Latitudinal gradients in butterfly population variability are influenced by landscape heterogeneity

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The variability of populations over time is positively associated with their risk of local extinction. Previous work has shown that populations at the high-latitude boundary of species' ranges show higher inter-annual variability, consistent with increased sensitivity and exposure to adverse climatic conditions. However, patterns of population variability at both high- and low-latitude species range boundaries have not yet been concurrently examined. Here, we assess the inter-annual population variability of 28 butterfly species between 1994 and 2009 at 351 and 18 sites in the United Kingdom and Catalonia, Spain, respectively. Local population variability is examined with respect to the position of the species' bioclimatic envelopes (i.e. whether the population falls within areas of the 'core' climatic suitability or is a climatically 'marginal' population), and in relation to local landscape heterogeneity, which may influence these range location – population dynamic relationships. We found that butterfly species consistently show latitudinal gradients in population variability, with increased variability in the more northerly UK. This pattern is even more marked for southerly distributed species with 'marginal' climatic suitability in the UK but 'core' climatic suitability in Catalonia. In addition, local landscape heterogeneity did influence these range location – population dynamic relationships. Habitat heterogeneity was associated with dampened population dynamics, especially for populations in the UK. Our results suggest that promoting habitat heterogeneity may promote the persistence of populations at high-latitude range boundaries, which may potentially aid northwards expansion under climate warming. We did not find evidence that population variability increases towards southern range boundaries. Sample sizes for this region were low, but there was tentative evidence, in line with previous ecological theory, that local landscape heterogeneity may promote persistence in these retracting low-latitude range boundary populations.

Population dynamics are known to arise from a combination of demographic and environmental stochasticity and non-linear effects from intra- and inter-specific interactions (Bjørnstad and Grenfell 2001). Therefore, unpicking the primary drivers of population dynamics can be difficult. Yet, summary metrics describing population dynamics, such as inter-annual variability, may be useful for applied conservation (Oliver et al. 2012a). Both theory and empirical work have shown that high inter-annual population variability is positively associated with local extinction risk. This has led to the adoption of population fluctuations as a risk criteria in IUCN Red List species assessments (IUCN 2011).

Both local and landscape-level habitat and topography can influence population variability. For example, Kindvall (1996) showed that a diversity of vegetation heights promote more persistent Orthoptera populations; Oliver et al. (2010) showed that the diversity of broad habitat types in landscapes (1–5 km radii) around monitoring sites

and also topographic diversity reduced the variability of butterfly populations. In addition to these effects of local site and landscape composition, population variability has been shown to exhibit broader spatial and temporal patterns. Latitudinal gradients in population variability have been demonstrated in a few cases (e.g. microtine rodents: Hansson and Hentonnen 1985, butterflies: Thomas et al. 1994, Oliver et al. 2012b). These studies have suggested increased population variability towards high-latitude range boundaries.

Population variability has also been shown to change over time. Population dynamics in butterflies were dampened in the latter half of a three decade recording period, especially for southerly-distributed species that were closer to their high latitude climatic range boundaries in the study region (Great Britain; Oliver et al. 2012b). This effect was consistent with expectations for species inhabiting locations with environmental conditions close to their (minimum temperature) climatically-determined fundamental niche

threshold (sensu Hutchinson 1957), and exposed to climate warming.

Therefore, the interactions between landscape structure (habitat and topography) and climate conditions which strongly impact population dynamics are starting to be understood. However, to date, studies have focussed primarily on species' high-latitude leading range edges. Patterns of population variability at both high- and low-latitude species range boundaries have not yet been concurrently examined; probably because monitoring data spanning species' ranges is uncommon.

In theory, if low-latitude range boundaries are also climatically determined, we would expect these populations to also show greater variability than populations in areas of 'core' climatic suitability. We test this hypothesis with an analysis of the inter-annual population variability of 28 butterfly species between 1994 and 2009 from 315 and 18 sites in the United Kingdom and Catalonia, Spain, respectively. We examine population variability with respect to the position of the species' current modelled suitable climate space across Europe, i.e. whether the population forms part of the 'core' climatic distribution or is a climatically 'marginal' population in each country. We also assess how large scale spatial patterns in population variability are modified by local landscape heterogeneity, in terms of habitat and topographic heterogeneity (Oliver et al. 2010). Such effects might provide potential for managing landscapes for climate change adaptation; for example, prioritising conservation in locations of high topographic heterogeneity and managing sites and landscapes to increase habitat heterogeneity (Hopkins et al. 2007, Heller and Zavaleta 2009). We predict that local landscape heterogeneity will have the greatest influence in dampening population variability closer to the edges of species' distributions, where populations are likely to have more unstable population dynamics in the absence of any other modifying factors.

