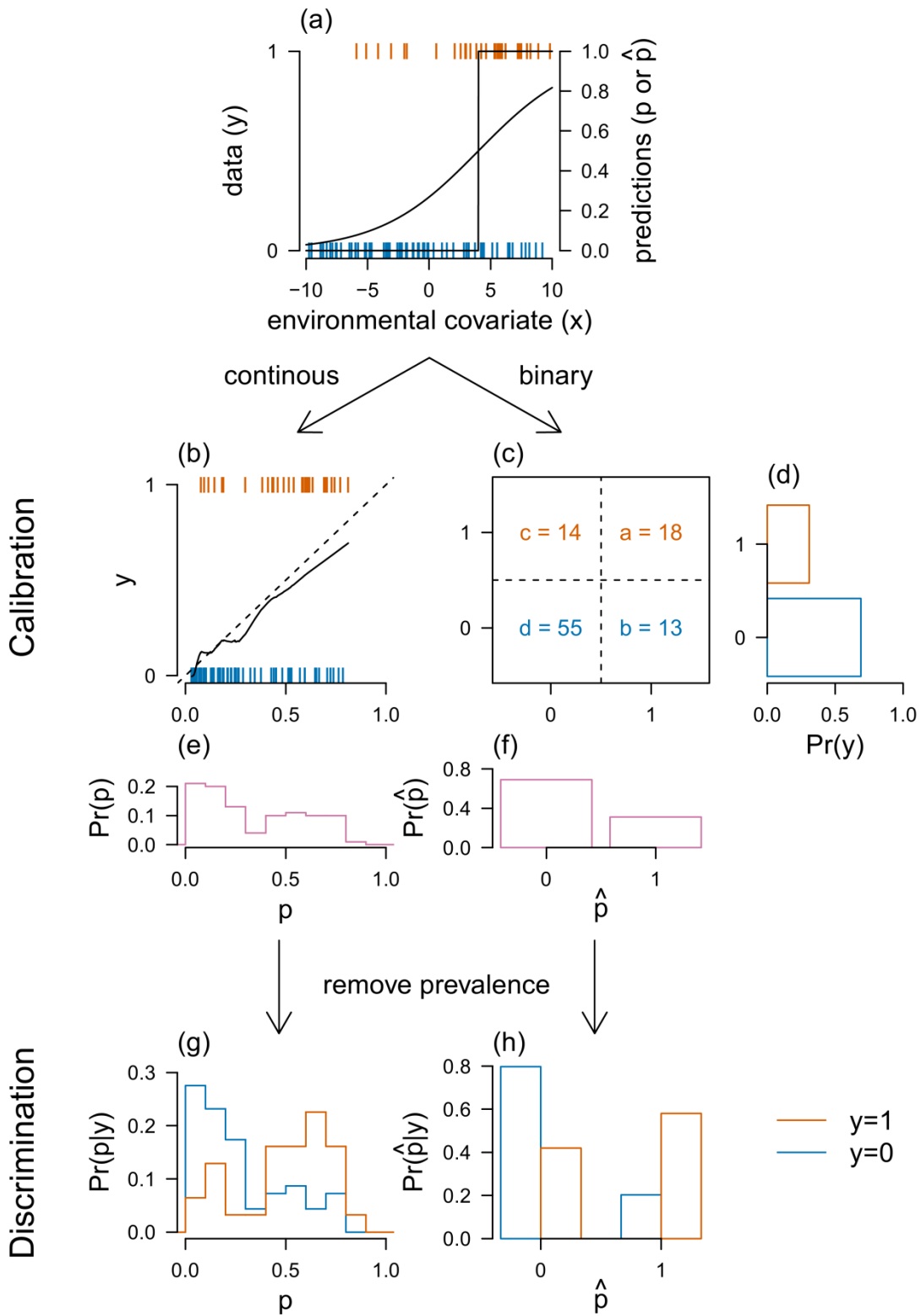


Figure 5.1: A conceptual framework for performance metrics. A dataset y of presences (red) and absences (blue), collected over different environments x , is compared to predicted probabilities of presence p or binary presence-absence predictions \hat{p} (a). The calibration (numerical accuracy) of the

predictions can be assessed using the joint distribution of predictions and observations (b,c; solid line indicates a smoothed relationship between predictions and observations, dotted line indicates a 1:1 relationship representing “perfect” calibration). Marginal distributions can also be calculated showing how commonly each prediction was made (marginal distribution of the predictions: e,f) and how frequently the species was present in the dataset as a whole (marginal distribution of the data, also known as prevalence: d). If prevalence is factored out of the joint distribution, the conditional distributions of predictions for presence and absence observations (g, h) can be compared to assess the discrimination ability of the predictions, but not their calibration.

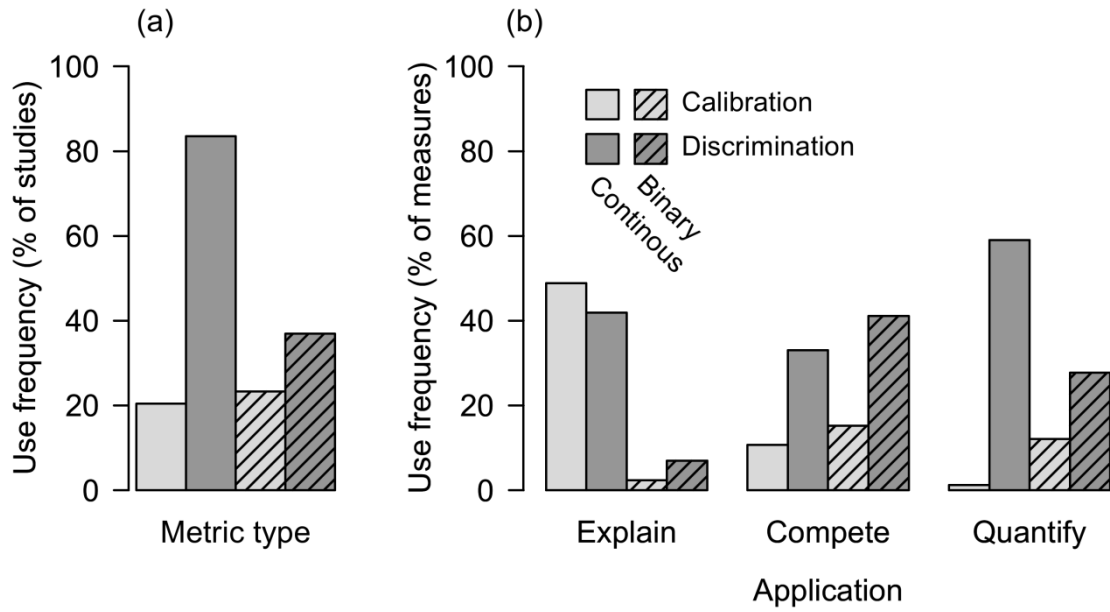


Figure 5.2: Use frequency of different performance metrics based on a literature survey of 100 SDM studies and using classifications derived from the conceptual framework (Figure 5.1, Table 5.2). Panel (a) shows overall frequency of use per study; panel (b) shows which metrics were used most frequently for particular applications (Explain=to test hypotheses on environmental determinants of species presence; Compete=to compete different models to find out which was best for prediction; Quantify=to summarise the performance of a single model; see Appendix 5A.1).

