



Topographic microclimates drive microhabitat associations at the range margin of a butterfly

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The habitat associations of individuals underpin the dynamics of species distributions. Broad-scale gradients in climate can alter habitat associations across species' geographic ranges, but topographic heterogeneity creates local microclimates which could generate variation in habitat use at finer spatial scales. We examined the selection of microhabitats for egg-laying by populations of a thermally-constrained butterfly, the skipper *Hesperia comma*, across 16 sites with different regional temperatures and topographic microclimates. Using models of thermal microclimate, we examined how the association between eggs and warm bare ground microhabitats varied with ambient temperature, and predicted bare ground associations in 287 existing *H. comma* populations, to investigate the relative impacts of regional temperatures and topographic microclimates on microhabitat use. Eggs were most strongly associated with bare ground in relatively cool sites, indicating climate-driven changes in microhabitat use. The majority of temperature variation between study sites was attributable to topographic microclimates rather than regional temperature differences, such that changes in microhabitat associations occurred principally between north- and south-facing slopes within the same region. Predicted microhabitat associations across the UK distribution of *H. comma* showed that, due to the large temperature differences generated by topography, most of the between-population variation in microhabitat use occurs locally within 5 km grid squares, with a smaller proportion occurring at a regional level between 5 km squares. Our findings show how microclimatic variation generated by topography alters the habitat associations of populations at fine spatial scales, suggesting that microclimate-driven changes in habitat suitability could shape species' distribution dynamics and their responses to environmental change.

The concept of habitat underpins our understanding of species' ecological requirements and our capacity to predict their responses to environmental change (Johnson 1980, Beyer et al. 2010). Definitions of habitat are generally based on the concept of the ecological niche, in which the presence or absence of organisms of a given group is linked to combinations of environmental variables (Peterson et al. 2011). However, ecologists working at different temporal and spatial scales often view habitat in different ways: in biogeographical studies and conservation biology, habitat requirements are typically viewed as species-level attributes, with the implicit assumption that the habitat associations of individuals remain constant across space and time (Oliver et al. 2009, Peterson et al. 2011); in contrast, behavioural ecologists investigate how the habitat associations of individuals change with both their internal state and external environmental conditions (Mysterud and Ims

1998, McLoughlin et al. 2010, Matthiopoulos et al. 2011). Nonetheless, if different habitats provide different reproductive and survival payoffs, changes in habitat selection behaviour can have important impacts on population and geographic distribution dynamics at broad spatial scales (McLoughlin et al. 2010, Matthiopoulos et al. 2011).

Observed changes in habitat associations may have two underlying causes. First, if the availability of a favoured habitat is reduced, the density of individuals in that habitat is expected to increase (providing that the population size remains constant), even if the underlying behavioural processes remain the same (Singer 2000, Beyer et al. 2010) (this effect is often referred to as a functional response in habitat selection; Mysterud and Ims 1998, Godvik et al. 2009, Matthiopoulos et al. 2011). Second, habitat preference itself may change as external conditions such as weather alter an individual's requirements or change the perceived values of different habitat types (Johnson 1980, McLoughlin et al. 2010, Morris and Dupuch 2012). For example, shorter vegetation heats up more quickly than longer vegetation in

direct sunlight, providing microclimates that are warmer than ambient temperatures (Suggitt et al. 2011); consequently, individuals exposed to cooler-than-optimal ambient conditions can achieve their thermal requirements by seeking shorter vegetation, but may show reduced association with short vegetation, and/or an increased association with longer vegetation, under warmer ambient temperatures (Thomas et al. 1999, Angilletta 2009). Climate-dependent microhabitat use has been demonstrated empirically in several species: for instance, bark crevice use by arthropods (Prinzing 2005), nest orientation in tree pipits *Anthus trivialis* (Burton 2006), the height of vegetation selected by larvae of the butterfly *Parnassius apollo* (Ashton et al. 2009), and the relative use of sunny versus shaded habitats by wood turtles *Glyptemys insculpta* (Dubois et al. 2009) all vary with ambient temperature (see Angilletta 2009 for further examples). Developing an understanding of such climate-driven changes in habitat use could improve predictions of species' occupancy patterns and responses to environmental change ('how much suitable habitat is or will be available for species X?') and the design of conservation management strategies ('which microhabitats should be provided for species X?') (Thomas et al. 1999, Oliver et al. 2009, McLoughlin et al. 2010).