Material and methods

Data collation

Butterfly data were obtained from the UK and Catalan Butterfly Monitoring Schemes (<www.ukbms.org/>; <www.catalanbms.org/>). These schemes employ identical methodologies of Pollard transect walks, with weekly counts aggregated into an annual index after accounting for missing weeks (Pollard and Yates 1993, Rothery and Roy 2001). In order to analyse spatial patterns in population dynamics, time series need to be of sufficient length and with sufficient spatial replication. Therefore, we set a minimum threshold for species inclusion of at least 3 sites in each region (UK or Catalonia) with at least 8 yr consecutive data with a mean count of greater than 9 at each site. These criteria were selected to make results comparable to a previous analysis by Thomas et al. (1994), and to achieve a balance between sufficient number of sites for analysis and sufficient quality of time series at each site, in order to optimise statistical power. We tested sensitivity to other minimum data criteria (results not shown), and found results to be qualitatively

similar but with weaker relationships. This data filtering gave a total of 28 species for analysis, with a mean number of sites of 124 ± 18 or 10 ± 1 per species in the UK and Catalonia respectively. Average lengths of time series were 13.0 ± 0.04 yr and 13.5 ± 0.2 yr in the UK and Catalonia respectively.

Each of the 28 species was classified a priori to analyses depending on the distribution of suitable climate space with respect to the UK and Catalonia. We used a visual assessment of maps of macroclimatic suitability in Settele et al. (2008) in order to categorise each of the UK and Catalonia into either climatically 'core' (i.e. in the central zone of climatic suitability) or climatically 'marginal' (i.e. at the edge of suitable climate space) for each butterfly species (Supplementary material Appendix 1, Table A1). Species were classified as climatically 'core' in the UK if their bioclimatic envelope covered the UK and extended into Scandinavia. They were classified as climatically 'core' in Catalonia if their bioclimatic envelope extended into most of southern Europe. In one case in the UK (*Leptidea sinapis*), a species' bioclimatic envelope covered the UK and Scandinavia (i.e. climatically 'core') but the species had very limited distribution in the UK. In this case, the species was still classified as climatically 'core' (under the assumption that some other factor such as habitat loss had restricted distribution extent). In another case, the species *Vanessa cardui* has a distribution extending across S. Europe and far north beyond the UK (making it a climatically 'core' in both areas under our classification) but does not overwinter in the UK or Catalonia (Stefanescu et al. 2013). The contribution of these (spring and summer) European generations to the whole population system could be more important than previously thought, as is the case for the *Autographa gamma* system (Chapman et al. 2012). However, we tested sensitivity to our classifications by re-running our analyses and treating *V. cardui* as 'marginal' in both regions, and *L. sinapis* as marginal in the UK. In both cases, overall results were qualitatively similar.

Each species could then be grouped into one of three mutually exclusive categories: 'core UK only' species (i.e. Catalonia is climatically marginal), 'core UK and Catalonia species' or 'core Catalonia only' species (i.e. the UK is climatically marginal).

For each monitoring site we assessed landscape structure in terms of habitat and topographic heterogeneity. Habitats on each butterfly monitoring route were grouped into broad categories by recorders. Habitat categories were chosen to be analogous to those from habitat maps available across each region. For the UK, we use the LCM 2000 map (Fuller et al. 2002). For Catalonia, we used a map compiled by botanists at the 1:50 000 scale. Habitat heterogeneity was calculated separately for each species, and only included habitat types used reasonably frequently by a species. More specifically, for each species in each country, habitat types were ranked by their mean species density. Only habitat types including 95% of the cumulative total density were selected, in order to avoid including habitat types where only vagrant individuals were spotted (i.e. where no resources are being used by the species). A Shannon–Wiener H' Index (Krebs 1999) was then

calculated on the habitat areas in landscape radii of 1, 2 and 5 km around monitoring sites. In addition, we assessed topographic heterogeneity in these landscape radii as the standard deviation of altitude values from a 50 m resolution digital elevation map (Morris and Flavin 1990).

Patterns in population variability at high- and low latitude range edges

We calculated population variability as the coefficient of variation in butterfly abundance over time at each site. We were interested in inter-annual variability, yet a number of different factors are known cause biases in using CV to assess inter-annual variability (e.g. length of time series, mean abundance, long term population trends; Pimm and Redfearn 1988, McArdle et al. 1990, Lepš 1993). Therefore, we included these as control variables in our statistical models. Mean abundance was logged before including in models to account for the power law relationship between abundance and variability, where slopes in a log-log transformed model can be different from 2 (i.e. using CV as a measure of population variability does not completely ensure that it is independent of mean abundance, and so we included log mean abundance as a covariate; Taylor 1961, Hanski and Tiainen 1989, Lepš 1993). Species' long term population trends for each site were assessed using the slope value from a log-linear regression of abundance versus year. Additionally, we included the length of each time series (number of years) and the northing of each site (km north).