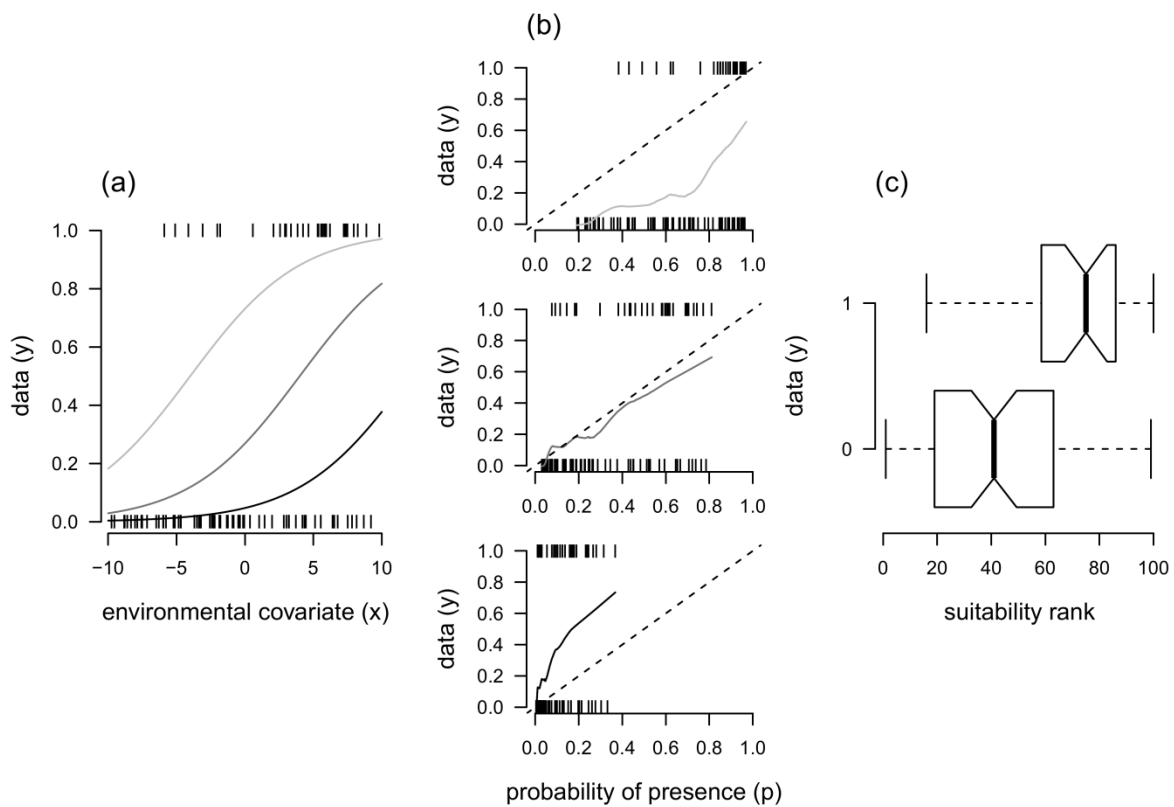


Figure 5.3: Model parameterisation example demonstrating the importance of prevalence for the calibration of continuous predictions. The performance of three models, each with different prevalence predictions (intercept values) is assessed based on a dataset of presences and absences (a). The intermediate grey predictions are well-calibrated because the predicted probabilities of presence are a good match to the observed probabilities of presence, but the light and dark grey predictions are poorly-calibrated and over- and under-predict species prevalence, respectively (b: solid lines represent smoothed relationships between predictions p and observations y ; dotted line represents 1:1 line indicating “perfect” calibration). However, all three models place the observations in the same rank order of occurrence probabilities, and consequently have the same discrimination ability (c); their performance is equivalent once prevalence has been factored out.

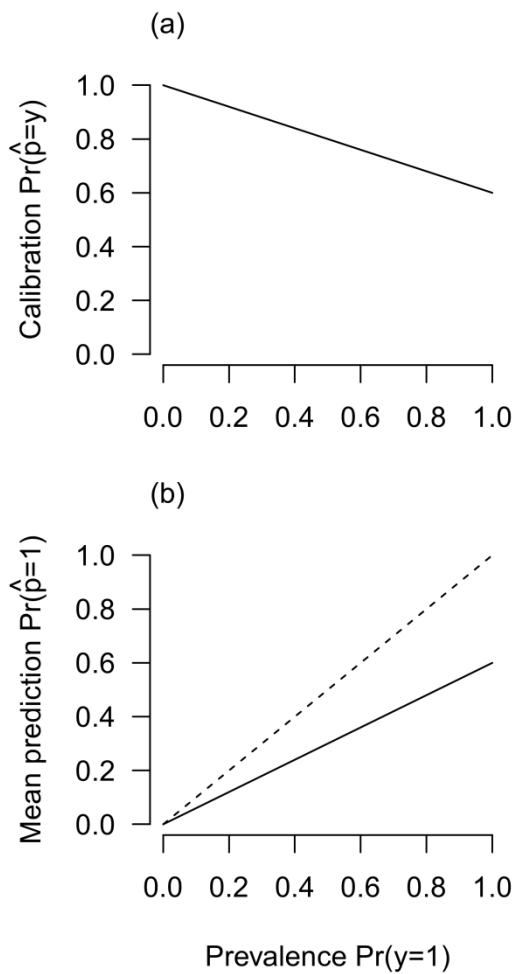


Figure 5.4: Model prediction example demonstrating the importance of prevalence \bar{y} in the calibration of binary predictions \hat{p} . The predictions in this example have constant discrimination ability, such that absences are always correctly predicted as absent (specificity=1), and presences are mistakenly predicted as absences 40% of the time (sensitivity=0.6; TSS=0.6). Panel (a) shows how the calibration of the predictions, measured as overall accuracy, changes with prevalence; (b) shows how the average predicted probability of presence $\bar{\hat{p}}$ (solid line) relates to prevalence \bar{y} (dotted line). At low prevalence, most observations are absences, and the model is well-calibrated: the predicted prevalence is a good match to the observed prevalence. However, as prevalence increases, presences become more common and the chance of making a false presence prediction increases, leading to a decrease in calibration.

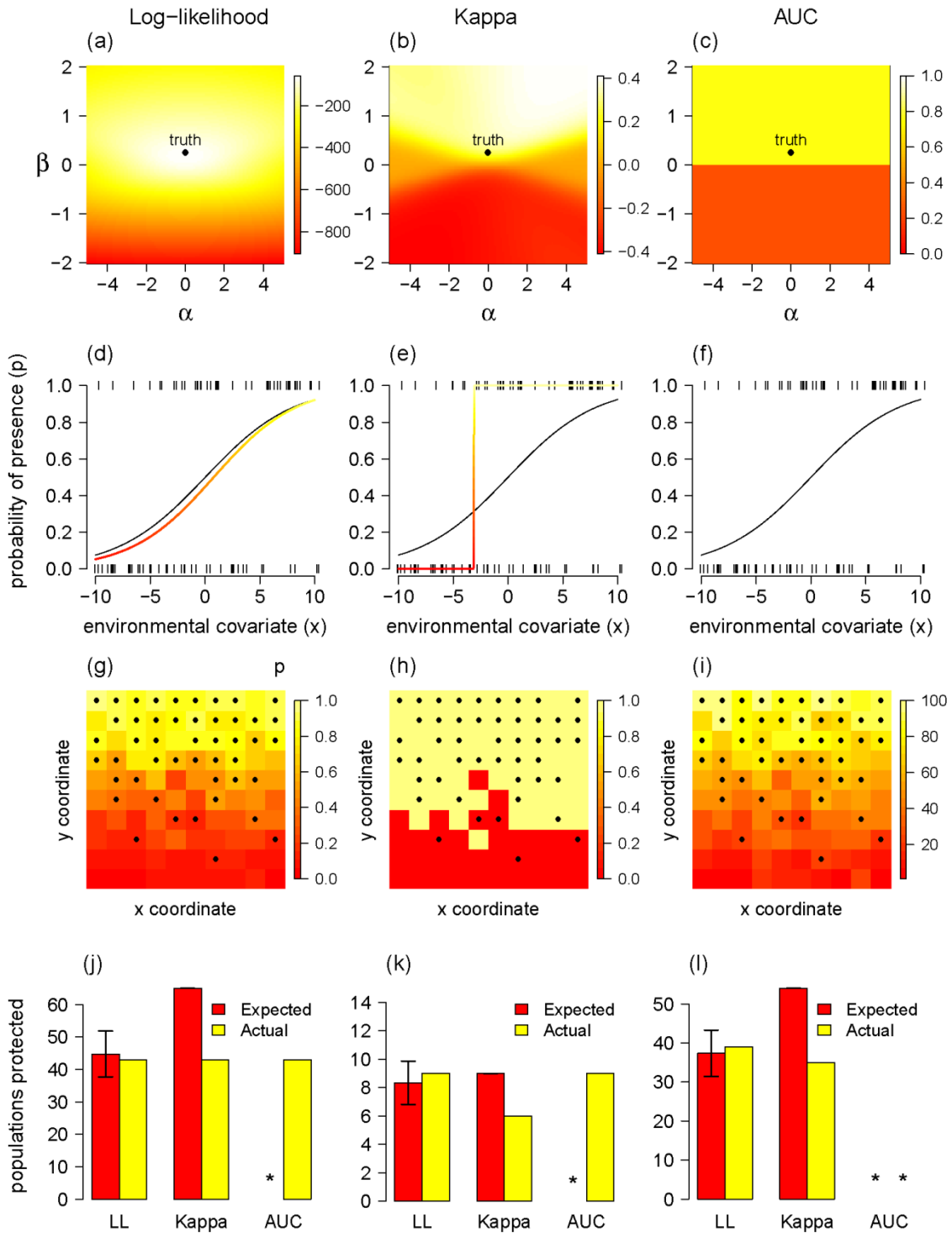


Figure 5.5: Application of performance metrics to a simple conservation scenario. Predictive models were parameterised on a training dataset using three performance metrics: log-likelihood, Kappa and the Area Under the Curve (AUC). Panels a-c show performance scores of different parameter sets (values of α and β) based on each metric, and d-f display best-fitting models. Panels g-i show the