By altering behaviour, climate can generate changes in population-level patterns of microhabitat use, particularly in ectothermic animals. In the UK, threatened invertebrate species are disproportionately associated with warm, early successional microclimates (Thomas 2005): for instance, decreased association with short vegetation has been observed in the silver-spotted skipper *Hesperia comma* during a warmer summer compared with a cooler summer (Davies et al. 2006), and in larvae of the Adonis blue *Polyommatus bellargus* in summer compared with spring (Roy and Thomas 2003). In addition to these temporal temperature changes, spatial gradients in climate can also generate changes in habitat use among populations. Oliver et al. (2009) studied the habitat associations of 41 butterfly species at their northern (poleward) range margins; in 29 of these species, the proportion of individuals associated with the species' 'favoured' habitat type increased in populations that were closer to their climatic range limits, indicating a narrower range of habitat associations in less climatically suitable sites. Existing work thus supports the idea that broad-scale spatial patterns in climate, such as latitudinal gradients in temperature, can alter habitat use between geographic regions (Thomas et al. 1999, Vázquez and Stevens 2004), although the number of studies investigating interactions between climate and population-level habitat use remains small (Oliver et al. 2009).

The ambient temperatures experienced by individuals depend not only on regional climate, but also on microclimates created by landscape topographic structure (Bennie et al. 2008). In the northern hemisphere south-facing slopes receive more insolation than north-facing slopes, and the temperature difference between two hillsides of different aspects can exceed 15°C on sunny days (equivalent to several times the rise in global temperatures predicted over the next century, or the difference in mean temperature of two locations several hundred km apart; Bennie et al. 2008). Topographic microclimates could thus have considerable effects on population-level habitat associations, but practical difficulties make their effects difficult to

quantify. First, data is needed at spatial resolutions fine enough to assess the distribution of individuals, yet from sufficiently large spatial extents to capture regional climate patterns (Wiens 1989). Second, the limited spatial resolution of conventional climate models makes the impacts of topography on ambient temperatures difficult to quantify (Potter et al. 2013). Third, habitat associations must be studied in a sufficiently large number of populations to differentiate between the impacts of climate and habitat availability on habitat use, a step which is essential to ensure the generality of conclusions (Beyer et al. 2010, Matthiopoulos et al. 2011).

Here, we examine how microclimate influences the egg-laying microhabitat associations of a thermally-constrained butterfly, the silver-spotted skipper *Hesperia comma* (Hesperiidae). We couple fine-scale models of thermal microclimate (Bennie et al. 2008, 2013) with mixed effects models of habitat association (Hebblewhite and Merrill 2008, Duchesne et al. 2010, Matthiopoulos et al. 2011) to assess how microhabitat use varies between 16 populations exposed to different temperatures. We quantify the effects of temperature on egg-laying microhabitat associations whilst controlling for habitat availability effects, and use our models to predict microhabitat use across the UK distribution of *H. comma*, to assess how regional climate and topographic microclimates combine to influence the spatial scale at which habitat associations vary.

Material and methods

Study species

The study took place in the UK, where *H. comma* reaches the north-western limit of its range. The UK distribution of *H. comma* is strongly constrained by both habitat and temperature: eggs are laid 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), and adult 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 the UK, from fewer than 70 populations in 1982 to over 300 populations by 2009 (Thomas et al. 1986, Lawson et al. 2012, 2013). The dynamics of range expansion have been linked to topographic microclimates, with populations more likely to be established (Thomas et al. 2001, Bennie et al. 2013) and less likely to suffer extinction (Lawson et al. 2012) on warmer south-facing slopes. A comparison of the microhabitats selected for egg-laying between two time periods (1982 and 2001/2002) within a single site indicated a weakened association with bare ground cover in the second (warmer) period (Davies et al. 2006), consistent with a climate-driven change in microhabitat use, although this study did not account for changes in habitat availability.

Sampling design

The selection of sites for egg-laying was sampled in 16 *H. comma* populations in 2010 (Fig. 1a, b). 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. 1a, b; Lawson et al. 2012). Sampling took place between 26 August and 30 September 2010 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, 25 × 25 cm quadrats were sampled for the presence of *H. comma* eggs (Fig. 1c, d). Because egg densities were low, a combined presence-only and random sampling design was adopted, necessary to obtain a sufficient number of presences for model-fitting (i.e. we employed a case-control design in which controls were sampled for presences or absences; Manly et al. 2002). On 'presence-only' transects, we searched for eggs across a 1 m search zone, and took quadrats wherever eggs were found. On 'random' transects, stratified samples of five quadrats, each 1 m apart, were taken at regular intervals (usually 20 m; Fig 1d). All presence-only quadrats contained eggs, but some quadrats on random transects also contained eggs, and were counted as presences. Therefore, there are two types of quadrat at each site: with and without eggs (present and absent). We chose to analyse egg presence/absence rather than egg abundance,

because female *H. comma* will often lay more than one egg on the same plant (Lawson unpubl.) such that the presence of each egg cannot be treated as an independent event; 97% of quadrats contained one egg or less, so this decision is unlikely to have substantially influenced our conclusions.

