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RESEARCH ARTICLE OPEN ACCESS

Local Climatic Effects on Colonisation and Extinction Drive Changes in Mountain Butterfly Communities

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Received: 10 May 2024 | **Revised:** 10 December 2024 | **Accepted:** 18 December 2024

Editor: Rob Cooke

Funding: This work was supported by Ministerio de Ciencia, Innovación y Universidades, MCIN/AEI/10.13039/501100011033, PID2021-126293OB-I00, RTI2018-096739-B-C21 and PRE2019-091025. Biodiversa+, PCI2022-135061-2.

Keywords: climate change | community temperature index (CTI) | extirpation | immigration | lepidoptera | local climate | spatial heterogeneity | thermophilisation

ABSTRACT

Aim: The capacity of cool refugia to protect cold-adapted species against climate change may depend on both their initial climatic conditions and how quickly these change. We test how local climatic conditions influence mountain butterfly communities via their effects on colonisation and local extinction.
Location: Four mountain ranges in Central Spain.
Methods: We used community temperature index (CTI), based on the climatic niches of constituent species (species temperature index, STI), to estimate thermal affinities for butterfly communities sampled in 1984–2005 to 2017–2022. We related CTI to local temperature, estimated using the model *Microclima*, and tested for changes to local temperature and CTI over time. We used standard deviation in CTI (CTI_{SD}) and species richness to detect effects of colonisation and local extinction on community change. Finally, we tested for differences in thermal affinity and thermal niche breadth (STI_{SD}) between species undergoing local extinction or colonisation at each site.
Results: CTI was positively related to local temperature in both periods. However, there were regional differences in rates of change in CTI and local temperature. CTI increased overall, even though temperatures decreased at many sites; and CTI increases were greatest in historically cool sites. Neither CTI_{SD} nor species richness changed overall, suggesting that communities experienced equivalent numbers of colonisations and extinctions. Colonising species had warmer thermal affinities than those undergoing local extinction, and species with broader thermal niches increased their occupancy most over time.
Main Conclusions: Local climatic conditions influenced changes to community composition based on species thermal tolerances, resulting in the loss of communities where cool-affinity species predominated, and a narrower range of community thermal affinities overall. Our results suggest that a regional perspective to identifying climate change refugia is needed to provide a wide range of local climate conditions and rates of change to help adapt conservation to climate change.

Diversity and Distributions, 2025; 31:e13967
https://doi.org/10.1111/ddi.13967

1 | Introduction

Ecosystem resilience in response to climate change is a topic of broad concern (Parmesan et al. 2022; Trisos, Merow, and Pigot 2020). As geographic ranges shift polewards and uphill in response to warming (Chen et al. 2011; Lenoir et al. 2020), communities are increasingly dominated by species with warm thermal affinities (community 'thermophilisation') (Lajeunesse and Fourcade 2023; Sagarin et al. 1999). Thermophilisation results from colonisation by species with warm affinities (tropicalisation) and/or local extinction of species with cool affinities (deborealisation) (McLean et al. 2021). However, the relative roles of colonisation and local extinction, and consequences for ecosystem function, have rarely been assessed (Gaget et al. 2021; Hemberger and Williams 2024; Khaliq et al. 2024). Landscapes that can accommodate range shifts while supporting cold-adapted species may be critical for conservation (Fourcade et al. 2021), as exemplified by 'refugia' that provide localised cool or stable climatic conditions (Ashcroft et al. 2012; Dobrowski 2011). Extinction risk at a landscape scale (10 km) was reduced for warming-sensitive insects and plants in the most climatically heterogeneous landscapes in England (Suggitt et al. 2018). However, local climatic heterogeneity could benefit cold-adapted species either by providing some extremely cool localities that retain suitable conditions despite regional warming, or because local climatic conditions do not change uniformly, warming more slowly or even cooling down in some places (Maclean et al. 2017; Stark and Fridley 2022). Here, we assess the effects of local climatic conditions on communities, to improve our capacity to anticipate community change, prioritise microrefugia and adapt conservation to climate change.

The thermal affinity of a species or species temperature index (STI) can be estimated as the average temperature across its geographic range (Devictor et al. 2008). Community-level effects of climate change can then be assessed via changes to the community temperature index (CTI), the average STI of species present (Bowler and Böhning-Gaese 2017). Thermophilisation has been deduced from CTI increases in many taxa (Khaliq et al. 2024; Lajeunesse and Fourcade 2023). The respective roles of colonisation and local extinction can also be inferred, from changes either in the range of thermal affinities (standard deviation in STI values, or $\mathrm{CTI}_{\mathrm{SD}}$; Gaget et al. 2021) or in species richness (Álvarez et al. 2024). Both $\mathrm{CTI}_{\mathrm{SD}}$ and species richness should increase if colonisations exceed extinctions, decrease if extinctions prevail, but not change if there are equivalent rates of colonisation and extinction (Figure 1). CTI increases driven primarily by extinctions are concerning since they imply that many species have already begun to exceed thermal thresholds in parts of their geographic ranges (Pigot et al. 2023).