predictions of each best model when applied to an “unseen” geographic distribution, simulated from the same parameter values as the training dataset (simulated presences shown as dots; cell colours represent either probability of presence estimates [g,h] or rank suitability scores [i]). Panels j-l show the estimated (red bars) and actual (yellow bars) number of populations saved using conservation strategies designed by each of the three best models, under three different scenarios: equal cell costs with conservation funds sufficient to protect all populations (j); equal cell costs with conservation funds insufficient to protect all populations (k); and different cell costs (l). Error bars indicate 95% confidence intervals around predicted number of populations saved; asterisks indicate that the success of the strategy could not be estimated (expected bars) or implemented (actual bars).

Appendix to Chapter 5

5A.1. Literature review methods

We conducted an ISI web of knowledge search for papers published between January 2011 and May 2012. We searched using the keywords "*species distribution model**" in ecology and evolution journals with a 2010 impact factor ≥ 3 . This included the following journals: AM NAT, ANNU REV ECOL EVOL S, BIOL CONSERV, BIOL INVASIONS, BIOL LETTERS, CONSERV BIOL, DIVERS DISTRIB, ECOGRAPHY, ECOL APPL, ECOL LETT, ECOL MONOGR, ECOLOGY, FRONT ECOL ENVIRON, FUNCT ECOL, GLOBAL CHANGE BIOL, GLOBAL ECOL BIOGEOGR, J ANIM ECOL, J APPL ECOL, J BIOGEOGR, J ECOL, LANDSCAPE ECOL, MOL ECOL, OECOLOGIA, OIKOS, P ROY SOC B-BIOL SCI, PLOS BIOL, PLOS ONE, TRENDS ECOL EVOL, WILDLIFE MONOGR.

We only selected papers that reported the results of single-number measures of SDM performance. We only reported measures that tested goodness-of-fit between a predicted and an observed or simulated distribution. Where studies included multiple analyses of different datasets (3 studies), we separately noted down the performance metrics used.

We classified each study by the type of data used in each analysis, according to one of the following categories: presence-absence, presence-pseudoabsence, presence-background, presence-only, abundance (numeric or ordinal categorical), or percentage cover. We excluded presence-only, abundance and percentage cover studies from all subsequent analyses. This left 100 studies and 103 analyses remaining.

For each analysis, we recorded the following:

- The performance metrics used (maximum = 6 per study).
- Whether the study made comparisons of the absolute values of performance metrics among datasets.

- Whether the study used a calibration plot (plot of predicted values on x-axis against observations on y-axis).
- Whether the study presented predictions and/or data in the form of maps.
- Whether the study presented plots of predictions and/or data in environmental space.
- Whether the study subsequently used the tested model for quantitative inference or prediction.

We also categorised the primary application of each performance metric into one of the following groups:

- *Explanation*: used to test hypotheses on environmental determinants of presence/absence.
- *Quantification*: used to summarise the goodness-of-fit of a single model to a dataset.
- *Competition*: used to compare different models (parameter combinations or modelling method) to find out which was best for prediction.

5A.2. Description of performance metrics

5A.2.1. Additional notation

To display formulas for the following performance metrics, it is necessary to introduce notation additional to that in Table 5.1 in the main paper.

Symbol	Description
\mathbf{p}_{y1}	Vector of predictions given for cells that contained presences
\mathbf{p}_{y0}	Vector of predictions given for cells that contained absences
n_{y1}	Number of cells to contain presences
n_{y0}	Number of cells to contain absences
\bar{p}_{y1}	Mean prediction given for cells that were presences
\bar{p}_{y0}	Mean prediction given for cells that were absences
s_p	Standard deviation of all predictions
\mathbf{r}_p	Vector containing ordinal ranks of predictions
\bar{r}_{y1}	Mean rank of predictions given for cells that were presences
\bar{r}_{y0}	Mean rank of predictions given for cells that were absences

Table 5A.1: Additional notation for metric calculation. Primary notation is described in Table 5.1 in the main text.

5A.2.2. Description of performance metrics

Table 5A.2 (see following page) provides descriptions and formulae from the most commonly-used performance metrics identified by our literature review. Figure 5A.1 displays the frequency of use of these performance metrics in the SDM literature. Other performance metrics not encountered in our literature search are reviewed in Liu *et al.* (2011) and Wilks (2011).

5A.2.3. Skill scores

We include here a brief discussion of the concept of *skill*, which is useful both for understanding the mechanics of performance metrics (Tables 5A.2 and 5A.3), and for explaining the findings of simulation studies (5A.4). *Skill scores* are performance metrics that involve a comparison of the performance of the predictions p to the predictions of a null model p_{null} (Wilks 2011). Skill scores place model performance on a scale that lies between 0, in which performance is equal to the null

model, and 1, in which performance is equal to a “perfect” model p_{perf} whose predictions match the observed data y exactly:

$$Skill = \frac{m(p) - m(p_{null})}{m(p_{perf}) - m(p_{null})}$$

Here, m indicates another metric used to calculate the performance of the predictions; this could be any “basic” performance metric (*i.e.* any metric that is not itself a skill score; Table 5A.2). Often, either the mean prediction (\bar{p}) or prevalence of the dataset (\bar{y}) is used as the null model, such that $p_{null} = \bar{p}$ or $p_{null} = \bar{y}$ for all observations. However, the choice of the null model is subjective and others may be used (Beale et al. 2008, Wilks 2011, Beale and Lennon 2012, Hijmans 2012). The skill scores that will be most familiar to ecologists are R-squared (based on variance or likelihood; UCLA 2012), Cohen’s Kappa, and the True Skill Statistic (definitions and formulae given in Table 5A.3).

Although skill scores can give a useful “ball park” indication of how well the model is predicting the data in comparison to the chosen null model, it is important to realise that the absolute value of any skill metric depends on both the choice of null model and the properties of the data. Consequently, using a skill metric does not resolve the issues of comparing performance among datasets (see main text).

Metric Name	Description	Formula	Calibration	Binary
Sensitivity	Proportion of occupied cells correctly predicted to be occupied (true positive rate)	$\frac{a}{a + b}$	No	Yes
Specificity	Proportion of unoccupied cells correctly predicted to be unoccupied (true negative rate)	$\frac{d}{c + d}$	No	Yes
Area under the curve of the receiver operating characteristic (AUC of ROC) Also known as Concordance Index (c-index)	Proportion of presence-absence pairs that are ranked in the correct order	$\frac{\sum_j \sum_k g(p_{y1,k} p_{y0,k})}{n_{y1} n_{y0}}$ $g(p_{y1}, p_{y0}) = \begin{cases} 1, & \text{if } p_{y1} > p_{y0} \\ 0.5, & \text{if } p_{y1} = p_{y0} \\ 0, & \text{otherwise} \end{cases}$	No	No
Point biserial correlation coefficient	Pearson's correlation coefficient between predictions and binary data	$\frac{\bar{p}_{y1} - \bar{p}_{y0}}{s_p} \sqrt{\frac{n_{y1} n_{y0}}{n^2}}$	No	No
Rank biserial correlation coefficient	Spearman's correlation coefficient between predictions and binary data	$\frac{2(\bar{r}_{y1} - \bar{r}_{y0})}{n}$	No	No
Overall accuracy	Proportion of predictions that were correct	$\frac{a + d}{n}$	Yes	Yes
Mean squared error (MSE)	Mean squared difference between the predictions and the observations	$\frac{1}{n} \sum_i (p_i - y_i)^2$	Yes	No
Root mean squared error (RMSE)	Square root transformation of MSE	\sqrt{MSE}	Yes	No
Log-likelihood	Log transformation of the likelihood of observing the data, given the predictions	See "demonstration of likelihood performance metrics", Appendix 5A.6.	Yes	No
Deviance	Mathematically convenient transformation of likelihood		Yes	No
Akaike's information criterion (AIC)	Deviance with model complexity penalty		Yes	No
Bayesian information criterion (BIC)	Deviance with model complexity penalty		Yes	No

Table 5A.2: definitions of common performance metrics; see Table 5A.1 for explanation of notation additional to that in the main paper.