Variables

Three types of data were recorded in each quadrat: 1) whether eggs were present; 2) the percentage cover of bare ground; and 3) the percentage cover of the host plant, *F. ovina*. Percentage cover measurements were estimated by eye to the nearest percent, using quadrats with 25 (four percent) subdivisions. Three site-level variables were calculated: vegetation surface temperature, estimated 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).

Site-level temperatures were modelled using a 5 × 5 m resolution model of grassland surface microclimate (Bennie et al. 2008, 2013). 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. 2006) over the August flight period, during which time the vast majority of *H. comma* egg-laying takes place (Thomas et al.

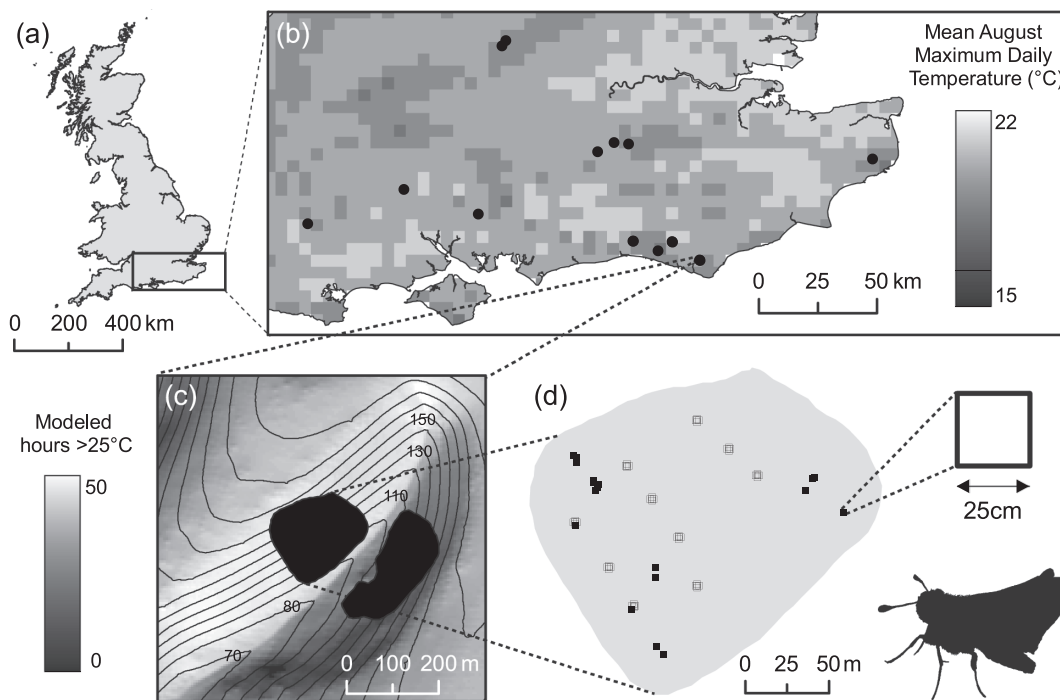


Figure 1. Study sampling design. Sites were chosen to span the extent of *H. comma*'s distribution in Britain (a). We surveyed populations from a range of large-scale climates (black circles indicate surveyed areas) with mean August maximum daily temperatures generally cooler in the north-western and coastal areas (lighter grid squares indicate warmer temperatures, based on mean daily maximum temperature in 2010 for each 5 km square). We also chose populations from a range of aspects, to include topographic variation in temperature; (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 (Material and 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; Material and methods). Within each quadrat, we recorded the percentage cover of bare ground and the host plant *F. ovina*.

1986). Predictions from the microclimate model have been empirically validated using ground-truthed data in a previous study (Bennie et al. 2008); a description of the empirical validation procedures is given in Appendix B. Modelled temperatures thus reflect the combined effects of regional climate (Fig. 1b) and microclimates generated by topography, with south-facing slopes being warmer than north-facing slopes (Fig. 1c; full details in Bennie et al. 2008). Sampled sites were digitized as polygons in ArcMap 9.3 (ESRI 2009; Fig. 1c). The mean number of hours exceeding 25°C during the August flight period was calculated for each polygon in 2010, using hourly climate data from the UK MET office (Perry and Hollis 2005) and a 5 × 5 m resolution Digital Elevation Model (Intermap Technologies 2011) as inputs. Therefore, although thermal microclimate was modelled at a 5 × 5 m resolution, the temperature values used in the analysis were spatially averaged across each habitat patch to give a measure of site-level temperature.