First, we fitted a hierarchical linear mixed effects model to assess if patterns in population variability between the UK and Catalonia differed depending on the distributions of species' suitable climate space (i.e. whether they were 'core UK only', 'core UK and Catalonia' or 'core Catalonia only', Eq. 1).

$$\log(\text{CV})_{ij} = \text{Reg} \times \text{C}\textit{Suit}_i + \text{TSlength}_{ij} + \log(\text{meanAb})_{ij} \\ + \text{AbTrend}_{ij} + i + j + \varepsilon_{ij} \quad (1)$$

Where *Reg* is a categorical variable with two levels indicating the region (UK/Catalonia); *CSuit*$_i$ is a categorical variable indicating the distribution of suitable climate space of species *i* across the two regions (either 'core UK only', 'core UK and Catalonia', or 'core Catalonia only'); TSlength$_{ij}$, log(meanAb)$_{ij}$ and AbTrend$_{ij}$ are, respectively, the length of the time series, natural log transformed mean abundance and log-linear abundance trend over time of species *i* at site *j*. Both species identity (i) and site (j) are categorical random effects, and ε_{ij} is the normally distributed residual error. We used the R software package lme4 to fit mixed models and a Bayesian package MCMCglmm to obtain significance scores (Bates et al. 2008, Hadfield 2010, R Development Core Team).

We found a significant interaction effect between the variables *Reg* and *CSuit* (i.e. patterns in population variability between the UK and Catalonia differed depending on the distributions of species' suitable climate space). Therefore, we subsequently fitted separate models for the three *CSuit* species groups (i.e. to assess differences in population variability between the UK and Catalonia for

'core UK only', 'core UK and Catalonia' and 'core Catalonia only' species separately, Eq. 2).

$$\log(\text{CV})_{ij} = \text{Reg} + \text{TSlength}_{ij} + \log(\text{meanAb})_{ij} \\ + \text{AbTrend}_{ij} + i + j + \varepsilon_{ij} \quad (2)$$

Finally, we tested whether local landscape heterogeneity could influence these range location–population dynamic relationships. For this analysis, each region (UK or Catalonia) was analysed separately in order to consider differences between species depending on whether the country constituted part of the 'core' climatic range, or was climatically 'marginal'. Hence, we fitted four models (for each combination of: UK or Catalonia, and species climatically 'core' or 'marginal' in the respective country), with local habitat and topographic heterogeneity added as continuous explanatory variables (Eq. 3).

$$\log(\text{CV})_{ij} = \text{ShanDiv}_{ij} + \text{SDAlt}_j + \text{TSlength}_{ij} \quad (3) \\ + \log(\text{meanAb})_{ij} + \text{AbTrend}_{ij} + \text{SNorth}_j \\ + i + j + \varepsilon_{ij}$$

Where ShanDiv$_{ij}$ is the species-specific Shannon–Wiener H' Index of habitat diversity, and SDAlt$_j$ is the standard deviation of altitude values. These were initially calculated at 1 km radius around the monitoring site *j*, then analyses were repeated with variables calculated at 2 and 5 km resolution. Control variables remained the same as the previous models, except that we additionally included the northing of the site in km (SNorth$_j$) to account for latitudinal patterns in population variability within each country (Thomas et al. 1994, Oliver et al. 2012b). Random effects remained the same with a random intercept for species (i) and site (j).

We tested for spatial autocorrelation in model residuals using the ncf package in R (Bjørnstad 2009), but in no cases was significant spatial autocorrelation present.