Name	Basic metric	Null model	Calibration	Binary
Cohen's Kappa	Accuracy	Mean prediction \bar{p}	Yes	Yes
True Skill Statistic*	Accuracy	Mean prediction \bar{p} (numerator) Prevalence \bar{y} (denominator)	No	Yes
R-squared	Mean squared error	Mean prediction \bar{p}	Yes	No
McFadden's R-squared	Likelihood	Mean prediction \bar{p}	Yes	No

Table 5A.3: definitions of common skill scores. See Table 5A.2 for definitions of “basic” performance metrics used in the calculation of skill scores. Definitions of other likelihood-based R-squared metrics can be found online (UCLA 2012). *Note that TSS can also be calculated as $TSS = Sensitivity + Specificity - 1$.

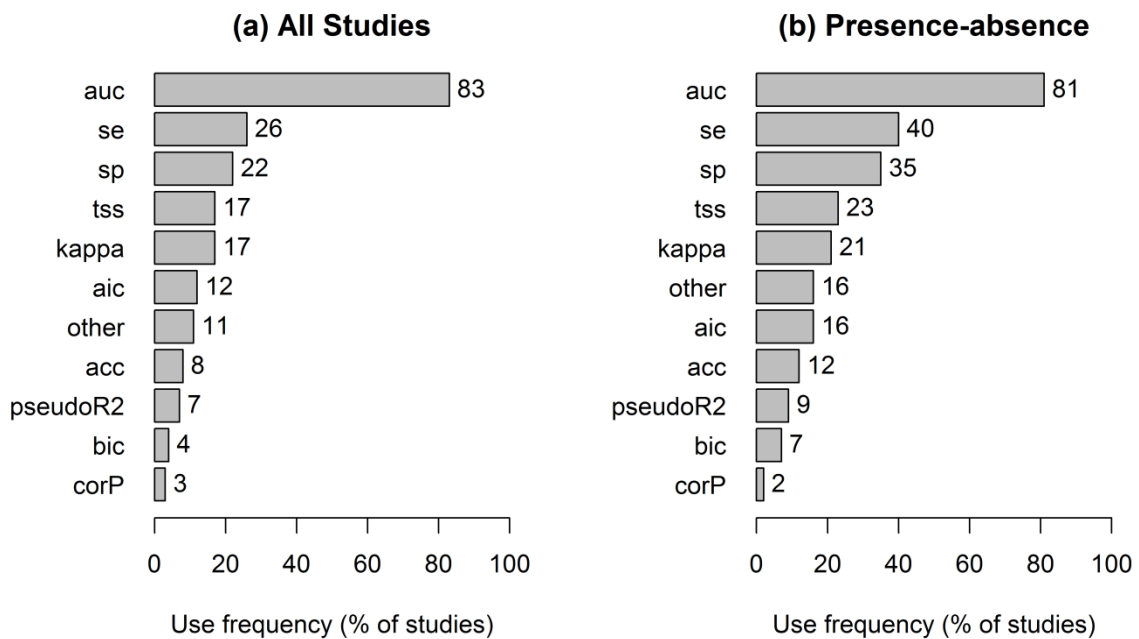


Figure 5A.1: Most frequently used metrics across (a) all studies and (b) evaluations using true presence-absence data. Key to metric names: auc=area under the curve; se=sensitivity; sp=specificity; kappa=Cohen's kappa; aic=Akaike's information criterion; bic=the Bayesian information criterion; acc=overall accuracy; corP=Pearson's correlation (point biserial correlation); pseudoR2=any likelihood-based R^2 ; other=any other metric. To produce this figure, we have grouped metrics that have identical or near-identical mathematical formulae; for example, we have grouped overall

accuracy with mean absolute prediction error, since these two metrics are effectively the same (see Appendix 5A.3). Full descriptions of metrics are given in Tables 5A.1 and 5A.2.

5A.3. Analytical demonstrations

5A.3.1. Proof that AUC is equivalent to TSS for binary models

Assuming that all predictions (and observations) are binary, let:

a = proportion of prediction-observation pairs that were true positives ($\hat{p} = 1, y = 1$)

b = proportion of prediction-observation pairs that were false positives ($\hat{p} = 1, y = 0$)

c = proportion of prediction-observation pairs that were false negatives ($\hat{p} = 0, y = 1$)

d = proportion of prediction-observation pairs that were true negatives ($\hat{p} = 0, y = 0$)

AUC is the proportion of presence-absence pairs that were ranked in the correct order. For each pair, there are three possible ranking outcomes:

1. Presence correctly ranked above absence (frequency ad)
2. Presence ranked equally with absence (frequency $ab + cd$)
3. Absence ranked above presence (frequency cb)

The relative frequency of presence-absence pairs is $(a + c)(b + d)$. Since equal ranks (ties) are “half-right”, receiving a score of 0.5, the frequency of correct ranking (AUC) is therefore:

$$AUC = \frac{ad + \frac{1}{2}(ab + cd)}{(a + c)(b + d)}$$

$$2(AUC - 0.5) = \frac{ad - bc}{(a + c)(b + d)} = TSS$$

5A.3.2. Proof that binary (confusion matrix) performance measures are improper

We consider a single environment in which a species is present with probability ψ . A prediction is made that the species will be present with probability p . We assume that a large number of samples are taken from this distribution, and a measure of performance $f(p, \psi)$ calculated.

All confusion matrix performance functions f aim to maximise the proportion of cells that were either:

- Correctly predicted presences, with frequency $a = p\psi$
- Correctly predicted absences, with frequency $d = (1 - p)(1 - \psi)$

If the performance metric only rewards correct predictions of one type (either a or d), performance will be maximised by:

- Predicting every cell as present in the case of rewards for a .
- Predicting every cell as absent in the case of rewards for d .

For example, sensitivity (the proportion of presences that were correctly predicted as present) is maximised by predicting every cell as present, whilst specificity (the proportion of presences that were correctly predicted as absent) is maximised by predicting every cell as absent.

If the metric rewards both correctly predicted presences a and correctly predicted absences d , the performance function f will be monotonic in both $p\psi$ and $(1 - p)(1 - \psi)$. Since $0 \leq p \leq 1$ and $0 \leq \psi \leq 1$, it follows that $f(p, \psi)$ is convex in p . Thus, the expected value of $f(p, \psi)$ is maximised by either $p = 0$ or $p = 1$, depending the value of ψ and the relative rewards for a and d .

For example, for overall accuracy (Table 5A.2):

$$\begin{aligned} f(p, \psi) &= p\psi + (1 - p)(1 - \psi) \\ &= 2p\psi - p - \psi + 1 \\ &= p(2\psi - 1) - \psi + 1 \end{aligned}$$

As such, overall accuracy is maximised by:

$$p = \begin{cases} 1, & \text{if } \psi > 0.5 \\ 0, & \text{if } \psi < 0.5 \end{cases}$$

...with $f(p, \psi)$ equal for any value of p in the special case of $\psi = 0.5$.

Thus, for any underlying probability of presence ψ , binary predictions ($p = 0$ or $p = 1$) receive higher or equal performance scores than predictions which match the true probability of presence ($p = \psi$).

This proof holds for a single probability of presence value (e.g. in a single environment). However, because confusion matrix methods are calculated using a summation over all cells, it extends to any number of probabilities (environments).

The finding that binary metrics are maximised by binary predictions applies not only to metrics that traditionally use a confusion matrix, but also to any “threshold-independent” method that can be formulated as a confusion matrix. For example, the mean absolute prediction error (MAPE) is ostensibly a threshold-independent method (Liu, White & Newell 2011):

$$MAPE = \frac{\sum_{i=1}^n |y_i - p_i|}{n}$$

However, it can also be written:

$$\begin{aligned} MAPE &= 1 - \frac{\sum_{i=1}^n [y_i p_i + (1 - y_i)(1 - p_i)]}{n} \\ &= 1 - \frac{a + d}{n} \\ &= 1 - \textit{overall accuracy} \end{aligned}$$

As a consequence, mean absolute prediction error (a continuous metric) is also an improper scoring rule.