The relative contributions of regional climate and topographic microclimate to variation in temperatures between our study populations were assessed using hierarchical partitioning (Mac Nally and Walsh 2004). Regional climate for each site was measured using mean August maximum daily temperatures during 2010, based on a 5 km-resolution dataset from the UK MET office (Perry and Hollis 2005). Topographic microclimate was approximated using a solar index measure which incorporates variation in slope and aspect, with steep south-facing aspects providing the warmest microclimates (see Lawson et al. 2012 for details). The independent and joint contributions of regional climate and topographic climate to variation in modelled microclimate were measured using R-squared, implemented using the hier.part package in R (Mac Nally and Walsh 2004).

Model-fitting

Generalised linear mixed models (GLMM) were used to model the probability of egg presence in a quadrat (Manly et al. 2002, Matthiopoulos et al. 2011). The full model consisted of the following processes: 1) a site-specific intercept, modelled as a random factor, to account for variability in the proportion of presences sampled among different sites. 2) Quadrat-level main effects of percent bare ground and percent host plant cover. 3) Site-level main effects of temperature (hours > 25°C) and habitat availability (mean bare ground and mean host plant cover). 4) Interactions between quadrat-level variables and site-level habitat availability (mean bare ground and mean host plant cover), to investigate whether the amount of bare ground and/or host plant cover selected depended on the availability of bare ground or host plant across the whole site. 5) An interaction between bare ground and temperature, to investigate whether the 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, Supplementary material Appendix 1 presents additional results demonstrating that there was no statistical support for this interaction.

The full model was therefore:

$$\begin{aligned} \text{logit}(p_{ij}) = & \alpha_j + \beta_1 b_{ij} + \beta_2 h_{ij} \\ & + \beta_3 \bar{b}_j + \beta_4 \bar{h}_j + \beta_5 T_j \\ & + \beta_6 b_{ij} \bar{b}_j + \beta_7 b_{ij} \bar{h}_j \\ & + \beta_8 h_{ij} \bar{b}_j + \beta_9 h_{ij} \bar{h}_j \\ & + \beta_{10} b_{ij} T_j \\ \alpha_j \sim & \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \\ \gamma_{ij} \sim & \text{Bernoulli}(p_{ij}) \end{aligned}$$

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 . 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 . Egg-laying site selection was thus modelled 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 employing resource selection functions, our models estimate relative rather than absolute probabilities of presence (Manly et al. 2002).

Statistical tests

Microhabitat association models were fitted using the lmer function in the lme4 package (Bates et al. 2011), assuming a binomial error structure. The empirical support for each model was assessed using the corrected form of Akaike's information criterion (AICc; Burnham and Anderson 2002). Seven different models were competed, representing seven different hypotheses about the roles of habitat availability and temperature in determining egg-laying locations; these models are specified in Table 1.

Microhabitat association predictions

Following model selection, the full and temp models were re-parameterised using a Bayesian approach in the software WinBUGS, via the R2WinBUGS package (Sturtz et al. 2005). The advantage of switching to a Bayesian approach here is that it allows integration over derived parameter estimates (representing the strength of association with bare ground and the host plant) to calculate their uncertainty. Bayesian approaches often deliver more accurate estimates of uncertainty in derived parameters, with fewer assumptions than maximum likelihood approaches (Kery and Schaub 2011). Flat priors were used for all parameters, which were estimated using 3 chains of 50 000 draws, with a thinning rate of 25 and a burn-in of 10 000 (Kery and Schaub 2011).

Table 1. Empirical support for different models of *H. comma* microhabitat associations, based on sampled egg locations. All fitted models are shown; the constituent main effects and interaction terms are described in the Methods section. Terms included in each model are indicated by plus signs (+) with empty spaces indicating terms that were not included. K = number of parameters; AIC = Akaike's information criteria score; δ AIC = difference in AIC between current and highest-ranked model; AICwt = AIC weights.