Results

Patterns in population variability at low and high latitude range boundaries

In the model for all species in both regions, UK and Catalonia, we found a significant interaction effect between region (Reg) and the location of species suitable climate space (*CSuit*), i.e. differences in population variability between UK and Catalonia differed depending on whether the countries constituted 'core' or 'marginal' climatic space (Supplementary material Appendix 1, Table A2). Therefore, we subsequently fitted separate models for the three *CSuit* species groups ('core UK', 'core UK and Catalonia' or 'core Catalonia' species). We found that species with a core climatic distribution in the UK and marginal in Catalonia showed no significant difference in inter-annual population variability between the two regions (Supplementary material Appendix 1, Table A3, Fig. 1). Species with a core distribution in both regions showed increased inter-annual population variability in the UK compared with Catalonia (Supplementary material Appendix 1, Table A4, Fig. 1). The effect was even more
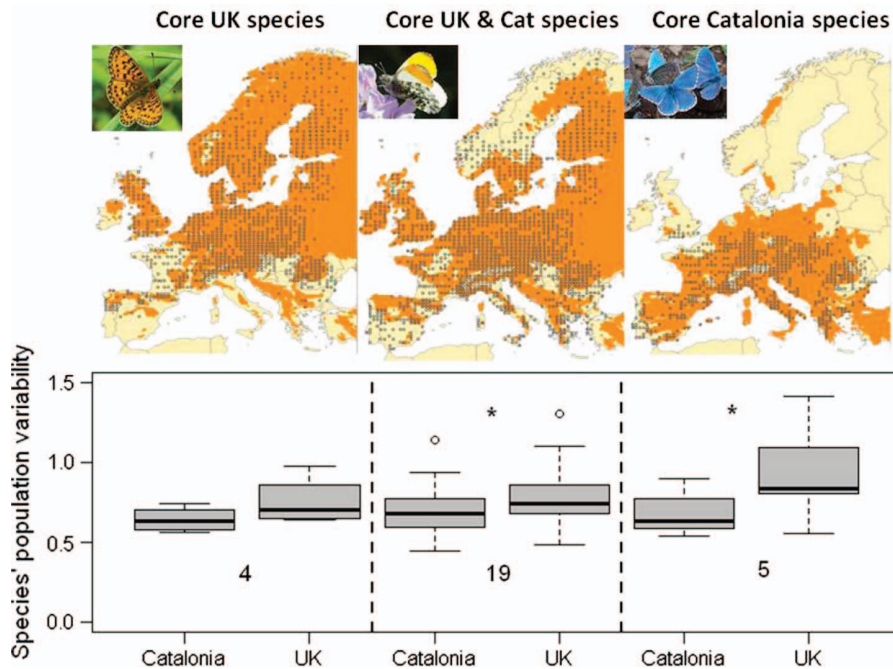
Figure 1. Box and whisker plots of species' mean population variability across all sites in Catalonia and the UK. Species were divided by their European distribution into three groups: those with 'core' climatic suitability in the UK and 'marginal' climatic suitability in southern Europe (left hand panel, with *Boloria selene* showing an example of this distribution pattern), those with 'core' climatic suitability in both regions (middle panel, *Anthocharis cardamines* shown as an example) and those with 'marginal' climatic suitability in the UK but 'core' in southern Europe (right hand panel, with *Polyommatus bellargus* shown as an example). The number of species in each category is listed in each panel. Asterisks show significant differences in species' population variability between Catalonia and the UK. Maps credited to Settele et al. (2008).

marked for species with a marginal distribution in the UK but core distribution in Catalonia (Supplementary material Appendix 1, Table A5, Fig. 1).

The control variables had significant effects on the CV measure of variability in the directions expected i.e. longer time series, those with smaller populations, and those which showed long term trends in abundance tended to have higher values of CV (Supplementary material Appendix 1, Table A3–A5).

Influences of local habitat heterogeneity on population variability

Within each region separately (UK and Catalonia), we assessed the ability of local landscape heterogeneity to mediate population dynamics for groups in the core or at the margin of their bioclimatic envelopes. Statistical models were fitted with topographic and habitat heterogeneity assessed at either 1, 2 or 5 km radius around monitoring sites. We found very little difference in goodness of fit between spatial scales due to the highly correlated nature of explanatory variables measures at different scales (Supplementary material Appendix 1, Table A6). Therefore, we primarily present results at the intermediate spatial scale of 2 km. Results were qualitatively similar across scales, except that some marginally significant results became significant (at p < 0.05) with landscape variables

assessed at either 1 or 5 km, where goodness of model fit was marginally better.

We found that habitat heterogeneity tended to have an effect in dampening inter-annual population variability, but the magnitude and strength of the association varied between region and species groups. In the UK, there was a significant effect of habitat heterogeneity for species for which the UK comprised the 'core' climate zone. Species for which Britain is climatically marginal, i.e. those with more southern European distributions, showed larger effects of habitat heterogeneity on average (Supplementary material Appendix 1, Table A7, A8). These effects were marginally non-significant across species for habitat heterogeneity assessed at 1 and 2 km radius, but became significant (at p < 0.05) at 5 km radius (Fig. 2, Supplementary material Appendix 1, Fig. A1, A2).