5A.4. Investigation of prevalence bias

The idea that prevalence-dependent metrics increase or decrease systematically with prevalence stems from simulation studies that showed an apparently unimodal relationship between Kappa and prevalence, in which Kappa scores are always higher for datasets with intermediate prevalence (McPherson et al. 2004, Allouche et al. 2006). However, we argue below that this finding is based on a questionable assumption.

The unimodal relationship between Kappa and prevalence occurs due to a combination of two reasons. First, the calculation of Kappa involves comparing the performance of the predictions p to those of a *null model*, which uses the mean prediction \bar{p} for all observations (see above). Second, the performance of the null model changes with prevalence, due to the uncertainty inherent in presence-absence models. A Bernoulli or “single coin-flip” distribution is used for the stochastic part of a presence-absence model, because each cell always contains either a presence or an absence (Clark 2007, Bolker 2008). In contrast to models with normally distributed error, the variance of the Bernoulli distribution changes with the value of the underlying probability ψ : variance is highest when presence and absence are equally likely ($\psi=0.5$), and lowest at extreme (high or low) probabilities of presence (Fig. 5A.2). For example, if a species is always present ($\psi=1$), we can predict the outcome with certainty; but when $\psi=0.5$, even a perfectly calibrated model will be “half-wrong” (incidentally, this explains why R-squared values for presence-absence models are often disappointingly low). Thus, it is genuinely easier to predict the outcome of any single presence/absence event at extreme probabilities of presence.

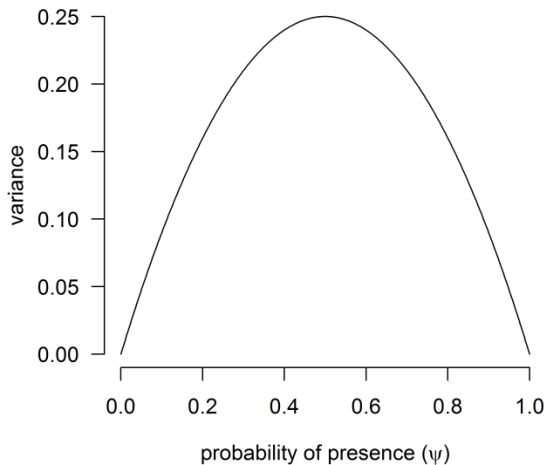


Figure 5A.2: *The relationship between the underlying probability of presence and the variance among presence-absence observations, assuming a Bernoulli sampling distribution.*

This same unimodal relationship (Fig. 5A.2) dictates the performance of a null model in a dataset with a given prevalence; for example, the null prediction performs poorly when the dataset consists of 50% presences and 50% absences ($\bar{p} = 0.5$), but delivers a perfect forecast for datasets consisting entirely of presences or absences ($\bar{p} = 0$ or $\bar{p} = 1$).

Because Kappa is calculated by referencing the performance of the predictions p to the performance of a null model \bar{p} , and the null model achieves a higher performance for datasets with extreme prevalence (as $\bar{p} \rightarrow 1$ or $\bar{p} \rightarrow 0$), a set of predictions with a *given predictive performance* (overall accuracy) will be credited with lower Kappa score (McPherson, Jetz & Rogers 2004; Allouche, Tsoar & Kadmon 2006). However, this conclusion rests on the assumption that the predictions p perform no better on datasets with extreme prevalence. This might be considered unlikely because, as already explained, predicting the outcome of any given rare or common event (with low or high probability) is genuinely easier than predicting the outcome of an intermediate probability event, such that we would expect that calibration of the tested model to improve for datasets with more extreme prevalence values. Put simply, if the data become easier to predict by chance, but the model fails to improve, it deserves a lower skill score.

5A.5. Additional information on simulation methods

This section describes in more detail the methods for our simulation example (Figure 5.5, main text).

As stated in the main text, we simulated the distribution of a species whose true probability of presence ψ in cell i can be described by a logistic function of a single environmental covariate x :

$$\text{logit}(\psi_i) = \alpha + \beta x_i$$

$$y_i \sim \text{Bernoulli}(\psi_i)$$

We simulated environmental variable (x) values for a training landscape with 100 cells. We created a gradient in x values: we first choose a mean x value for each of the ten rows (evenly dispersed along the interval $[-10,10]$), and then simulated an x value for each cell from a normal distribution with mean defined by the row mean, and standard deviation of 2. These parameters were chosen arbitrarily, with the intention of creating a distribution of environments with a range of different probabilities of presence.

Once this initial “training” landscape had been simulated, we generated a species distribution using the logistic function above and the *rbinom* function in R (R Development Core Team 2011). To parameterise the best model under each performance metric, we wrote functions to calculate the performance of a given parameter set for each metric, and used R’s *optim* function (Bolker 2008) to locate the parameter set that maximised each performance function.

Next, we simulated a new, “test” environment following the same procedure above, for which a conservation strategy needed to be designed. We assigned a protection cost to each of the 100 cells, using two different cost scenarios: (a) each cell had a unit cost of 1, such that all cells had the same costs; (b) each cell had cost simulated from a uniform distribution in the range $[0,2]$, such that cells had different costs. We also varied the resources available for protection, and consequently, the

number of cells that could be protected. The combination of these factors gave us the three scenarios explored in the paper (Table 5A.3).

Scenario	Relative protection costs	Resources available
1	Equal (1)	Exactly equal to number of occupied cells (47)
2	Equal (1)	Limited (10)
3	Different (simulated from uniform distribution [0,2])	Exactly equal to number of occupied cells (47)

Table 5A.4: protection cost scenarios for which conservation strategies needed to be designed.

Using the x values of the test environment as inputs, we calculated the probability of presence in each cell using model parameters selected by each metric. We calculated a “protection efficiency” by dividing the expected probabilities of presence by the associated cost for each cell. We then used a simple ranking algorithm to allocate resources to cells: we selected the combination of cells which gave the highest total protection efficiency, given the available resources for protection.

We calculated the expected number of populations saved as $\sum_{i=j} p_i$, where j indexes the protected cells. We also calculated the 95% confidence intervals around this expectation, based on the probabilistic uncertainty of the predictions for protected cells, using $var(p) = \sum_{i=j} p_i(1 - p_i)$, where var denotes the variance of the expected value (Fig. 5.5j-l, main text). For simplicity, we ignored other sources of uncertainty, including that in parameter estimation (i.e. we focused on variability from the Bernoulli process, not in it; Clark 2007).

5A.6. Demonstration of likelihood performance metrics

We feel that likelihood-based performance metrics, as proper scoring rules, continue to offer one of the most useful ways to evaluate SDM calibration. Below, we provide formulae and R code for those wishing to use likelihood-based metrics to assess the performance of SDMs.

The log-likelihood of observing a presence-absence dataset \mathbf{y} given a set of predictions \mathbf{p} is simple to calculate, assuming independence among observations:

$$\log L_p = \sum_i \log(p_i y_i + (1 - p_i)(1 - y_i))$$

```
loglikP <- sum( log( p*y + (1-p)*(1-y) ) )
```

To quantify the performance of an given model with log-likelihood L_p relative to a null model with log-likelihood $\log L_{\bar{p}}$, a likelihood-based R-squared value (skill score; see above) can be used (McFadden 1973, Guisan and Zimmermann 2000, UCLA 2012):

$$R^2 = \frac{\log L_p - \log L_{\bar{p}}}{0 - \log L_{\bar{p}}}$$

```
loglikN <- sum( log( mean(p)*y + (1-mean(p))*(1-y) ) )
```

```
rsq <- (loglikP-loglikN)/(1-loglikN)
```

Further examples of likelihood-based R-squared metrics are provided online (UCLA 2012). It is important to remember that likelihood-based R-squared values, as with all performance metrics, cannot easily be compared among datasets.

For competing models and testing hypotheses, information criteria such as Akaike's information criterion (AIC) or the Bayesian Information Criterion (BIC) can be calculated (Burnham and Anderson 2002b, Bolker 2008):

$$AIC = -2\log L_p + 2k$$

$$BIC = -2\log L_p + k \log(n)$$

```
aic <- -2*loglikP + 2k
```

```
bic <- -2*loglikP + k*log( length(p) )
```

Here, n indicates the total number of observations (grid cells), and k indicates the estimated number of parameters, so that more complex models receive penalised AIC and BIC scores. Both of these performance metrics multiply the log-likelihood by -2 to obtain $-2\log L_p$, a quantity known as the deviance of the model.

