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Heterogeneity in habitat and microclimate delay butterfly community tracking of climate change over an elevation gradient

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ABSTRACT

Gradients in community diversity and composition rarely track rates of warming, prompting efforts to understand the factors causing non-equilibrium responses to climatic change and their implications for conservation. Here, we test the roles of fine-resolution habitat heterogeneity and microclimate in delaying butterfly community responses to warming over a mountain elevation gradient. We assess species diversity and Community Temperature Index (CTI) in 2004–2005 and 2017 across 120 transect sites in the Sierra de Guadarrama (Spain), modelling temperatures based on topography, and vegetation structure based on LiDAR. A humped elevation gradient in species diversity was maintained over time. However, diversity in the later period was more positively related to vegetation heterogeneity, and sites with reduced rates of warming and greater forest cover maintained or increased their diversity. Site CTI declines with increasing elevation, showing little evidence of systematic change over the gradient between periods, although CTI increased most in locations with the greatest rates of spring microclimatic warming. Our results show that delays in community tracking of climatic conditions could result partly from positive effects of habitat and topographic heterogeneity providing microclimatic buffering against warming to existing communities; although barriers to colonization could also delay diversity increases and community thermophilization at high elevations. We suggest that protecting and managing complex habitats with high community diversity, and identifying localized microclimates that buffer populations against negative effects of warming, are more immediate conservation priorities over elevation gradients than efforts to ensure that communities track prevailing rates of warming.

1. Introduction

Rapid and large-scale changes to global ecosystems challenge the capacity of ecological systems to maintain equilibrium in space and time, in contrast with the dynamic equilibrium hypothesis (Prentice et al., 1991; Webb, 1986), with implications for conservation (Newbold and Siikamäki, 2015). Regarding biodiversity responses to climate change, if species' climate tolerances are constant over time (Pearman et al., 2008; Wiens et al., 2010) they will shift their distributions to track changes in the climate (La Sorte and Jetz, 2012; Parmesan et al., 1999). As species ranges move to higher latitudes and elevations, latitude and elevation diversity gradients are expected also to shift, with communities increasingly dominated by warm-associated species (community "thermophilization") (Sagarin et al., 1999). In practice, patchy habitat availability imposes barriers on range expansion (Fourcade et al., 2021) whilst microclimatic variability can buffer populations against negative climate change impacts (Suggitt et al., 2018). As a result, time lags in community responses to climate change ("climatic debt") have been widely observed (Devictor et al., 2008; Lajeunesse and Fourcade, 2023). The ability of management to influence these non-equilibrium community responses to warming, by facilitating range expansions or delaying local extinctions, is important for adapting conservation to climate change (Jackson and Sax, 2010; Gaget et al., 2021; Schuurman et al., 2022).

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Changes over time in elevation gradients of diversity and community composition present opportunities to infer the extent to which communities are maintaining equilibrium with climatic conditions. Species can move much shorter distances to track climate change in mountains than in flatter landscapes, because temperature changes more steeply over elevation than latitude gradients (Jump et al., 2009). However, changes to species' elevation ranges generally lag behind rates of warming (Chen et al., 2009) because of delays both in local extinction at low elevations ("extinction debt") and colonization at high elevations ("colonization credit"), as shown widely for mountain plants (Geppert et al., 2020; Rumpf et al., 2019). Animals have tracked climate warming with reduced delays (Lenoir et al., 2020), but the thermophilization of animal communities over elevation gradients has neither been ubiquitous nor at the pace expected from rates of warming (e.g., Herrando et al., 2019; Nieto-Sánchez et al., 2015).

Community thermal associations can be quantified using the Community Temperature Index (CTI), a measure based on the average temperature experienced across the geographic ranges of constituent species (Bowler and Böhning-Gaese, 2017; Devictor et al., 2008). Typically, higher elevation communities are composed by species associated with cooler conditions across their geographic ranges (i.e., CTI is lower at higher elevations; Nieto-Sánchez et al., 2015). As the climate warms, colonization by warm-adapted species and/or local extinction of cool-adapted species are expected to cause indices of the thermophilization of communities such as CTI to increase (Devictor et al., 2008). At the same time, local (alpha) diversity of communities often declines as elevation increases, or shows a humped pattern with elevation (McCain and Grytnes, 2010). As conditions warm, if species primarily experience range contractions at their lower limits, and expansions at their upper limits, then initial alpha diversity is expected to reduce at low elevations but increase at high elevations. Latitudinal range shifts also influence species richness especially at low elevations, but may not compensate for species lost to uphill shifts if the regional species pool is less species rich at lower latitudes (García-Barros et al., 2022), or if limitations to connectivity or habitat availability prevent species from colonizing (Wilson et al., 2007; Fourcade et al., 2019). If elevation gradients in alpha diversity or CTI do not change, among-site differences can be used to infer the roles of microclimate or landscape heterogeneity in delaying widespread climate-related community responses, and hence as potential tools for adapting conservation to climatic change.

Previous evidence suggests a time lag in butterfly community responses to warming, across both elevation and latitudinal gradients (e.g., Europe, Devictor et al., 2012; Menéndez et al., 2006). In the Sierra de Guadarrama mountain range in Spain, butterfly CTI increased over the last four decades of the twentieth century, but not as quickly as rates of warming (Nieto-Sánchez et al., 2015). Subsequently, in 24 annually monitored sites between 2005 and 2018, butterfly species population trends depended on species' vegetation associations but not their climatic associations (Caro-Miralles and Gutiérrez, 2023). Here, we test the roles of habitat heterogeneity and microclimate in delaying butterfly community responses to warming over the 1600 m elevation gradient in the Sierra de Guadarrama. We assess species diversity and CTI across an independent set of 120 butterfly communities that were sampled twice, 13 years apart (2004–2005 and 2017). We model 30 m resolution temperature conditions in the survey years based on site topography, as well as fine-resolution vegetation structure based on 3D LiDAR data. Communities responding to climate warming would be expected to show increases in CTI either because of the loss of cool-adapted species, the gain of hot-adapted species (referred to as "deborealization" and "tropicalization" respectively in marine ecology; McLean et al., 2021), or both processes operating together. In addition, communities undergoing these processes are expected to show decreases in initial alpha diversity at low elevations but increases at high elevations, because here latitudinal species expansions should not compensate for extirpations at low elevations since in the Iberian Peninsula butterfly species richness is higher in mountains and in the north (García-Barros et al., 2022). We set out first to establish how diversity and CTI varied with elevation and habitat heterogeneity over the two sampling periods, and then to test the effects of micro-habitat characteristics (microclimate and vegetation structure) on changes to diversity and CTI over time. Evidence that microclimatic conditions or habitat heterogeneity can delay these changes would provide support for their importance in managing community responses to climate change.