In Catalonia, species whose 'core' climatic distribution occurred in Catalonia showed no evidence that habitat heterogeneity influences inter-annual population variability despite reasonable sample sizes (Fig. 2, Supplementary material Appendix 1, Table A9, Fig. A1, A2). Species for which Catalonia was climatically marginal, i.e. those tending to have more northerly European distributions showed large effects of habitat heterogeneity. These effects were non-significant, but it should be noted that this group had very small sample sizes, with very limited statistical power to detect significant effects (Fig. 2, Supplementary material Appendix 1, Table A10, Fig. A1, A2).
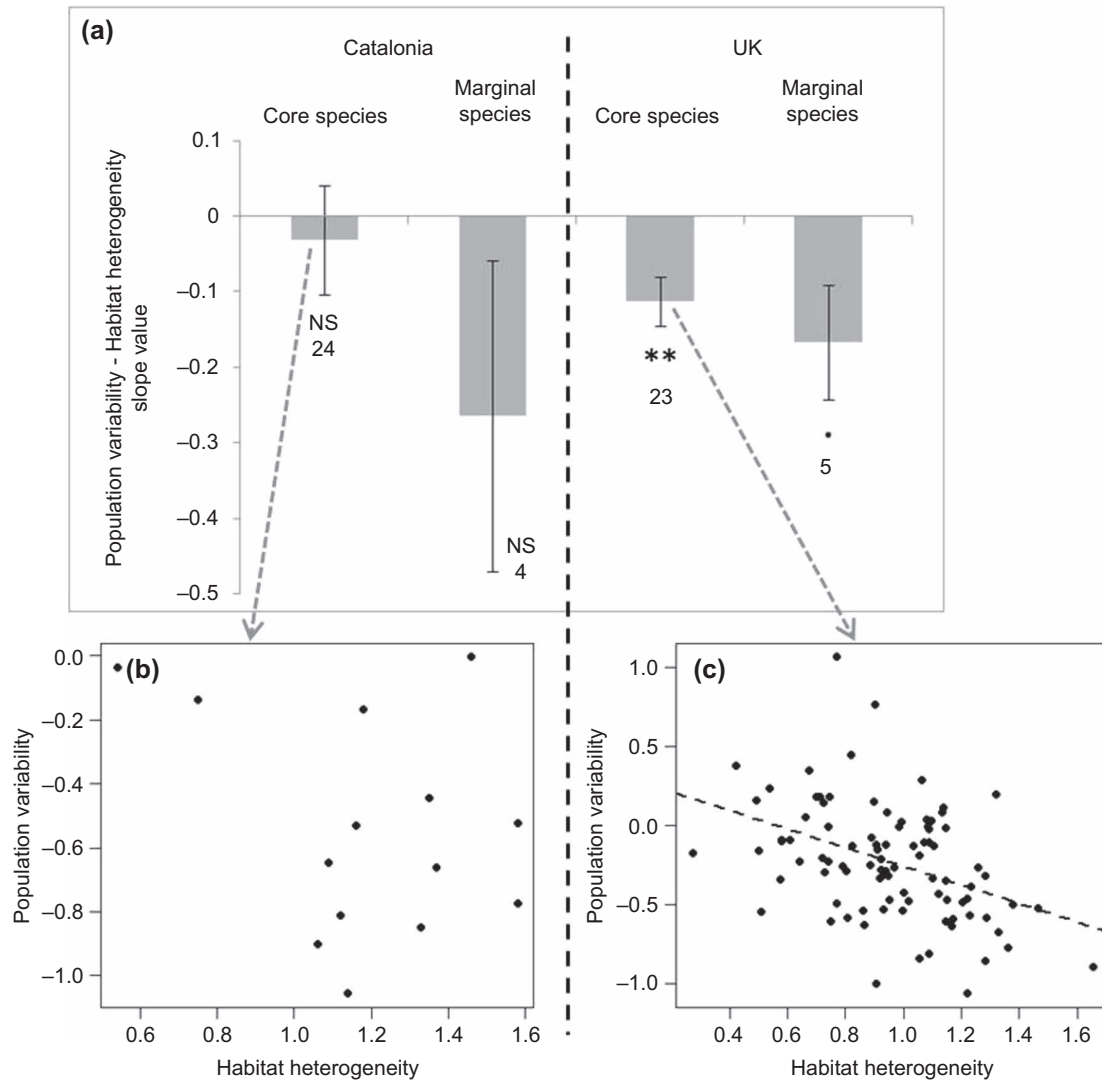
Figure 2. Relationships between butterfly population variability and habitat heterogeneity in the UK and Catalonia, assessed at 2 km radius around monitoring sites. In each region, species are split into those for which the region falls within the species' area of 'core' climatic suitability and those for which the region constitutes 'marginal' climatic suitability. The number of species in each group is listed below the bars in (a). The significance of the population variability–habitat heterogeneity relationship for each group is also indicated (NS non-significant; · marginally non-significant at $p < 0.05$; **$p < 0.01$). (b) and (c) show example relationships for an individual species, *Lycaena phlaeas*, chosen to best represent average trends across other species.