Chapter 6: General discussion

6.1. Summary

Global warming provides both an opportunity and an imperative to develop understanding of species' responses to climate change. This thesis has presented studies on a temperature-limited habitat specialist species, the silver-spotted skipper butterfly *Hesperia comma*, at its expanding range margin in Britain. Fine-resolution surveys of changes to the distribution and habitat associations of *H. comma* have demonstrated the way in which microclimate can generate patterns of local population extinction during range expansions (Chapter 2) and alter patterns in habitat use in times and places with different climates (Chapter 4). The findings have also provided empirical evidence for the ways in which range expansions can be facilitated through conservation management at different spatial scales (Chapter 2) both inside and outside of protected area networks (Chapter 3). In addition, I have developed a framework for measuring the performance of presence-absence models, which are widely applied to predict changes in species' distributions in response to climate change (Chapter 5). The principal roles of this work have therefore been to develop a fine-scale understanding of how to facilitate range expansions under climate change, and to improve the ways in which climate change predictions are modelled and assessed. I now discuss the findings and implications of individual chapters, as well as questions that they raise for future research in climate change ecology.

6.2. Chapter 2: patch-scale management prevents setbacks in range expansion

Chapter 2 used the range expansion of *H. comma* in Britain as a case study to improve understanding of the dynamics and management of climate-driven range shifts. Two findings in particular stand out as important for conservation under climate change.

First, I found lower population densities and higher rates of population extinctions on cooler north-facing slopes, demonstrating how microclimates alter the spatial pattern of range expansion. Metapopulations persist as a balance between extinction and colonisation events, and the delay between the stochastic extinction of a population and recolonisation of the patch means that some habitat patches are unoccupied even when suitable (Hanski 1998). It is expected that the process of range expansion should be similarly dynamic, occurring in fits and starts as new colonies are repeatedly established and extinguished (Hill et al. 2008, Walther 2009, Early and Sax 2011). Climate-driven range expansions could be especially dynamic, because short-term variability in climate among years is likely to drive fluctuations in population size, accentuating extinction risk in unfavourable years and generating waves of colonisation in favourable years (Drake 2005, Boyce et al. 2006). The results from Chapter 2 conform to this dynamic view of range expansion (see also Thomas et al. 2001b), and illustrate that the spatial pattern of extinctions is closely related to the distribution of microclimates, an effect that would have been missed by coarser-resolution distribution surveys (Wiens and Bachelet 2010, Peterson et al. 2011). The link between microclimate and local extinction means that range shifts may be realised as a semi-contiguous “rising tide” of periodical colonisations and extinctions within a narrow expanding front of relatively homogenous habitats, or conversely, as repeated “in-filling” of cooler microclimate pockets within a broader distribution of heterogeneous habitats, depending on whether microclimates are organised into continuous bands or are patchy across the landscape. Indeed, changes to the UK distribution of *H. comma* illustrate that continuous expansions and in-filling may occur within the same range expansion: the continuous range expansion along largely north-facing escarpments in Sussex stands in contrast to the mosaics of expansion and retraction observed in the Chilterns, where the topography is more heterogeneous (Chapter 2).

Second, Chapter 2 illustrates that management to protect populations may play an important role in facilitating range shifts. The idea of managing habitat to secure populations at the range edge challenges current ideas on facilitating range expansions, which have been largely focussed on

increasing the colonisation of new habitat (Crooks and Sanjayan 2006, Pearce-Higgins et al. 2011; but see Hodgson et al. 2009, Oliver et al. 2012). The emphasis on increasing colonisation, rather than population survival, probably predominates for two reasons: (a) most studies of range-shifts have been at coarse spatial resolutions (Pearson and Dawson 2003, Peterson et al. 2011), such that local extinctions may often go unnoticed (particularly if the pattern of microclimates is heterogeneous; see above); and (b) the idea of protecting populations in habitat that is becoming increasingly suitable may seem somewhat counter-intuitive. However, in the context of a dynamic range expansion, it is important both to enhance colonisation rates and maintain populations once colonisation has occurred, to preserve the gains made and provide larger and closer sources of dispersing individuals for further expansion (Chapter 2; Hodgson et al. 2009). Chapter 2 shows that increased population survival can be achieved through increasing the size or quality of individual habitat patches (Chapter 2), an encouraging result for regions in which purchasing land to create new habitats is costly or otherwise difficult to achieve.

In addition to demonstrating the roles of microclimates and patch-scale management in range expansion, Chapter 2 also illustrates the importance of connectivity for facilitating range shifts. The idea that increasing the number, size, or proximity of source populations can enhance colonisation rates is well-established in metapopulation theory (Hanski 1998) and has been widely advocated as a way of promoting climate-driven range shifts in fragmented habitats (Crooks and Sanjayan 2006, Hannah et al. 2007, Krosby et al. 2010). The finding that connectivity enhances both colonisation and population survival rates is thus unlikely to come as a great surprise to many conservation biologists. However, Chapter 2 provides rare empirical evidence for the benefits of connectivity in the context of a range expansion, demonstrating that theory developed for metapopulations in static habitats (Hanski 1998) transfers well to more dynamic situations. Moreover, the strong effect of “indirect connectivity” highlights the importance of multiple “stepping-stone” colonisations, opening the possibility of managing landscapes well in advance of the expanding range margin to facilitate runs

of colonisation events (Krosby et al. 2010). These findings will inform and contribute to the evidence base for conservation under climate change.

The findings of Chapter 2 suggest several productive directions that future research might take. Given the importance of microclimate in range expansions revealed by Chapter 2, it would be interesting to conduct analytical and/or simulation studies of the ways in which microclimate impacts the dynamics of range expansion. In particular, it would be useful to examine the way in which the microclimate structure of the landscape (the frequency and magnitude of climatic fluctuations through space) interacts with patterns of temporal variability in climate (the frequency and magnitude of climatic fluctuations through time) to determine the responses of species' distributions to climate change. This work would be especially relevant given that temporal variability in climate (Easterling et al. 2000, Boyce et al. 2006) and temporal autocorrelations in climate (van de Pol et al. 2011) may alter under global warming.

From a more applied perspective, an important priority for future research is to establish the relative merits of competing ways to increase connectivity. Chapter 2 highlights that connectivity can be enhanced by increasing the *number* of dispersing individuals (by increasing the number or size of extant populations), as well as by increasing the *per capita* dispersal success (e.g. through corridor creation). However, there has been relatively little exploration of which of these methods is likely to be more effective in terms of delivering greater benefits for range-expanding species under different scenarios. As hinted in Chapter 2, I suspect that an analysis incorporating realistic costs of these competing measures may find that increasing abundance and population persistence could, under many circumstances, be a more efficient way to facilitate range expansions in comparison with other, more commonly discussed methods such as the creation of habitat corridors. Quantitative tests of the extent to which increasing abundance can help to facilitate range shifts would thus be welcome.

6.3. Chapter 3: current conservation practice can effectively facilitate range expansions

Using the models of colonisation and population survival developed in Chapter 2 as a starting point, Chapter 3 conducted an empirical analysis of the combined effects of protected areas and active conservation management on the range expansion of *H. comma*. As in Chapter 2, this analysis represents an empirical test of applied conservation management under climate change. However, Chapter 3 examined the extent to which existing conservation plans, originally designed to protect remnant populations of threatened species with relatively static ranges, can facilitate range shifts.

The results of Chapter 3 suggest that pre-existing conservation plans offer effective means to help species to shift through fragmented habitats and track their suitable climate space. This result is somewhat contrary to theoretical and modelling studies which have suggested that protected area networks will be rendered inadequate by climate change (Lovejoy and Hannah 2005, Hannah et al. 2007, Araujo et al. 2011). However, it supports and develops the results of empirical work which found that protected areas can effectively facilitate range expansions (Thomas et al. 2012). The major advance delivered by Chapter 3 is an explanation of why protected areas are colonised more frequently than unprotected areas: rather than merely preventing important habitats from being degraded, protected areas encourage active conservation management to improve and maintain habitat quality, and it is the combined effects of protection and active conservation that increase colonisation chances. The results of Chapter 3 thus offer encouragement that existing conservation practice will not become outdated under climate change, but rather, will form an important contribution to overcoming the combined threats of habitat fragmentation and global warming (Travis 2003).