2. Materials and methods

2.1. Study area

The Sierra de Guadarrama mountain range has been classified as a priority site for butterfly conservation as it supports Iberian endemic species (Munguira et al., 2003) and species at their warm range margins that are expected to suffer decreasing distribution sizes or extirpations as conditions warm (Wilson et al., 2005). The mountain range is located in the centre of the Iberian Peninsula (from 40°20′ N, 4°40′ W south-west to 41°28′ N, 3°36′ W north-east) and has a maximum elevation of 2430 m.a.s.l. (Fig. 1a). Mean annual temperature for the last two decades in the mountain range (2000 to 2022) has increased by an average of 0.067 °C per year, based on linear regression of mean annual temperature at Puerto de Navacerrada meteorological station (1894 m elevation; $n = 23$ years, $R^2 = 0.38$; Fig. 1b), albeit with wide interannual variation. The temperature lapse rate is approximately 5.8 °C for each 1000 m increase in elevation (Nieto-Sánchez et al., 2015; Wilson et al., 2005). Hence the average warming experienced over 2004/05 to 2017 is equivalent to an uphill shift of approximately 130–150 m in isotherms (the absolute difference in mean temperatures between survey years was 1.7 °C, equivalent to 300 m; Fig. 1b).

2.2. Butterfly sampling

120 sites were located throughout the regional altitudinal gradient (601–2253 m) (Supplementary material, Fig. S1). The sites consisted of accessible clearings within the available habitats (forest, scrubland, and meadow). Butterflies were counted on standardized 500 m long x 5 m wide transect walks during suitable conditions (sunshine and low wind, between 10:00 h and 17:00 h European Summer Time) (Pollard and Yates, 1993). Butterflies were sampled in three years encompassing two periods separated by a decade, i.e., years 2004 and 2005 (hereafter 2004–2005: 62 sites sampled in 2004 and 58 in 2005), and year 2017 (all 120 sites sampled). Transects were visited approximately every three weeks between May and August (the main butterfly flight season: four visits per site in 2004, five visits per site in 2005 and 2017). Individuals were identified either perched or in flight, or caught with a net, identified on site, and immediately released. We excluded from our analyses two genera from the family Hesperiidae which are not straightforward to identify in the field (*Pyrgus* and *Carcharodus*) and which represented a very small percentage of the total number of butterflies observed (0.10 % in 2004/05, 0.17 % in 2017).

2.3. Environmental data

2.3.1. 3D spatial information on vegetation

Laser imaging detection and ranging (LiDAR) data represent landscapes and features through three-dimensional (3D: x, y, z) point clouds, which can be processed into a digital height model of surface objects (DHM: the difference of digital terrain models vs digital surface models) and used to measure 3D characteristics (e.g., vegetation height) (Kedron et al., 2019). However, LiDAR data are not suitable for traditional two-dimensional analyses (e.g., through the software FRAGSTATS), so different approaches have to be implemented (Kedron et al., 2019). For this study, LiDAR data were extracted from the Spanish PNOA database: flight cover of 2010 "primera cobertura" (sensor Leica ALS50)