Model	Terms Main effects					Interactions					K	AIC	δ AIC	AICwt
	Quadrat		Site-level			Bare ground		Host plant		Temperature				
	b_{ij}	h_{ij}	\bar{b}_i	\bar{h}_j	T_j	$b_{ij}\bar{b}_j$	$b_{ij}\bar{h}_j$	$h_{ij}\bar{b}_j$	$h_{ij}\bar{h}_j$	$b_{ij}T_j$				
Full	+	+	+	+	+	+	+	+	+	+	12	1178.90	0.00	0.97
Inthabitat	+	+	+	+		+	+	+	+		10	1186.21	7.31	0.03
Intbare	+	+	+			+	+				8	1205.83	26.93	0.00
Inthost	+	+		+				+	+		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

Model predictions were used to assess the extent to which spatial variation in temperature drives changes in the microhabitat associations of *H. comma* at different spatial scales. We predicted the strength of association with bare ground in 287 occupied habitat patches identified in a distribution survey conducted in 2009, encompassing the majority (ca 95%) of *H. comma* populations in Britain (Lawson et al. 2012). Occupied habitat patches were grouped into 5 km squares, adopting the origin of the UK Ordnance Survey British National Grid (southwest corner with coordinates [0,0]). The strength of bare ground association was modelled in each patch using parameters from the full model, preserving between-patch variation in microclimate but using the same landscape-level mean values of bare ground and *F. ovina* cover for all patches, so as to eliminate habitat availability effects. Site-level microclimates were estimated based on the mean number of hours $> 25^\circ\text{C}$ during August for each patch over a 27-yr period (1982–2009, chosen to coincide with the period over which the distribution of this species has been documented in detail; Lawson et al. 2012), using the microclimate model described above. We took the average hours $> 25^\circ\text{C}$ over this 27-yr period because we wanted to focus on how spatial variation in temperature influences patterns of microhabitat use in an average year; although we could also have predicted temporal changes in habitat use, we could not have tested the necessary assumption that habitat use changes in the same way in both space and time, because our models were calibrated using samples from a single year (2010). Habitat availability was based on estimates of mean percentage bare ground cover and *F. ovina* cover across all patches in the 2009 survey (Lawson et al. 2012). A variance components analysis (Crawley 2007, p. 546) was used to partition variance in bare ground association strength into two components: within and between 5 km squares.

Results

In total, 1317 quadrats were sampled, of which 338 contained eggs (presences) and 979 represented absences. The number of presence-only and random quadrats taken varied between sites: the mean numbers of presences and absences

sampled at each site were 21.1 (standard deviation = 4.1) and 61.2 (standard deviation = 37.9), respectively.

The data provided strong support for the full model (Table 1; δ AIC between full model and next best model = 7.31). The coefficients of this model (Supplementary material Appendix 3) 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. 1986). Second, the interaction between bare ground cover and site-level temperature (models including an interaction between temperature and bare ground cover outperform those without this interaction, Table 1) demonstrates that eggs were most strongly associated with bare ground in relatively cool sites (Fig. 2a). In the hottest sites, eggs were only weakly associated with high values of bare ground (coefficient near zero, Fig. 2a). Third, the interactions of quadrat-level effects of bare ground cover and host plant cover with site-level habitat variables (Table 1: models including interactions with bare ground and host plant availability, e.g. the full and inthabitat models, outperform models without these interactions, e.g. the temp model), supports the idea that microhabitat associations depended on habitat availability.

The strength of bare ground association decreased as the availability of bare ground increased, such that butterflies disproportionately selected quadrats with high levels of bare ground in sites where bare ground was relatively rare (Fig. 2b). There was an indication that bare ground associations 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.

To further explore the relationships identified by the full model, we individually assessed the parameters to test whether they were statistically different from zero. This was done in two ways, to ensure that our conclusions were robust to the statistical method used: first, we plotted the posterior distributions of the parameters from the full