An obvious but important expansion to Chapter 3 is to conduct similarly fine-resolution analyses of protected area effectiveness for a wider variety of range-shifting species. Studying distribution change at a spatial resolution sufficiently high to identify individual populations is necessary to quantify the effects of management decisions at the level of individual patches, which often

constitute the principal level at which conservation decisions are made (especially in the UK; Chapter 3). Moreover, with detailed information on patch attributes, it becomes more feasible to identify the causal impacts of management and ensure that protection status is not simply a “label” for high-quality patches that would have been colonised anyway (Chapter 3). However, obtaining data with this level of detail, and over a length of time sufficient to observe the dynamics of range shifts, is no easy challenge.

Comparisons of current protected areas with more flexible methods of reserve network design (Lovejoy and Hannah 2005, Hannah et al. 2007) are closely related to questions about the best ways to increase connectivity (see previous section). Consequently, there is some overlap between the directions for future research suggested by Chapters 2 and 3. For example, many simulation studies comparing current and proposed methods of protected area network designation would benefit from incorporating realistic costs of buying and selling land. It is fairly unsurprising that reserve networks which adapt to range shift patterns are predicted to be more effective at facilitating colonisation than those which stay static (Hannah et al. 2007), but the costs and logistical challenges of implementing flexible or adaptive strategies could be much higher than those associated with maintaining static networks (Cabeza and Moilanen 2001, Carroll et al. 2009). Given that Chapter 3 suggests static protected area networks could provide effective means to facilitate range shifts, there is a need to demonstrate that more flexible networks would deliver benefits over and above current conservation policy, in a cost-effective manner.

6.4. Chapter 4: habitat associations shift as climate changes in space and time

Chapter 4 examined the distribution of *H. comma* at a yet finer spatial resolution than in Chapters 2 and 3, surveying the locations of individuals (at the egg life stage), and relating these distributions to patterns of microhabitat. By surveying the egg-laying microhabitat associations of *H. comma* at

different sites and years of varying climates, I quantified the relationship between microhabitat use and (micro)climate.

The finding that patterns of microclimate use vary predictably with larger-scale variation in temperature supports a more nuanced treatment of habitat associations in the context of climate change. There is a tendency in climate change ecology to view responses to climate and habitat separately, assuming that they have distinct and divisible impacts on species' distributions. This view is formalised in species distribution modelling, in which habitat and climate almost always enter presence/absence models as additive, rather than interacting terms (Araujo and Guisan 2006, Peterson et al. 2011). The results of Chapter 4 challenge this view, suggesting that, due to the influence of habitat (specifically, vegetation height) on microclimate, the definition of "suitable habitat" is likely to vary from place-to-place and from year-to-year. An especially striking implication of Chapter 4 is that microhabitat associations could vary on very fine spatial scales (between 10^2 and 10^3 m for *H. comma*) due to differences in microclimate, such as those generated by north- and south-facing slopes. Thus, Chapter 4 illustrates a hierarchical and interactive relationship between climate, habitat, and the locations of individuals.

An evident corollary of Chapter 4 is that the predictive power and biological relevance of species distribution models could be improved by the inclusion of interaction terms between habitat and climate variables. This recommendation would be most usefully implemented with process-based models (Buckley et al. 2010, Dormann et al. 2012), in which a sound biological understanding of the species being modelled is a necessary prerequisite. Including interactions in more exploratory or correlative models might be less advisable, especially in situations where many climate and habitat variables are included, because the number of possible interactions would quickly become large, leading to overparameterised models (Warren and Seifert 2011, Wenger and Olden 2011). Although it may thus be difficult to specify interactions between habitat and climate variables *a priori* for

many species, simply being aware that such interactions may occur could lead to improved predictions and hypothesis generation from species distribution models.

The changing patterns of microhabitat use documented in Chapter 4 provide further evidence for the importance of habitat heterogeneity under a variable climate (Opdam and Wascher 2004, Hodgson et al. 2009, Oliver et al. 2010). Developing understanding of microclimatic heterogeneity, including how and when it might be delivered by conservation management, represents a top priority for climate change ecology. Progress towards this goal will begin with developing a more solid conceptual basis for the term “microclimate heterogeneity”. Habitat heterogeneity actually represents two components: the number of different habitat types, and the frequency with which they appear across a landscape (i.e. their "grain size"; Fahrig et al. 2011). Microclimate heterogeneity could be similarly understood as the number of different microclimates (*i.e.* the absolute variation in climate generated), in combination with the frequency with which they appear in the landscape (which can also be thought of as the frequency of climate fluctuations in space). When posed in this way, it becomes clear that investigating the impacts of microclimatic variation on habitat use is very closely related to the issue of how microclimatic variation at larger scales (for example, as generated by topographic variation) affects range expansions (see discussion of Chapter 2), with the key difference being that habitat use is usually studied at the individual level, whilst range expansion is usually studied at the population level. I would therefore welcome simulation studies that explored the way in which microclimatic heterogeneity interacts with temporal fluctuations in climate to influence population persistence.

Finally, Chapter 4 raises a more general question for habitat use studies: how should habitat associations be modelled? Traditionally, and in Chapter 4, habitat use is modelled as the probability that an individual is present at a given location. This has led to misinterpretations of habitat use models, because the strength of association with a particular resource (bare ground and the host plant *F. ovina* in Chapter 4) varies with its availability (Beyer and Schultz 2010, Matthiopoulos et al.

2011). In Chapter 4, the effects of habitat availability were accounted for, but many previous studies have not been aware of this problem (e.g. Roy and Thomas 2003, Davies et al. 2006, Merrill et al. 2008). In my view, part of the difficulty arises from the counter-intuitive nature of the modelling approach: the question of interest usually relates to the probability that an environment is selected, given a set of available environments, rather than the probability that an individual is present at a given location (in which case the assumption of independence among locations is invalid). I suggest that habitat use studies might benefit from a more process-based approach, in which parameters relate directly to habitat selection decisions, rather than the resulting distribution of individuals across different locations.

6.5. Chapter 5: a framework for metrics of species distribution model performance

After the applied case studies of Chapters 2-4, Chapter 5 addressed a more theoretical question in climate change ecology: how to measure the match between predicted and observed species distributions. In some ways there is no “right” answer to this question, since the desired attributes of range shift predictions will depend on their objectives and applications. However, based on my literature review of species distribution modelling (SDM) studies, and the conceptual framework I developed, it is clear that SDM predictions are not being adequately assessed for the purposes to which they are applied. Chapter 5 showed that the key weaknesses of current studies are (a) the numerical accuracy of predictions is not considered, such that only their ability to place locations in rank order of relative suitability is assessed; and (b) the performance metrics used often produce binary (“present or absent”) predictions, which produce misleading conclusions when the presence or absence of the species in question is not certain. Given the extremely widespread application of SDMs to forecast species responses to climate change, appropriate validation of predictions is of paramount importance for developing reliable conclusions (Guisan and Zimmermann 2000, Peterson et al. 2011). My hope is therefore that this work will improve the accuracy of SDM predictions under

climate change by encouraging researchers to use more informative performance metrics, such as Akaike's Information Criterion (Burnham and Anderson 2002).

Accounting for spatial autocorrelation represents an important next step for SDM performance evaluation. Spatial autocorrelation is ubiquitous in species' distributions, because dispersal between neighbouring locations couples patterns of occupancy at those locations (Dormann 2007, Beale et al. 2008b, Beale et al. 2010). For example, if a metapopulation model is used to predict colonisation or extinction in two neighbouring patches, the colonisation or extinction of one patch will alter the chance of colonisation of another (Hanski 1998), these patches do not provide entirely independent tests of model fit. Some efforts have already been made to account for spatial autocorrelation in SDM performance assessment. For example, spatial autocorrelation functions can be used as null models to which the performance of an alternative model can be compared (Beale et al. 2008, Hijmans 2012). I would argue that explicit incorporation of autocorrelation into the performance of any given model – for example, by specifying the non-independence in likelihood functions – might offer an alternative assessment method that is not contingent on the choice of null model. Nonetheless, the conclusions of this method will still be dependent on the spatial autocorrelation structure assumed. This emphasises one of the most important messages from Chapter 5: SDM performance is relative, not absolute. It makes little sense to compare performance among datasets, and, contrary to current practice, there is no particular value of performance at which predictive power can be said to be “good”. Moving away from this “holy grail” of absolute performance values will promote more informative assessments of SDM predictive ability (Chapter 5).