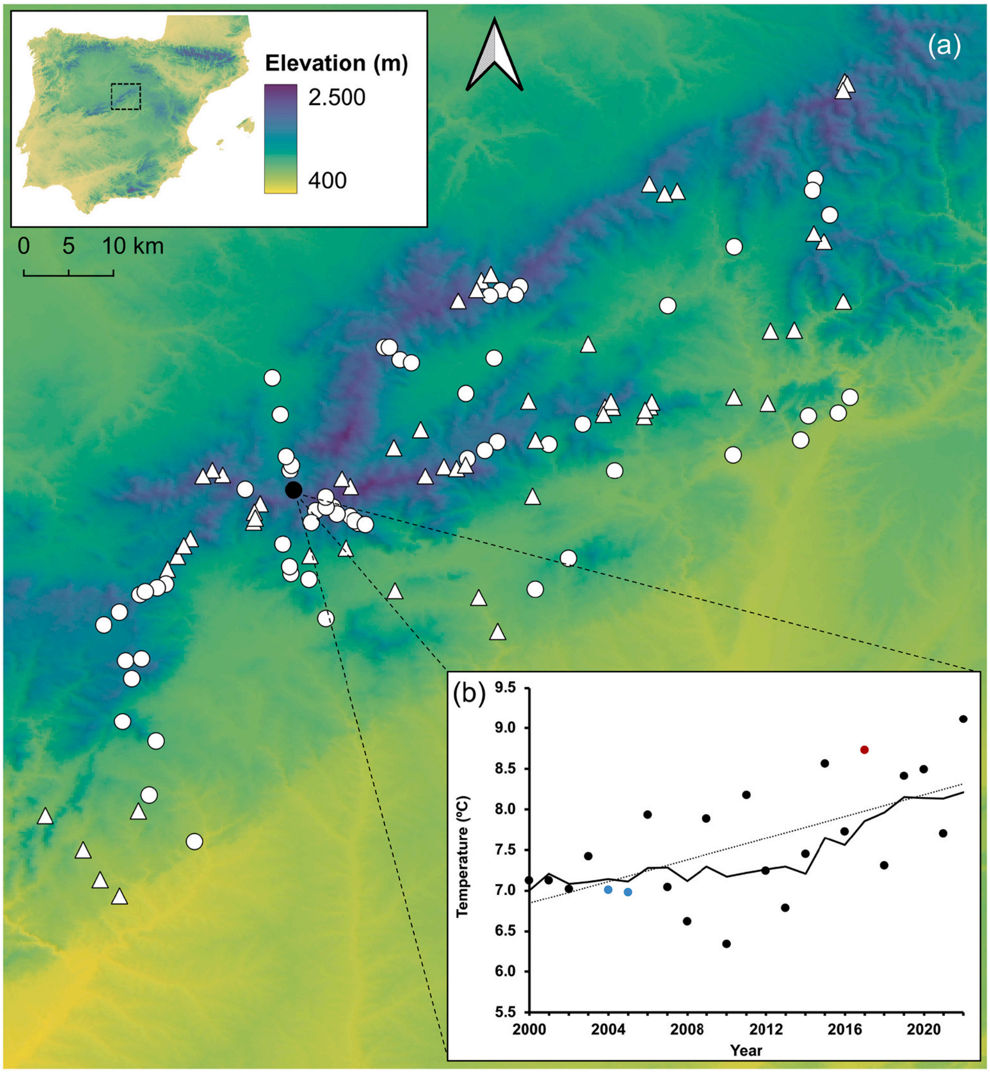

Fig. 1. Map of Sierra de Guadarrama (located between parallels 40° and 41°) with the location of the 120 sites visited in both periods: 2004–2005 and 2017 (a). Open circles and triangles show visits in 2004 and 2005, respectively. Filled circle shows the Puerto de Navacerrada Meteorological Station. Changes in mean annual temperature for the last 22 years (2000−2022) (i.e., increasing temperatures experienced in the area), with both periods highlighted (blue circles: 2004–2005; red circle: 2017) (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(https://pnoa.ign.es). Because vegetation within natural habitats is inherently interconnected (high adjacency), and thus, discrete non-adjacent patches cannot be produced correctly, we followed Kedron et al. (2019) by selecting height classes with a threshold approach based on DHM. In ArcGIS software (v. 10.5, www.esri.com), we made a buffer of 5 m around the 500 m transect for each of the 120 sites. We then extracted from the DHM the number of pixels (2 m) in each transect, and classified six vegetation classes (composition variables) based on maximum height in the pixel using the threshold approach, i.e., Forest-high (>15 m), Forest-mid (15–5 m), Forest-low (5–2 m), Scrubland (2–1 m), Meadow (1–0.5 m), and Meadow-Soil (<0.5 m), giving information on within-site habitat complexity. Finally, using pixel numbers in each class we extracted the proportion of each vegetation class in the buffers and calculated habitat heterogeneity as Shannon diversity index (SHDI) of LiDAR class (minus the sum of the pixels-based proportional abundance of each class multiplied by the natural logarithm of that proportion).

2.3.2. *Microclimate*

We used R software (R Developmental Core Team, 2023) to run all tests. R packages Microclima (Maclean et al., 2019) and NicheMapR (Kearney and Porter, 2017) were used to model the effects of topography on the temperature experienced near the ground. NicheMapR provides a vertical-flow air and soil microclimate model, and with the resulting data, Microclima calculates the effect of physical forcing on near-ground temperature. The resulting models allow for the estimation of hourly temperatures at fine spatial resolutions based on freely available high-temporal-resolution climate data (Kearney et al., 2020). We carried out microclimate modelling using the runauto function of package Microclima to integrate the mechanistic physical models of Microclima and NicheMapR for each of the 120 sites, using the centroid of each transect. We modelled microclimate based on open scrubland “H7” (Kearney and Porter, 2017), an intermediate openness class for the main vegetation found in the region, which ranges from meadows to pine forests. Soil and canopy albedo were set to 0.15 and 0.23 as default parameters. Microclima provides accurate measurements of maximum daily temperature near the ground in the Sierra de Guadarrama (Gómez-Vadillo et al., 2022). We estimated hourly temperatures 10 cm above the ground at 30 m resolution, and then calculated average monthly daily maxima for eight months: January to August (preceding and during the butterfly flight periods), for the sample years at each site.

2.4. Data analysis

2.4.1. Community diversity and thermal composition

To account for differences in abundance and survey effort in comparisons of species diversity, we took the recommended approach based on equal estimated sample coverage (Roswell et al., 2021). We used R package iNEXT (Hsieh et al., 2022) to calculate a diversity estimate for each site and period (2004–2005 versus 2017) accounting for the facts that abundance varied among sites and years, and that sites were visited 4 times in 2004 but 5 times in 2005 and 2017. iNEXT computes diversity estimates focusing on three measures of Hill numbers of order q: species richness ($q = 0$), Shannon diversity ($q = 1$, the exponential of Shannon entropy) and Simpson diversity ($q = 2$, the inverse of Simpson concentration) (Chao and Jost, 2015). The resulting diversity estimate qD (q 0 $\leq q \leq 3$) and the associated 95 % confidence intervals are calculated from the observed species counts and abundance data. We used the estimates of sample size-based sample coverage (SC) from iNEXT to set an equal threshold to compare diversity among sites and periods. SC for our observed data was $\geq$0.8 for all sites in both periods ($n = 240$), except for two sites in 2004–2005. Therefore, we estimated qD using rarefaction to SC = 0.8 for 237 sites, obtaining extrapolations to SC = 0.8 for 2004–2005 for these two sites and for the site at the threshold value.

We calculated the incidence-based CTI using the average Species Temperature Index (STI) – the long-term average experienced by individuals of a species over its range (Devictor et al., 2008) – of each species present at a site. We calculated one incidence-CTI per site and period using the STIs of butterflies based on mean 1981–2000 temperatures at 50 km resolution across their European ranges (Platania et al., 2020) (Supplementary material, Table S1).

2.4.2. Spatial autocorrelation and collinearity

Spatial autocorrelation can influence the reliability of spatial analyses, particularly for samples separated by short geographic distances. Mean distances among nearest neighbouring sites were 1.99 ± s.e.m. 0.15 km. The geographically closest sites were at high elevations (where accessibility was more limited but sites were widely separated in elevation), and at lower elevations most sites were much further apart (Supplementary material, Fig. S2). To examine spatial autocorrelation we created a contiguity-based spatial weights matrix for the transect buffers and centroids, and analysed local autocorrelation in GeoDa software (v. 1.20, geodacenter.github.io). There was no contiguity for the buffer (polygon) information. Conversely, centroid connectivity showed that there was geographical autocorrelation among 15 of 120 sites ($p < 0.01$), which were sites at higher elevations (Supplementary material, Fig. S2). Because spatial autocorrelation in these analyses does not account for elevation differences, we created higher order neighbours as *spatial lags* on the weights matrix using the R package spdep (Bivand et al., 2023) (set to order 3), i.e., all redundant and circular paths were removed (Anselin and Smirnov, 1996). Then to detect spatial autocorrelation in our response variables, we calculated Geary's C test of autocorrelation for qD and CTI in both periods with Monte-Carlo simulation in spdep. Geary's C is recommended instead of Moran's I when the response variable is not normally distributed (Schofield et al., 2007) because it takes into account the differences between observed values in two different sites, without using the average value of the response variable (Fortin and Dale, 2005). In this analysis, Monte-Carlo simulation ($n = 9999$) on Geary's C showed no autocorrelation for qD and CTI in both periods ($p > 0.05$). In both analyses 2.4.3. and 2.4.4. we also tested for spatial autocorrelation in the residuals of the selected models, using Moran's I because the residuals were Normally distributed.