Influences of local topographic heterogeneity on population variability

In the UK, we found no significant effect of local topographic heterogeneity (in terms of variation in altitude) for species with their 'core' climate envelope in the UK, neither for species that were marginally distributed in the UK (Fig. 3, Supplementary material Appendix 1, Table A7, A8, Fig. A3, A4). In Catalonia, effects of topographic heterogeneity for species with a 'core' climatic distribution in Catalonia were marginally non-significant when assessed at 2km and significant (at $p < 0.05$) when assessed at 5 km, with a negative coefficient (Fig. 3, Supplementary material Appendix 1, Table A9, Fig. A3, A4). Climatically marginal species in Catalonia had very small sample sizes and consequently very large error margins (Fig. 3, Supplementary

material Appendix 1, Table A10, Fig. A3, A4). Therefore, on balance, there was some evidence that topographic heterogeneity might be important for dampening population variability of Catalonian butterfly populations, but further support is required.

Discussion

To our knowledge, this is the first study to assess population dynamics of multiple species concurrently at high and low latitude range boundaries. We found a clear latitudinal gradient in butterfly inter-annual population variability across western Europe, with higher variability at higher latitudes. This was especially marked for southerly distributed species. Furthermore, we found that local habitat
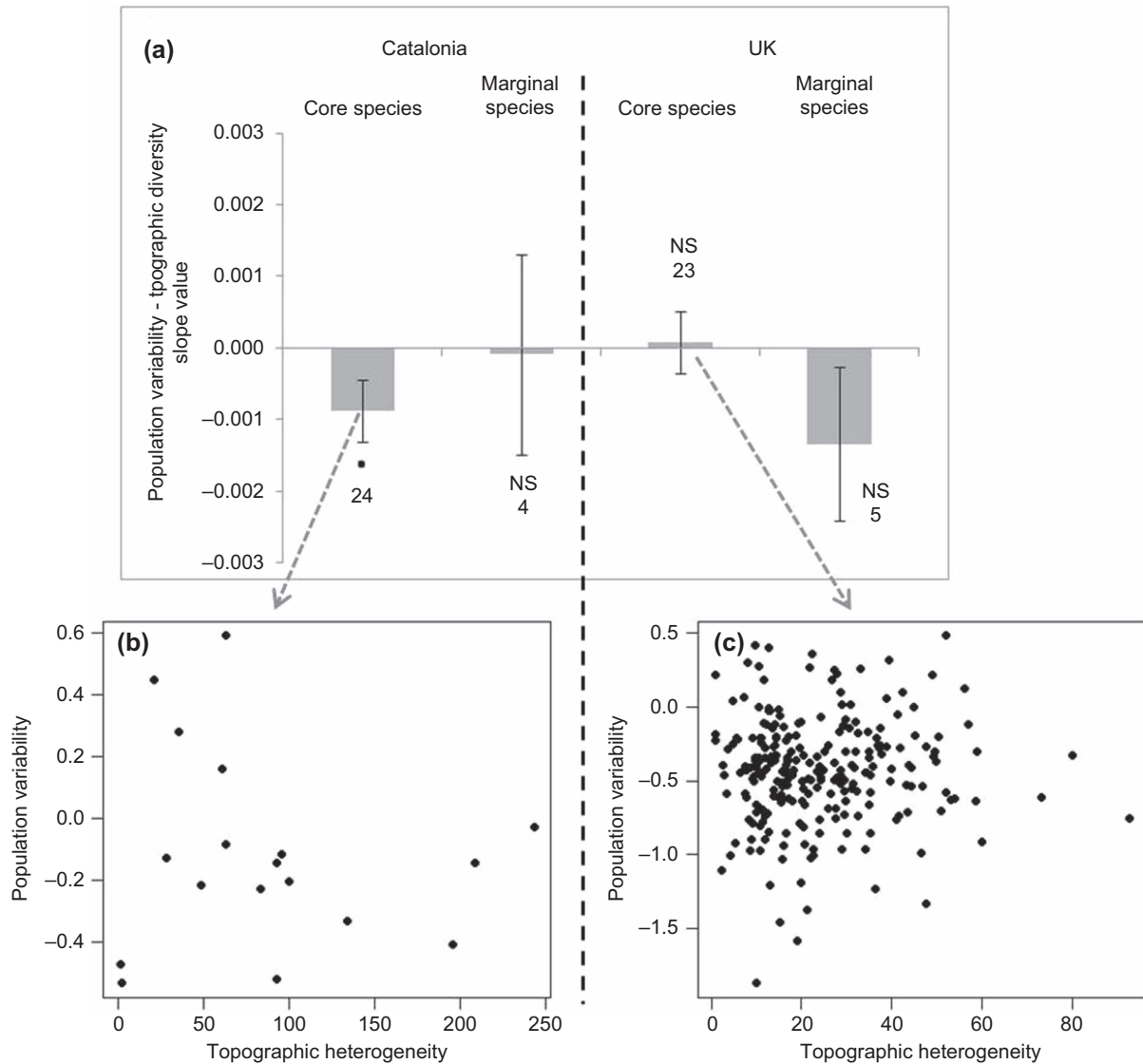
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Figure 3. Relationships between butterfly population variability and topographic heterogeneity in the UK and Catalonia, assessed at 2 km radius around monitoring sites. In each region, species are split into those for which the region falls within the species' area of 'core' climatic suitability and those for which the region constitutes 'marginal' climatic suitability. The number of species in each group is listed below the bars in (a). The significance of the population variability–habitat heterogeneity relationship for each group is also indicated (NS non-significant; · marginally non-significant at $p < 0.05$). (b) and (c) show example relationships for an individual species, *Pieris brassicae*, chosen to best represent average trends across other species.