One of the most concerning issues for climate-based SDM predictions is that the uncertainty of predictions is often ignored, or only given cursory consideration (Chapter 5). It is not widely appreciated that the uncertainty of predictions, as well as their mean or best-parameter estimates, is contingent on the assumptions of the SDM. It is common in climate change ecology papers to find mean predictions for a far-distant future climate scenario (e.g. 2080) that are unaccompanied by any

estimate of uncertainty, or acknowledgement that assumptions on which the model has been parameterised may not be robust to such long-term projections (Peterson et al. 2011, Araújo and Peterson 2012). When biologically-justified, process-based models have been constructed, it has frequently become evident that patterns of population spread are extremely difficult to forecast accurately, even a few generations in advance (Clark et al. 2001, Clark et al. 2003). In my view, the inherent uncertainty in range shifts limits the value of long-term SDM predictions to revealing semi-qualitative patterns, such as demonstrating that climate change could potentially result in severe increases in extinction risk (Thomas et al. 2004). Even in an ideal situation in which a species' relationship with climate is known exactly, long-term predictions are unlikely to provide precise forecasts of detailed *quantitative* patterns, such as the fine-scale spatial distribution of populations (Chapters 2-3). Thus, rather than merely searching for the "best" way to predict species' distributions, I would argue that furthering our understanding of the limitations of SDM forecasts represents an imperative for climate change ecology.

6.6. Conclusion

Developing a holistic understanding of how climate affects ecological processes will improve our capacity to anticipate and ameliorate the impacts of climate change on biodiversity. Using the silver-spotted skipper butterfly *Hesperia comma* as a model system, this thesis has examined the ecological effects of climate at a range of spatial scales, ranging from the distribution of individuals among microhabitats (Chapter 4), to the distribution of populations across a landscape (Chapters 2-3). This work has revealed the important influence of microclimate on the spatiotemporal dynamics of range expansion (Chapters 2-3) and habitat use (Chapters 4), provided empirical tests of the efficacy of conservation actions in facilitating range shifts (Chapters 2-3), and developed understanding of how to assess species distribution forecasts under climate change (Chapter 5). These findings have illustrated the complex relationship between species' distributions and climate, showing that global warming can generate varied and multifaceted changes in species' geographic

distributions (Chapter 2) and alter their relationships with habitat (Chapter 4). Nonetheless, whilst precise and accurate fine-scale predictions of distribution change may not always be possible (Chapter 5), the analyses in Chapters 2 and 3 of this thesis offer encouragement that ecological theory and traditional biodiversity conservation approaches, originally developed for relatively static distributions, may transfer well to facilitate range shifts under climate change.

6.7. References

- Araujo, M. B., D. Alagador, M. Cabeza, D. Nogues-Bravo, and W. Thuiller. 2011. Climate change threatens European conservation areas. *Ecology Letters* **14**:484-492.
- Araujo, M. B. and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33**:1677-1688.
- Araújo, M. B. and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**:1527-1539.
- Beale, C. M., J. J. Lennon, and A. Gimona. 2008. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of the United States of America* **105**:14908-14912.
- Beale, C. M., J. J. Lennon, J. M. Yearsley, M. J. Brewer, and D. A. Elston. 2010. Regression analysis of spatial data. *Ecology Letters* **13**:246-264.
- Beyer, L. J. and C. B. Schultz. 2010. Oviposition selection by a rare grass skipper *Polites mardon* in montane habitats: Advancing ecological understanding to develop conservation strategies. *Biological Conservation* **143**:862-872.
- Boyce, M. S., C. V. Haridas, and C. T. Lee. 2006. Demography in an increasingly variable world. *Trends in Ecology & Evolution* **21**:141-148.

- Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? *Ecology Letters* **13**:1041-1054.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and multimodel inference : a practical information-theoretic approach*. 2nd edition. Springer, New York, London.
- Cabeza, M. and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution* **16**:242-248.
- Carroll, C., J. R. Dunk, and A. Moilanen. 2009. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. *Global Change Biology* **16**:891-904.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *The American Naturalist* **157**:537-554.
- Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: what can we forecast and how well? *Ecology* **84**:1979-1988.
- Crooks, K. R. and M. A. Sanjayan. 2006. *Connectivity conservation*. Cambridge University Press, Cambridge.
- Davies, Z. G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology* **75**:247-256.
- Dormann, C. F. 2007. Assessing the validity of autologistic regression. *Ecological Modelling* **207**:234-242.
- Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X. Morin, C. Römermann, B. Schröder, and A. Singer. 2012. Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography* **39**:2119-2131.

- Drake, J. M. 2005. Population effects of increased climate variation. *Proceedings of the Royal Society B: Biological Sciences* **272**:1823-1827.
- Early, R. and D. F. Sax. 2011. Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters* **14**:1125-1133.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* **289**:2068-2074.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J.-L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* **14**:101-112.
- Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147-186.
- Hannah, L., G. Midgley, S. Andelman, M. Araújo, G. Hughes, E. Martinez-Meyer, R. Pearson, and P. Williams. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5**:131-138.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* **396**:41-49.
- Hijmans, R. J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* **93**:679-688.
- Hill, J., Y. Collingham, C. Thomas, D. Blakeley, R. Fox, D. Moss, and B. Huntley. 2008. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* **4**:313-321.
- Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology* **46**:964-969.

- Krosby, M., J. Tewksbury, N. M. Haddad, and J. Hoekstra. 2010. Ecological Connectivity for a Changing Climate. *Conservation Biology* **24**:1686-1689.
- Lovejoy, T. E. and L. J. Hannah. 2005. *Climate change and biodiversity*. Yale University Press, Michigan.
- Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalized functional responses for species distributions. *Ecology* **92**:583-589.
- Merrill, R., M. , D. Gutiérrez, O. Lewis, T., J. Gutiérrez, S. Díez, B. , and R. Wilson, J. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* **77**:145-155.
- Oliver, T., D. B. Roy, J. K. Hill, T. Brereton, and C. D. Thomas. 2010. Heterogeneous landscapes promote population stability. *Ecology Letters* **13**:473-484.
- Oliver, T. H., R. J. Smithers, S. Bailey, C. A. Walmsley, and K. Watts. 2012. A decision framework for considering climate change adaptation in biodiversity conservation planning. *Journal of Applied Ecology* **49**:1247-1255.
- Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117**:285-297.
- Pearce-Higgins, J. W., R. B. Bradbury, D. E. Chamberlain, A. Drewitt, R. H. W. Langston, and S. G. Willis. 2011. Targeting research to underpin climate change adaptation for birds. *Ibis* **153**:207-211.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**:361-371.

- Peterson, A. T., S. J. R. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. Ecological niches and geographic distributions. Princeton University Press, Princeton, N.J. ; Oxford.
- Roy, D. B. and J. A. Thomas. 2003. Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia* **134**:439-444.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**:577-581.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145-148.
- Thomas, C. D., P. K. Gillingham, R. B. Bradbury, D. B. Roy, B. J. Anderson, J. M. Baxter, N. A. D. Bourn, H. Q. P. Crick, R. A. Findon, R. Fox, J. A. Hodgson, A. R. Holt, M. D. Morecroft, N. J. O'Hanlon, T. H. Oliver, J. W. Pearce-Higgins, D. A. Procter, J. A. Thomas, K. J. Walker, C. A. Walmsley, R. J. Wilson, and J. K. Hill. 2012. Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences* **109**:14063-14068.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**:467-473.
- van de Pol, M., Y. Vindenes, B. E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. M. Tinbergen. 2011. Poor environmental tracking can make extinction risk insensitive to the colour of environmental noise. *Proceedings of the Royal Society B: Biological Sciences* **278**:3713-3722.

- Walther, G. R. 2009. Two steps forward, one step back.... *Functional Ecology* **23**:1029-1030.
- Warren, D. L. and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* **21**:335-342.
- Wenger, S. J. and J. D. Olden. 2011. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*.
- Wiens, J. A. and D. Bachelet. 2010. Matching the Multiple Scales of Conservation with the Multiple Scales of Climate Change. *Conservation Biology* **24**:51-62.