Collinearity of predictor variables is known to influence model estimation and prediction (Dormann et al., 2013). We produced pairwise Spearman Rank coefficient correlograms for all explanatory variables using the R package GGally (Schloerke et al., 2021), to inspect collinearity based on a threshold of correlation coefficients <0.7 between predictor variables as an indicator (Supplementary material, Fig. S3). LiDAR variables Meadow-Soil and Forest-low showed high levels of collinearity with the rest of the LiDAR variables, so we removed them from analyses. Further, all microclimatic variables (monthly temperature maxima) showed high levels of collinearity, but with less collinearity among variables in 2004–2005 than 2017. Thus, because there are two sets of microclimatic variables (i.e., one set per period) we also inspected the amount of variance explained by each variable within both periods using principal components analysis (PCA) (Supplementary material, Fig. S4). Microclimatic information for March and June (i.e., MicroC-03 and MicroC-06 respectively) were selected to perform further analyses because of (1) a main effect between clusters of variables on axes 1 and 2 of the PCA and (2) the importance of spring and early summer temperatures for butterfly phenology and dynamics in the region (Gutiérrez and Wilson, 2021). Habitat heterogeneity (SHDI of LiDAR class) was calculated using the LiDAR vegetation classes, and thus showed high collinearity with the selected LiDAR classes, but showed low collinearity with microclimatic information.

2.4.3. Modelling community variation over space and time

In our first analysis we tested how qD and CTI varied with elevation and habitat heterogeneity among the two sample periods by fitting generalized additive mixed models (GAMMs) using the R package mgcv (Wood, 2023). For all models a smoothing function was used setting the basis dimension k of the smoothing parameter to 3. By setting $k = 3$, we limit the number of turns the curve is allowed to make, equalling a quadratic function. Models were fitted with a smoothing function of elevation and SHDI of LiDAR class (henceforth "habitat heterogeneity"), with period as a factor (2004–2005 vs 2017), and the interactions of elevation and habitat heterogeneity with period. We included the study site identity and sampled year ($n = 3$: 2004, 2005, 2017) as random intercept effects, setting data family to quasi-Poisson to account for overdispersion, and the smoothing procedure to restricted maximum likelihood (REML).

2.4.4. Testing micro-habitat effects on community change

In our second analysis we sought to test how fine-scale variation in microclimate and vegetation classes were related to changes in qD and CTI over time. In these models the response variables were the changes to qD and CTI between periods ($q\mathrm{D}_{\mathrm{recent}}$ - $q\mathrm{D}_{\mathrm{historic}}$ and $\mathrm{CTI}_{\mathrm{recent}}$ – $\mathrm{CTI}_{\mathrm{historic}}$), and the explanatory variables were MicroC-03 (2004–2005), MicroC-06 (2004–2005), MicroC-03 difference, MicroC-06 difference (changes to the microclimate terms from 2004-05 to 2017), and the proportion of Meadow, Scrubland, Forest-high, and Forest-mid. To account for the effects of these multiple variables, we used multi-model inference (Burnham and Anderson, 2002). We fitted two generalized linear models (GLMs) as global models for the changes to qD and CTI between periods. Before model fitting, all explanatory variables were standardized (mean centred and scaled). Multi-model inference was conducted using all possible combinations of the predictors, with models ranked using the Akaike information criterion (AIC) (Burnham and Anderson, 2002). The significance and contribution of the variables was extracted only by model averaging of the best models setting ΔAIC <2. The procedure was computed using the R package MuMIn (Bartón, 2023).

3. Results

3.1. Community variation over space and time

Overall, we recorded 26,977 individuals of 101 butterfly species in 2004–2005, and 42,674 individuals of 106 species in 2017 (total: 106 species, supplementary material Table S1).

In the GAMM, qD showed a humped relationship with elevation, with the highest species diversity in mid-elevation sites (Fig. 2a), and a positive relationship with habitat heterogeneity (Fig. 2b). The