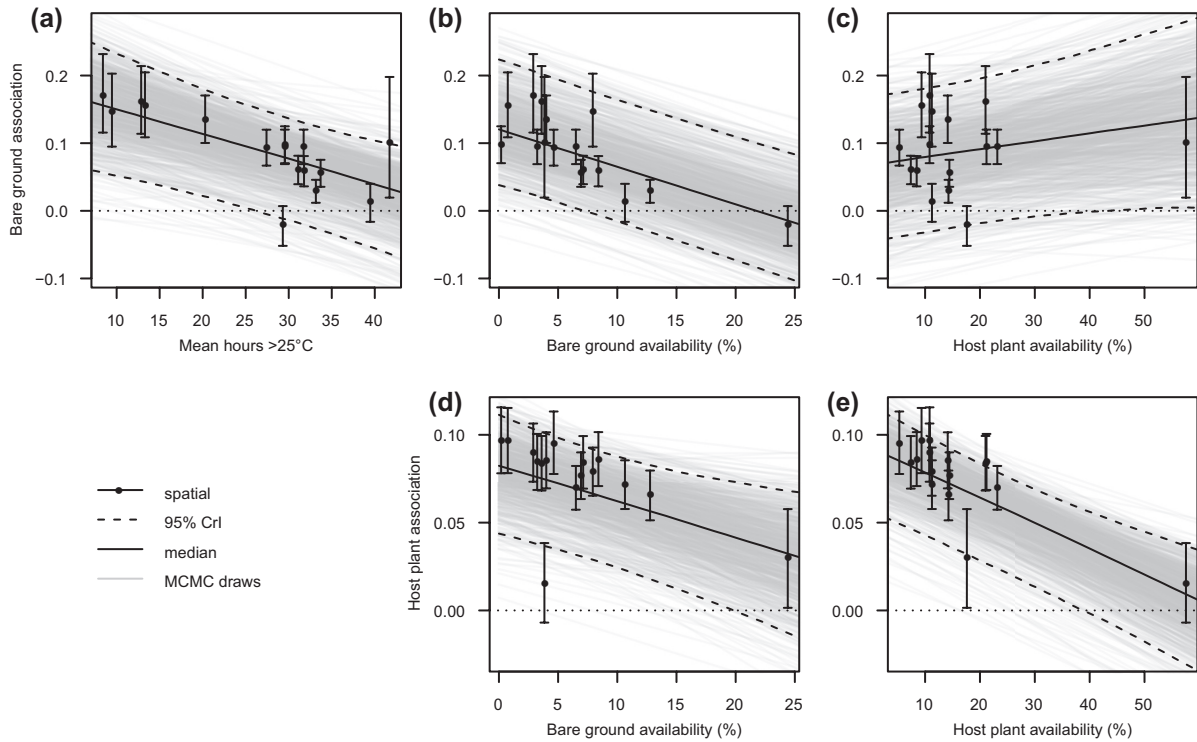


Figure 2. Coefficients indicating the association of *H. comma* eggs with bare ground (a–c) and the host plant *F. ovina* (d–e), in sites with different temperatures (a), bare ground availability (b, d) and host plant availability (c, e). Coefficients are derived from the full model, which includes effects of both climate and habitat availability on microhabitat use. The median (marginal) prediction across all sites is shown as a solid line, 95% population prediction intervals are shown as dashed lines, grey lines show random draws from the joint posterior distribution, and dotted lines indicate an association coefficient of zero, representing no relationship with between egg presence and bare ground. Site-specific (conditional) predictions are shown as circles along with 95% credible intervals (error bars).

model (as parameterised in WinBUGS) together with the 95% credible interval, and compared these distributions to zero (Supplementary material Appendix 3); and second, we calculated Z-scores for each parameter (as estimated using maximum likelihood methods in the lme4 package; Supplementary material Appendix 4). Both methods showed that all interactions shown in Table 1 were statistically different from zero, with the exception of the effects of host plant availability on bare ground associations (Table 1; Fig. 2c); this suggests that host plant availability had relatively weak effects on bare ground associations. However, following Matthiopoulos et al. (2011), we opted to preserve this parameter in the full model for the purposes of prediction; the use of a Bayesian approach allows us to propagate our uncertainty in this parameter through model predictions (Kery and Schaub 2011).

To ensure our findings were not solely driven by data from sites with unusually high bare ground or host plant cover, we re-analysed our data whilst excluding sites with the highest bare ground or host plant cover from the dataset (Supplementary material Appendix 5). In each case, the full model continued to outperform its simpler nested variants, suggesting that our findings were robust to the removal of these sites. Predictions and data for each site are shown in Supplementary material Appendix 6; note that the intervals shown in Fig. 2 and Supplementary material Appendix 7 are 95% population prediction intervals (PPIs) incorporating randomly-drawn values of bare ground, host plant cover,