heterogeneity can influence these range location-population dynamic relationships.

A few previous studies have demonstrated latitudinal gradients in population variability, although so far these tended to focus on high-latitude range margins (Hansson and Hentonnen 1985, Thomas et al. 1994, Oliver et al. 2012b; although see Curnutt et al. 1996, who considered variability towards edges of distributions in general). A number of explanations have been suggested for these patterns in population dynamics. Firstly, there may be spatial variation in interactions with other species, such as natural enemies. These interactions may be complex and also related to variation in the abiotic environment. For example, Hansson and Hentonnen (1985) found that two species of microtine rodent showed increased (cyclic)

variations in density over time in locations of higher latitude or with greater snow cover. They suggested that in these cooler locations predators have less alternative food sources present, which leads to stronger cyclic interactions with rodent prey species.

Abiotic conditions may of course have direct effects on population dynamics. Species close to the edge of their fundamental niche space (e.g. in cooler climates) may experience greater variability in population abundance due to threshold effects on growth and death rates and limited resources available due to reduced habitat associations (Nicholson 1933, Pollard and Rothery 1994, Lennon et al. 2002, Davies et al. 2006, Oliver et al. 2009, 2012b). In butterflies, additional evidence that climate may be directly responsible for patterns in population

variability comes from observations of increased population synchrony at northern range edges (Powney et al. 2010) and the fact that more southerly distributed species in the UK show greater variability than northerly distributed species (Oliver et al. 2012b).

A strong response of butterfly populations to climate fits with much existing research, showing increased species richness at lower latitudes (Kudrna et al. 2011), and close correlations between population abundance and annual weather (Roy et al. 2001). Therefore, our result that most species show positive gradients of inter-annual population variability with latitude in western Europe, and in particular southerly distributed species with 'core' climate areas only in the south, makes intuitive sense.

More surprising is the fact that northerly distributed species with 'core' climate areas in the north and apparently at the margins of their bioclimatic envelopes in the south, did not show significant latitudinal patterns in population variability. We had expected that these species may have had opposite patterns, with increased population variability in Catalonia compared with the UK. One possibility for this result could be that species populations are less influenced by climate at southern range margins. Previous authors have suggested a proportionally greater role of competition in determining the southern boundaries of species distributions compared with northern limits (Gaston 2003). However, for many species it is clear that inhospitable climate prevents range expansion southwards. These climatic constraints are obviously different to those experienced at the northern range limits, with moisture availability being a key factor (Hawkins and Porter 2003, Stefanescu et al. 2011). It is possible perhaps that limited moisture availability has a different effect on population dynamics compared with excessive cold temperatures, with the latter causing more variability due to rapid short-term changes and the former having a more gradual effect on suppressing mean abundance. In addition, the availability of wetter microhabitats which can buffer southern range margin populations from drought may be more common than warmer microsites that are sufficient to buffer northern margin populations from extreme cold snaps. However, we stress that these are speculative hypotheses and need further empirical testing. In addition, under future climate scenarios an increased frequency of extreme drought events are expected, and these would be expected to have large impacts on southern populations (i.e. especially if even the wetter microhabitats dry up; Della-Marta et al. 2007, Giorgi and Lionello 2008). Therefore, we may hypothesise an increase in variability over time in these populations, just as a decrease in variability in northern populations has been observed as climatic conditions have become less inclement (Oliver et al. 2012b).