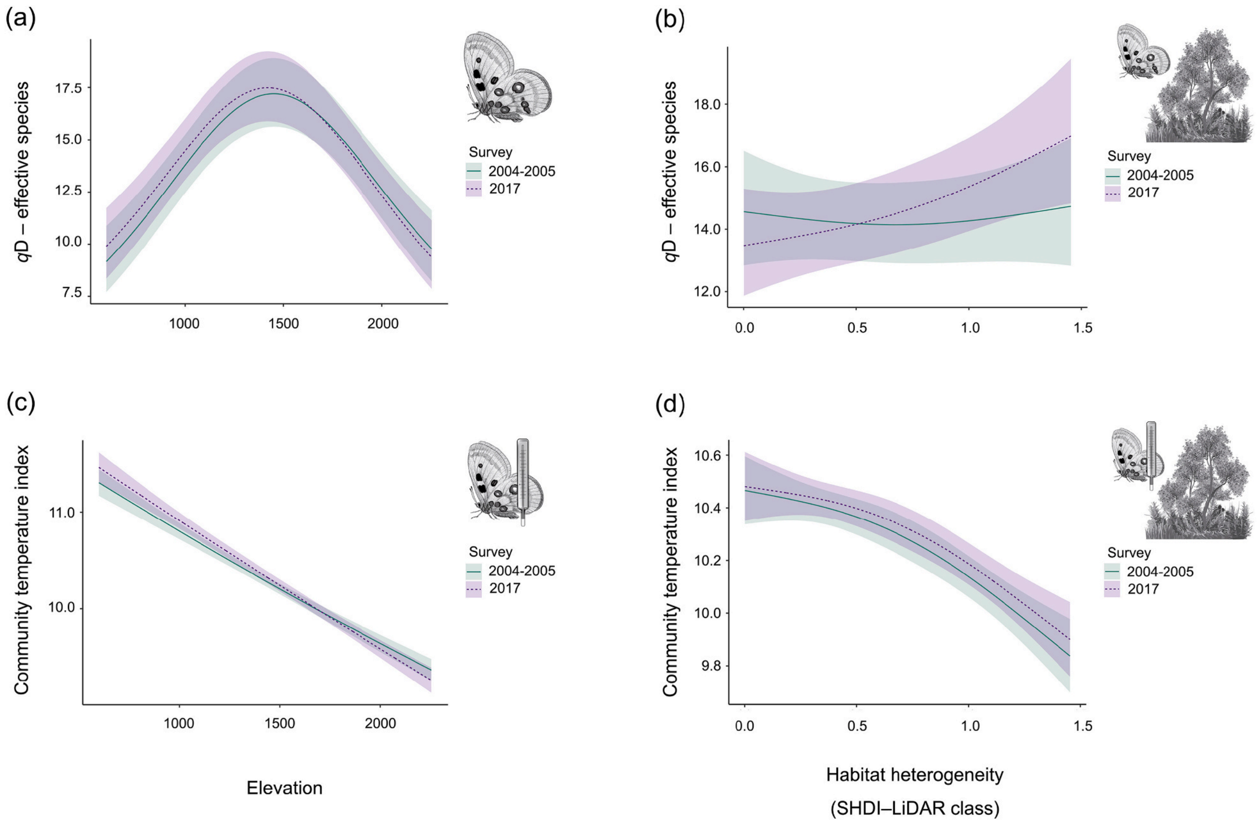

Fig. 2. Modelled relationships based on generalized additive mixed models (GAMMs) of the diversity estimator of order *q* (*q*D) and the community temperature index vs elevation (a, c) and habitat heterogeneity (SHDI of LiDAR class) (b, d). The tendencies are shown based on 120 sites in the Sierra de Guadarrama between two periods (2004–2005 vs 2017) ($n = 240$). *Parnassius apollo* illustration source: Das kleine Schmetterlingsbuch: Die Tagfalter, Insel- Bücherei No. 213.

relationship of *q*D with elevation did not differ between periods (2004–2005 vs 2017), but with habitat heterogeneity the relationship became stronger over time (i.e., significant interaction of period with habitat heterogeneity but not with elevation; Table 1). Therefore, when we plotted the response of *q*D integrating the effects of elevation and habitat heterogeneity, the highest *q*D values shifted from sites at middle and high elevations with mid-levels of heterogeneity, to the mid elevations with the highest heterogeneity (Fig. 3).

Table 1
Generalized additive mixed models (GAMMs) for community variation with elevation and habitat heterogeneity, for 120 sites over two periods (2004–2005 vs 2017) ($n = 240$). Community descriptors are the diversity estimator of order *q* (*q*D) and the community temperature index (CTI). Habitat heterogeneity is measured as the Shannon diversity index of LiDAR vegetation height class (SHDI-LiDAR class). Models were fitted with smoothing functions for the community descriptors against elevation, habitat heterogeneity and their interactions with period, including study site and sample year as random effects. Modelled relationships are shown in Fig. 2.

Response variable	Predictor	Estimate (parametric)	EDF (smooth)	*p* value		Adjusted R^2	Deviance explained	Family	Link function
qD	Period	0.012	–	0.541	n. s.	0.597	70.90 %	quasi-Poisson	Log
	Elevation	–	1.983	<0.001	***				
	Elevation:period	–	1.000	0.291	n. s.				
	Habitat heterogeneity	–	1.387	0.767	n. s.				
	Habitat heterogeneity: period	–	1.000	0.016	*				
	Study site (random effect)	–	64.720	<0.001	***				
	Sampled year (random effect)	–	1.60e-07	<0.001	***				
CTI	Period	0.002	–	0.214	n. s.	0.870	91.10 %	quasi-Poisson	Log
	Elevation	–	1.000	<0.001	***				
	Elevation:period	–	1.327	0.047	*				
	Habitat heterogeneity	–	1.792	<0.001	***				
	Habitat heterogeneity: period	–	1.001	0.632	n. s.				
	Study site (random effect)	–	69.170	<0.001	***				
	Sampled year (random effect)	–	2.88e-09	0.43	n. s.				