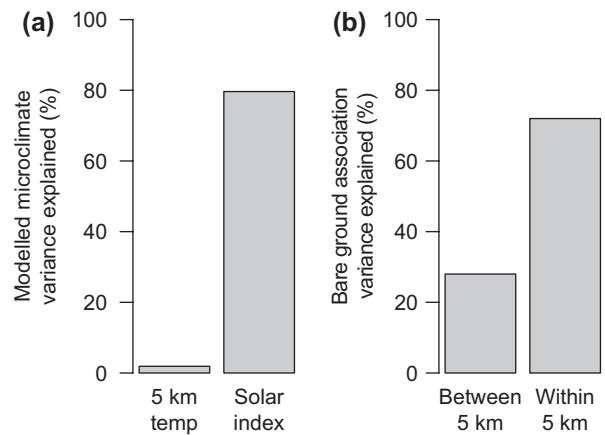


Figure 3. (a) Relative influence of regional temperatures (mean maximum daily temperature during August 2010, measured at 5 km resolution) and topography (measured using a solar index) on modelled site-level temperatures. Microclimatic variation generated by topography accounts for the vast majority of temperature variation experienced by the study populations. (b) Relative influence of regional (between 5 km) and local (within 5 km) temperatures on variation in predicted bare ground associations across the UK distribution of *H. comma*, showing that variation in microhabitat use within 5 km grid squares is considerably greater than the variation in microhabitat use between 5 km squares.

and/or site-level temperatures (see Bolker 2008, p. 255 for an explanation of PPIs).

Hierarchical partitioning showed that the majority of the variation in temperature between study populations was attributable to differences in slope and aspect, with only a very small proportion explained by 5 km-resolution differences in regional temperature (Fig. 3a). Solar index and regional temperature had largely independent effects on population-level temperatures (very small 'joint' effect, not visible in Fig. 3a). The variance components analysis of predicted bare ground associations across the UK distribution of *H. comma* revealed that the majority of climate-driven variation in bare ground associations is expected to occur between neighbouring populations within 5 km squares, with a smaller proportion occurring at regional scales between 5 km squares (Fig. 3b).

Discussion

This study shows how fine-scale temperature variation generated by topography drives spatial variation in the microhabitat associations of a thermally constrained butterfly, *H. comma*. Consistent with expectations derived from previous work on *H. comma* (Thomas et al. 1986, Davies et al. 2006), we found that populations exposed to higher temperatures were less likely to lay eggs next to warm microhabitats with high bare ground cover (Fig. 2a). The observed changes in microhabitat associations reflect the variable importance of microclimates created by bare ground for ovipositing *H. comma*: the preference for a certain temperature may remain unchanged (the 'thermal niche' is conserved), but the preference for microhabitats which are hotter than ambient temperatures decreases as ambient temperatures rise (Davies et al. 2006). The principal finding of this study is that thermal microclimates generated by topography can interact with these temperature preferences to produce considerable changes in habitat use at fine spatial scales.

Our results indicate that topographic microclimates have effects on microhabitat use which act in concert with the coarser-scale impacts of regional climate, such as the increases in habitat specialisation towards climate range boundaries reported for UK butterfly species (Oliver et al. 2009). Using high-resolution estimates of vegetation surface temperatures (Fig. 1c; Bennie et al. 2008, 2013) allowed us to integrate the effects of regional and topographic microclimates on the temperatures experienced by individuals, and hence explore their relative importance on the microhabitat associations of *H. comma*. This 'common currency' temperature modelling approach showed that the majority of variation in microhabitat use between our study populations was attributable to the effects of topographic microclimates, rather than regional temperatures (Fig. 3a). Furthermore, predicting microhabitat associations across the UK distribution of *H. comma* showed that, due to the large temperature differences created by topographic microclimates, microhabitat associations are expected to vary more between neighbouring populations within the same 5 km square than at a regional scale between 5 km squares (Fig. 3b). This shows that topographic microclimates can generate considerable differences in microhabitat use which, depending on the spatial extent

of the study, can be of greater or comparable magnitude to the effects of regional climates.

Changes in habitat availability can potentially mask or accentuate the impacts of climate on habitat use (Beyer et al. 2010, Matthiopoulos et al. 2011). In our study populations, *H. comma* eggs were less likely to be associated with microsites of high bare ground (Fig. 2b–c) or with high host plant cover (Fig. 2d–e) in sites with increased availability of these resources (Mysterud and Ims 1998, Godvik et al. 2009). This is because *H. comma* females allocate eggs to the 'best' microhabitats, relative to the other microhabitat available: for example, if bare ground offers favourable microclimates, a given microsite with high bare ground may be more attractive (and thus have a higher probability of being selected for egg-laying) when bare ground is limited than when it is widely available [this effect is analogous to the increased likelihood that an isolated host plant individual may receive more eggs (Mackay and Singer 1982), or that an isolated individual animal may experience a higher risk of predation than one within a herd (Connell 2003)]. In our study system, the low correlation between site-level temperatures and either bare ground or host plant availability meant that habitat availability effects were not mistakenly attributed to climate effects, so accounting for habitat availability did not seriously alter the estimated relationship between climate and microhabitat use (Supplementary material Appendix 7). This indicates that the importance of accounting for habitat availability in habitat use studies (Beyer et al. 2010, Matthiopoulos et al. 2011) is likely to be system-specific, depending on the strength of correlations between habitat and other environmental variables of interest.