In addition to large scale latitudinal gradients in population variability, we found that local landscape heterogeneity had a moderating influence on butterfly population dynamics. Higher habitat heterogeneity in the local landscape was associated with less variable butterfly populations, in line with previous research (Oliver et al. 2010), although trends were only significant in the UK. A lack of significance for Catalonian butterflies may have

been due to smaller sample sizes in this region (18 sites in Catalonia compared with 351 in the UK). However, relationship coefficients were negative as expected, indicating a qualitatively similar pattern as in the UK. We also hypothesised that populations in 'marginal' climate space within any given region would show a greater effect of landscape heterogeneity in buffering population dynamics, because these populations are closer to the edge of their fundamental niche space. Although effect sizes were much greater for marginal populations, these trends were not significant. This is possibly due to the smaller sample sizes of these groups, but it does mean we only have low confidence in this result.

For topographic heterogeneity, we did not find significant effects on population variability for either region, this is despite large sample sizes in the UK. A previous study in the UK found weak effects whereby variation in topographic aspect was associated with reduced population variability, although this effect was only evident for topography assessed at 1 km radius and for a larger set of 35 species (Oliver et al. 2010). Hence, the lack of effect of this study could be due to the larger spatial scale and smaller set of species examined (the species pool was smaller as species had to have sufficient data in both the UK and Catalonia for this analysis). For Catalonia, there was a negative relationship between topographic heterogeneity and population variability as expected for both climatically 'core' and 'marginal' populations. The trends were not significant, although they were very close to significance (at 2 km scale; and significant at 5 km) for climatically 'core' species' populations. However, other research suggests that these effects may be real. Weiss et al. (1988) found that topographic diversity was a key factor for the persistence of *Euphydryas editha* butterfly populations in California, especially in the face of drought. A number of other studies show that drought years can often limit insect populations to cooler wetter habitats or topographic formations (Ehrlich et al. 1980, Kindvall 1995, 1996, Sutcliffe et al. 1997, McLaughlin et al. 2002, Roslin et al. 2009, Suggitt et al. 2012). For Catalonian butterflies in particular, a recent analysis by Fernàndez-Chacón et al. (2013) on a broader set of species found that populations are more likely to persist in areas of high topographic heterogeneity. Therefore, on balance, although the current study only provides tentative evidence, we have reason to believe that topographic heterogeneity may be highly important for these species populations at their low-latitude climatic boundaries.

It is an interesting question to ask whether habitat or topographic heterogeneity is more important for population persistence, and at which spatial scale effects are most important. Some previous work has considered the relative importance of these heterogeneity measures at different spatial scales, and related this to broad species traits (Oliver et al. 2010). However, due to the difficulty in knowing that we have really measured heterogeneity in the right way for the species in question (e.g. at what spatial resolution, what habitat types/topographic aspects to include), it is very difficult to compare the relative importance of habitat versus topography in buffering population dynamics. We can conclude, however, that both seem to have qualitatively similar effects in dampening population variability, with subsequent expected effects on reducing

local extinction risk (Pimm et al. 1988, Lande 1993, Inchausti and Halley 2003, Oliver et al. 2012a). Therefore, the different aspects of heterogeneity may be substitutable to some degree, and in flatter locations improving habitat diversity may allow the persistence of species under climate change (Hampe and Petit 2005, Settele and Kühn 2009). Studies measuring microclimatic variability show that both variation in habitat type and topography can provide broad microclimatic gradients (Rosenberg 1974, Ashton et al. 2009, Suggitt et al. 2011). In practice, in the face of rapid climate change, we may want to maximise both aspects of heterogeneity, selecting priority sites in areas of high topographic diversity and manipulating landscapes and sites to increase habitat heterogeneity. There may even be ways to design interventions to increase micro-topographic diversity (e.g. repeated ploughing along an E-W line to create deep soil ridges). However, these interventions still need empirical testing and benefits to species would also need to be weighed up in terms of both economic and other environmental costs (e.g. below ground biota disruption and reduced carbon sequestration).

In conclusion, this study has demonstrated that many butterfly species consistently show latitudinal gradients in population variability, with increased variability in the higher latitude UK. This pattern is even more marked for southerly distributed species with a marginal distribution in the UK but core distribution in Catalonia. In addition, local landscape heterogeneity can influence these range location–population dynamic relationships. Habitat heterogeneity is particularly important in the UK, but there is tentative evidence that both topographic and habitat heterogeneity may be important for butterfly species at both high and low latitude range margins. These results have implications for the management of sites and landscapes to facilitate range expansion at high latitude boundaries and aid persistence at low-latitude boundaries in the face of rapid climate change.

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Supplementary material (Appendix ECOG-00608 at <www.ecography.org/readers/appendix>). Appendix 1.