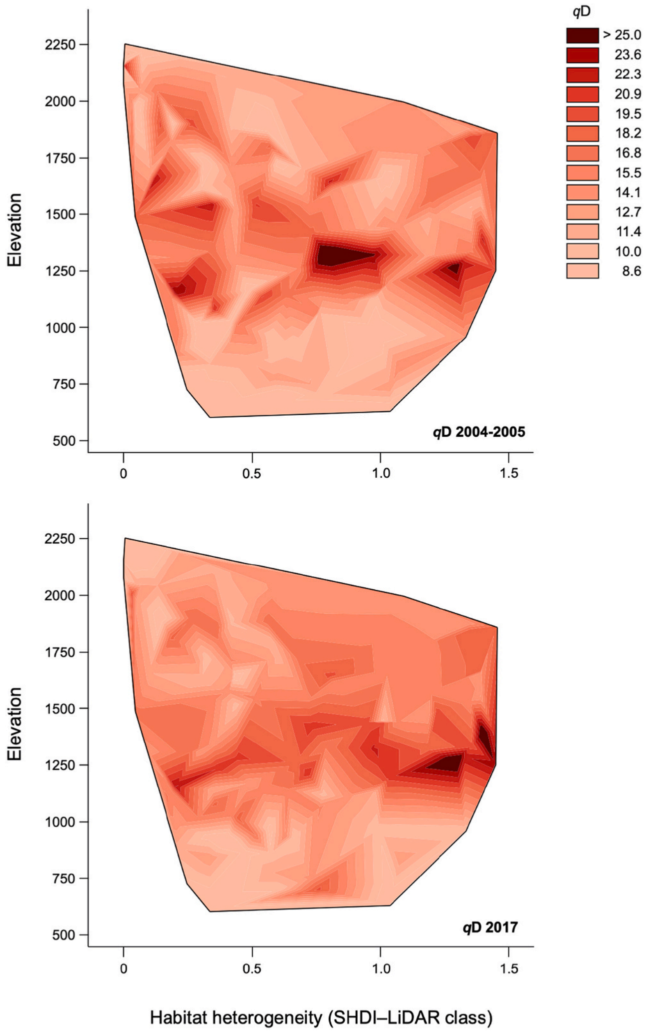

Fig. 3. Response of the diversity estimator of order *q* (*q*D) across elevation and habitat heterogeneity. The contour plots show the response values and desirable operating conditions. The predictor on the X axis was the Shannon diversity index (SHDI) of LiDAR class, and the predictors on the Y axis was elevation. Contour lines connect points that have the same adjusted response value integrating the data of *q*D across the 120 sites. The form of the aggregate is given by the variable in Y axes and sites.

CTI was negatively related to both elevation and habitat heterogeneity (Fig. 2c, d): in other words, incidence of warm-adapted species was greater at low elevations or in sites with less heterogeneous vegetation, whereas cool-adapted species predominated at high elevations or in more heterogeneous sites. We did not find evidence that CTI increased over time; instead, there was a significant interaction between elevation and period, suggesting that CTI reduced at high elevations over time, but no significant interaction between habitat heterogeneity and period (Table 1).

Habitat heterogeneity (SHDI of LiDAR classes) had a humped relationship with elevation, being greater at mid-elevation sites (Supplementary material, Fig. S5). GAMM residuals showed no spatial autocorrelation apart from in the case of *q*D modelled for 2017 (Supplementary material, Table S2).

3.2. *Micro-habitat effects on community change*

In the GLM model selection and averaging for change in *q*D, the only variables with significant effects were coverage of Forest-mid (positive) and MicroC-06 difference (negative) (Table 2). Thus, species diversity increased more in sites with relatively high cover of 5–15 m high forest, and where June temperatures did not increase.

Model averaging showed that microclimatic variables were the main factors explaining the difference in CTI between periods, with positive effects on CTI change from both 2004–2005 March temperatures (MicroC-03) and increases in March temperatures to 2017 (MicroC-03 difference) (Table 2). Hence, in sites where topography led to high and increasing spring temperatures, CTI also increased.

GLM residuals showed no spatial autocorrelation (Supplementary material, Table S2).

4. Discussion

In common with other taxonomic groups, butterflies have responded to climate warming with elevation range shifts and accompanying changes to community composition (Kerner et al., 2023; Parmesan, 1996; Wilson et al., 2007). However, community-level changes such as increases in the community temperature index (CTI) have rarely if ever kept pace with rates of climate change (Devictor et al., 2008, 2012; Lajeunesse and Fourcade, 2023; Nieto-Sánchez et al., 2015). This prompts efforts to understand the factors causing delayed responses to climatic change and their implications for conservation (Jackson and Sax, 2010; Rumpf et al., 2019). Elevation gradients in the diversity and composition of butterflies in the Sierra de Guadarrama showed little change between two periods separated by 12–13 years of warming. The results suggest that delays in community tracking of climatic conditions arise partly from positive effects of topographic and habitat heterogeneity providing microhabitats and microclimatic conditions that help to maintain alpha diversity and community temperature index. By extrapolation, delays in increases to species richness or CTI at high elevations could also result from barriers to colonization at species range edges.

4.1. *Gradients in diversity and composition*

Discrepancies between community responses to warming and rates of change in climatic gradients have been explained by fine-scale variation in both habitat and the microclimates that populations experience (De Frenne et al., 2013; Maclean et al., 2015). We therefore examined how the effects of habitat heterogeneity, quantified using LiDAR, and variation in topographically driven microclimates influenced elevation gradients in butterfly communities. A humped relationship between butterfly diversity and elevation (Gutiérrez Illán et al., 2010; Wilson et al., 2007) was maintained between 2004–05 and 2017, with no evidence of systematic changes related to warming (Fig. 2a). Instead, a positive relationship between butterfly diversity and habitat heterogeneity became stronger (Fig. 2b). Thus, although the diversity peak remained at mid-elevations (*c.* 1200–1400 m), by 2017 the most diverse communities were associated with more structurally diverse habitats (Fig. 3). The possible role of local habitat heterogeneity in maintaining or increasing species richness between periods is further indicated by the positive effect of forest cover on changes to diversity (*q*D) (Table 2).

As expected, there was a negative elevation gradient in butterfly CTI, with greater incidence of warm-adapted species in warmer, lower elevation sites. However, changes over time to CTI were not consistent over the elevation gradient, generally being more positive at low- and mid-elevation sites, but negative at high elevations (Fig. 2c). We found that where modelled spring temperatures increased most, thermophilization of the community was greater (CTI difference, Table 2). A previous study of changes to CTI across an independent set of communities in the same region found evidence of increasing CTI across the elevation gradient between 1967–73 and 2006–12, with reduced rates of CTI change in sites with greater cover of forest and meadows (Nieto-Sánchez et al., 2015). Our results show that variation in topographically-driven microclimates also influence rates of CTI change.

Table 2
Models for the effects of micro-habitat on changes in community diversity and CTI. Multimodel Inference summary statistics are shown for generalized linear models (GLMs) of the differences between 2004 and 05 and 2017 in site *q*D and CTI. The full sets of 255 models use as explanatory variables four vegetation LiDAR height classes, 2004–05 microclimatic maximum temperatures in March (MicroC-03) and June (MicroC-06), and changes to the temperatures between the two periods. Only variables and results returned from model averaging of the best models (ΔAIC <2 – see N overall models) are presented, with the number of selected models containing each variable shown. In both cases ΔAIC was >2 for the null model.