Climate-driven changes in habitat use may alter the quantity of suitable habitat and thereby affect population growth rates (Thomas et al. 1999, Roy et al. 2003). For *H. comma* populations in the UK, the increased breadth of microhabitats available for egg-laying in warmer sites may contribute to the higher population densities (Lawson et al. 2012) and rates of population establishment and survival (Thomas et al. 2001, Lawson et al. 2012, Bennie et al. 2013) observed on south-facing slopes. Warming summer temperatures associated with global environmental change are likely to increase the amount of suitable egg-laying habitat (see Davies et al. 2006 for data consistent with this idea), particularly on north-facing slopes, but could eventually reduce the availability of suitable habitat on south-facing slopes by restricting *H. comma* to cooler microhabitats. Realised changes in microhabitat associations will depend on the relative contributions of plasticity and local adaptation, and the rate of microevolutionary change (Chevin et al. 2010); the data presented here were sampled in a single year and thus cannot partition changes in microhabitat associations between populations into plastic and genetic contributions, but replicated sampling in future years could help to disentangle these factors and assess the rate at which microhabitat associations may broaden under climate change.

The findings of this study suggest that climate-driven changes in habitat use are likely to have scale-dependent impacts on species distribution dynamics, contingent upon both the spatial pattern of microclimatic variation and the spatial resolution of observation. Existing work indicates that gradients in regional climate could drive changes in

niche breadth (Davies et al. 2006, Oliver et al. 2009) which modify geographic range boundaries (La Sorte and Jetz 2012) and/or rates of range expansion (Pateman et al. 2012) at coarse spatial scales. However, when topographic microclimates generate much of the between-population variation in habitat use, the relationships between climate, habitat associations, and population presence may become difficult to detect at coarser spatial resolutions. In our study system, *H. comma* remains restricted to the same general vegetation type (short-sward calcareous grassland containing suitable *F. ovina* plants) despite changes in microhabitat use. This means that if high topographic variation exists within grid squares, and increases in abundance due to broader microhabitat associations on south-facing slopes are counteracted by decreases in abundance due to reduced availability of suitable microhabitat on north-facing slopes (or vice-versa), the impacts of microhabitat use on patch occupancy dynamics may be 'averaged away' to some extent at coarser spatial resolutions. Nonetheless, where topographic microclimates are similar within a region (such as along consistently north- or south-facing escarpments in some of the habitat networks considered here; see Lawson et al. 2012), their effects on microhabitat associations could have impacts on species distributions that are detectable at coarse spatial resolutions. Thus, where habitat use is influenced by microclimate (as in the butterflies *P. bellargus* and *P. apollo*, whose larvae are associated with different vegetation heights depending on ambient temperature; Roy and Thomas 2003, Ashton et al. 2009), and microhabitat temperatures are in turn influenced by topography, the spatial pattern of topography is likely to have important impacts on observed distribution dynamics. This may be of considerable importance to species conservation, given that many threatened invertebrates are associated with warm, early successional microclimates (Thomas 2005).

Developing a population-level understanding of how climate modifies habitat will help to anticipate and assist species' responses to environmental change. In the same way that region-specific conservation schemes could accommodate broad-scale gradients in habitat use (Oliver et al. 2009), adopting different management practices on north- and south-facing slopes could tailor microhabitat availability to the differing requirements of populations on those slopes. Similarly, promoting microclimatic heterogeneity within sites could ensure that some habitat provides suitable thermal conditions at any given time, buffering populations against inter-annual fluctuations in climate (Opdam and Wascher 2004). Our findings also highlight the advantages of incorporating microclimatic heterogeneity and population-level processes in species distribution models (Thomas et al. 1999, Bennie et al. 2013) and relaxing the common assumption of independence between climate and habitat effects (Mysterud and Ims 1998, McLoughlin et al. 2010, Matthiopoulos et al. 2011). Accounting for the impacts of fine-scale, short-term variation in climate on habitat use could thus improve understanding of how species will respond to environmental change.

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Supplementary material (Appendix ECOG-00535 at <www.oikosoffice.lu.se/appendix>). Appendix 1–7.