Variable	Predictor	Estimate	SE	Adjusted SE	z value	*Pr*(>|z|)		*N* containing models	*N* overall models
qD (difference)	(Intercept)	0.341	0.377	0.381	0.895	0.371	n.s.	–	12
	Forest-mid	0.930	0.437	0.441	2.109	0.035	*	2	–
	MicroC-06 difference	−1.014	0.440	0.444	2.282	0.023	*	7	–
	Forest-high	0.842	0.477	0.481	1.749	0.080	n.s.	1	–
	MicroC-06 2004-2005	0.744	0.543	0.547	1.360	0.174	n.s.	5	–
	Scrubland	0.423	0.414	0.418	1.012	0.312	n.s.	8	–
	Meadow	0.471	0.384	0.388	1.214	0.225	n.s.	3	–
	MicroC-03 2004-2005	0.328	0.406	0.410	0.801	0.423	n.s.	4	–
	MicroC-03 difference	−0.375	0.643	0.650	0.576	0.564	n.s.	6	–
CTI (difference)	(Intercept)	0.039	0.029	0.029	1.356	0.175	n.s.	–	5
	MicroC-03 2004-2005	0.099	0.043	0.043	2.293	0.022	*	2	–
	MicroC-03 difference	0.084	0.038	0.038	2.204	0.028	*	4	–
	Meadow	0.022	0.031	0.031	0.715	0.475	n.s.	1	–
	MicroC-06 difference	−0.057	0.031	0.031	1.822	0.069	n.s.	5	–
	MicroC-06 2004-2005	0.052	0.030	0.030	1.729	0.084	n.s.	3	–
	Scrubland	0.013	0.031	0.031	0.425	0.671	n.s.	6	–

4.2. Constraints on climatic equilibria

The consistent elevation gradients in species diversity and CTI in 2004–05 and 2017 provide little evidence that communities were tracking climate change over time. Our results particularly for diversity (*q*D) show that vegetation may play a key role in modulating the rates at which communities change. The Sierra de Guadarrama is characterised by less structurally diverse habitats at the highest (grasslands and shrubs) and lowest elevations (sclerophyllous woodland and pasture), with forest at mid-elevations (deciduous c. 1000–1500 m; pine c. 1500–2000 m). As in other regions of Mediterranean Europe, forest structure has changed recently, with tree densification following grazing abandonment (Morales-Molino et al., 2017; Pardo and Gil, 2005; Tellería, 2020). Butterflies associated with closed vegetation in the Sierra de Guadarrama (Caro-Miralles and Gutiérrez, 2023) and other regions of Spain (Barea-Azcón et al., 2023; Mora et al., 2022; Ubach et al., 2020) have recently shown the most positive population trends. In our system there is likely to be some increase of species richness caused by the colonization of increasingly wooded habitats by these species associated with closed conditions (Fig. 4). Expansions by woodland associated birds in response to afforestation have also counteracted responses expected from warming for bird communities in the Sierra de Guadarrama (Tellería, 2020), and other mountain systems in Spain (Clavero et al., 2011).

In addition, changes to both *q*D and CTI suggest a role of persistence by species in locations where topography has reduced microclimatic warming. *q*D change over time showed a negative relationship with microclimatic warming in June (i.e., where summer temperatures increased more, diversity decreased), whereas CTI change was positively related to March microclimatic warming (community composition changed more where spring temperatures warmed the most). These results suggest that sheltered locations such as narrow river valleys or north-facing slopes which experience reduced rates of warming (Fridley, 2009; Maclean et al., 2015; Stark and Fridley, 2022) might have buffered populations against possible negative impacts of warming, maintaining species richness and delaying increases in CTI.

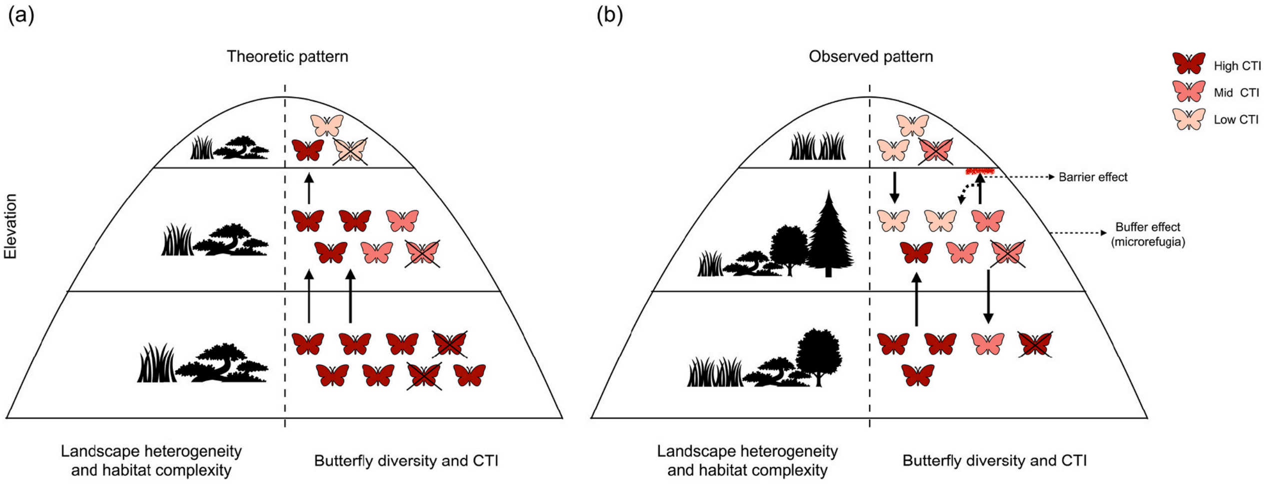

Fig. 4. Patterns of change in local communities over elevation gradients in mountains. Theoretically, if species' climate tolerances are constant over time they will shift their distributions to track climate warming (equilibrium process), so in the absence of lowland colonizations by species at leading edges of their latitud range diversity is expected to reduce at low elevations but increase at high elevations producing community thermophilization (communities increasingly dominated by warm-associated species). This pattern may be possible only if vegetation is the same over the altitudinal gradient (a). Conversely, the observed pattern suggests species local extinctions over the gradient but with colonizations towards mid elevations of both cold and warm-associated species due to microrefugia created by higher habitat heterogeneity (buffer effect) and constraints produced by low levels of resource availability at mountain peaks (barrier effect) (b). The pattern is based on Community Temperature Index (CTI) of butterfly local communities in the Sierra de Guadarrama.

The changes we observe over this elevation gradient illustrate possible buffering versus barrier effects of landscape structure on community responses to climate change (Fig. 4). Towards warming low-elevation limits, populations can persist by exploiting cool microclimates in topographically variable locations (Suggitt et al., 2018) or shady habitats (McGinn et al., 2023). In contrast, although animals may be dispersive enough to reach sites above existing cool range limits, suitable habitat or host resources may not be present (Gutiérrez et al., 2016), especially if resource species are shifting uphill more slowly than their consumers (Kerner et al., 2023). Furthermore, because climatic conditions are not warming uniformly over time, newly founded small populations of ectotherms occupying marginal climates may be vulnerable to stochastic local extinction (Bennie et al., 2013). The uniform distribution of resources and gradual rates of warming that would lead to consistently higher rates of colonization by warm-associated species at higher elevations (Fig. 4a) is rarely likely to occur, producing delays in the rates at which communities track climate change over elevation gradients (Bowler and Böhning-Gaese, 2017; McCain and Garfinkel, 2021). Instead, we show how community responses can be delayed when habitat heterogeneity and microclimatic conditions vary over space and time (Fig. 4b). Delays in colonization at the leading edges of elevation ranges are always likely to be present because of limitations to dispersal, resource availability and effects of environmental stochasticity on newly founded small populations (Rumpf et al., 2019). On the other hand, whereas climatic extremes might cause rapid population losses at trailing edges, recolonizations during cooler years may be possible as long as some populations of cool-associated species are able to persist nearby in cool microrefugia provided by habitat heterogeneity or topography (Suggitt et al., 2018), delaying increases in CTI (Mingarro et al., 2021).

The use of temporal snapshots to detect ecological responses to global change has limitations because of interannual variation in environmental conditions and population dynamics (Stuble et al., 2021). In this respect, variability in insect populations can undermine evidence of changes to their abundance or distribution (Didham et al., 2020). We used rarefaction to ensure that our measures of butterfly diversity over space and time were comparable; and the estimated sample completeness for species included in our calculations of site CTI were high (average = 0.951 ± 0.002). However, we acknowledge that changes to the abundance and detectability of component species from year to year superimpose noise on underlying changes to distributions and communities. We note, however, that the potentially wide stochasticity of environmental conditions and hence dynamics at environmental range limits (Oliver et al., 2012) is a factor likely to delay the tracking of underlying trends in the climate.

5. Conservation implications

Delays in community responses to warming provide opportunities to adapt conservation management, but demand understanding of the factors favouring persistence on the one hand or colonization on the other. Fourcade et al. (2021) noted for fragmented lowland landscapes that persistence of cool-adapted or declining species was favoured by large, high-quality habitats, whereas hot-adapted expanding species benefited from widely spread habitats in the landscape (see also Fernández-Chacón et al., 2014). As a result, in north-Western Europe the ranges of declining species have become increasingly patchy as they contract to refugial landscapes, whereas advancing species show aggregated distributions around expanding fronts (Wilson et al., 2004). Species should find it easier to shift their ranges over elevation gradients, because the distances are shorter and habitats are often less degraded (Fernández-Chacón et al., 2014), but most evidence suggests significant delays in apparent tracking of climatic conditions by communities over elevation gradients (e.g. Rumpf et al., 2019). Our results suggest that this is at least partly because local microclimatic variation, which may not be detected using coarser scale data, permits populations to persist or undergo short distance relocations to exploit the microclimatic variation created by topography (see also Maclean and Early, 2023). Our microclimate models did not include the effects of vegetation, but the positive effects we find of vegetation complexity on diversity could also be because vegetation is modulating microclimates over and above the effects of topography (De Frenne et al., 2013). Maintaining, managing, and monitoring a wide range of habitats occurring in varying topographic conditions over elevation gradients is therefore likely to be valuable in conserving communities in a changing climate (see Suggitt et al., 2018).

In terms of the limits to range expansion, in the case of phytophagous insects the speed with which larval resources are able to expand their distributions is likely to be a limiting factor (Gutiérrez et al., 2016; Kerner et al., 2023). At high elevations or other cool range limits, high levels of environmental stochasticity also reduce chances of population establishment, although establishment is favoured by high connectivity between habitats or landscape permeability (Bennie et al., 2013; Fernández-Chacón et al., 2014). Overall, however, evidence that heterogeneity in topography, vegetation and hence in the microclimates that populations experience can reduce risk of local extinction across wide environmental gradients mean that it makes sense to concentrate conservation resources on the core of species ranges, and moreso because we do not yet have ubiquitous or accurate estimates of fine-resolution microclimates and species' climatic limits (Maclean and Early, 2023). In the case of elevation gradients, concentrating resources on locations of highest diversity or unique (e.g. endemic) taxa is a greater priority than ensuring that communities are tracking climatic change. In large flat anthropogenic landscapes which provide reduced variability in microclimate or habitat complexity, in contrast, there may be more concern about ensuring that species can colonize at their leading range edges (Platts et al., 2019).

Apart from the importance of including fine-resolution information on habitat heterogeneity or microclimate, the results also suggest the possible importance of understanding the factors driving the responses of different component species in communities. We included microclimatic temperatures for March and June in our models, which are known to influence butterfly phenology and population dynamics in the region (Gutiérrez and Wilson, 2021), and found effects of both on diversity and CTI. Both periods are likely to be important for the butterfly community, particularly for larvae feeding in springtime and for adult activity in summer, but different species show differences in sensitivity periods, which appear to be key for individual species population trends, and hence for understanding and managing how communities change (see Colom et al., 2022).

Overall, our results suggest that it is unlikely that gradients in community diversity and composition will track prevailing changes to the climate, or at least that there will be substantial delays in the rates that they do so. Instead, local effects on population dynamics of variation in habitat structure, resource availability, and microclimate could play important roles both in buffering local populations against warming, or in imposing barriers to range expansion, leading to delays in overall community responses. Understanding these factors and their effects will provide valuable guidance for adapting conservation to climate change.

CRediT authorship contribution statement

HA, EW and RW conceptualized the study. JPC, LB and RW developed methodology and undertook field investigation. JPC, LB, GU and MM curated data. HA, MM, GU and EW developed and conducted formal analysis, validation and visualisation of results. RW acquired funding, administered and supervised the project. HA, EW and RW prepared the original draft. All authors contributed to writing review and editing.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110389.

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