Changes to community thermal affinities over latitude or elevation gradients can demonstrate whether communities are tracking climate change (Devictor et al. 2012; Hemberger and Williams 2024). In many taxa, including butterflies, rates of thermophilisation have not tracked warming (Howard et al. 2023; Lajeunesse and Fourcade 2023; Nieto-Sánchez,

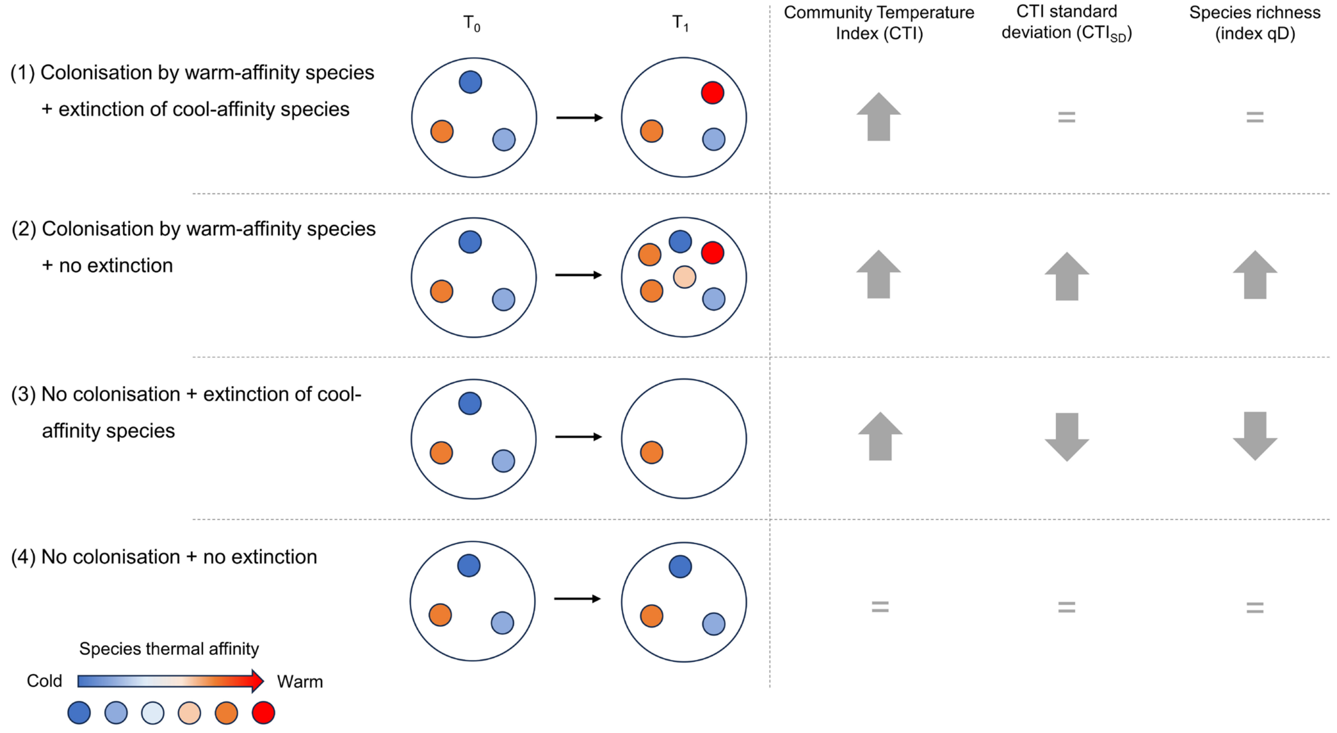

FIGURE 1 | Expected results for community metrics (CTI, $\mathrm{CTI}_{\mathrm{SD}}$ and species richness) depending on which process is dominant in community turnover. T_0 represents historical communities and T_1 recent communities. Community temperature index (CTI) is the average across all species thermal affinities present in a community. CTI standard deviation ($\mathrm{CTI}_{\mathrm{SD}}$) is the variation across these thermal affinities. Species richness (qD) represents the number of species in a community. $\mathrm{CTI}_{\mathrm{SD}}$ is expected to increase where colonisation predominates (because species with warm affinities extend the range of STIs), to decrease where local extinction is more important (because losing species with cool affinities reduces STI range), but not to change if there are similar rates of colonisation and extinction. Figure adapted from Gaget et al. (2021).

Gutiérrez, and Wilson 2015). In the Iberian Peninsula, for example, butterfly CTI has not increased at a regional scale (10 km) despite rising temperatures, especially where topography provides heterogeneous climatic conditions and/or slower local rates of warming, such as in inland mountain ranges (Mingarro et al. 2021). Climatic conditions experienced by organisms in mountains are influenced by elevation, slope, aspect and shading by topography or habitat (Pincebourde et al. 2016), and this fine-scale variation affects responses by small ectotherms (Pincebourde and Woods 2020). However, local climate effects on colonisation and extinction in mountains have rarely been assessed because of few sufficiently fine-scale meteorological data (Kilibarda et al. 2015). This need for reliable estimates of temperatures can now be overcome using mechanistic models such as *Microclima* (Kearney et al. 2020; Maclean, Mosedale, and Bennie 2019). Temperatures estimated by *Microclima* have been validated using in situ temperature data (Baker et al. 2021; Brusse et al. 2024; Gómez-Vadillo et al. 2022), and have been used to assess ecological effects of local climate in several taxa (Ramos et al. 2023; Turner and Maclean 2022).

Here, we test how local climate influences community change via the processes of colonisation and extinction, by combining fine-scale field data on mountain butterfly communities with a mechanistic climatic model. First, we analyse how local climate and its temporal change influence community thermal associations using CTI, and whether community change has resulted predominantly from colonisation or extinction, using $\mathrm{CTI_{SD}}$ and species richness. Second, we test for differences in thermal affinities between species experiencing colonisation and local extinction, and whether temporal change in species occupancy is explained by their thermal affinity or their thermal niche breadth. Both analyses are based on data across four mountain ranges in Central Spain to account for regional differences in prevailing temperatures and rates of change. Overall, we aim to test at a fine spatial resolution how the capacity of localised refugia to protect warming-sensitive taxa from climate change is linked to historically cool conditions or rates of change.

2 | Methods

2.1 | Study Area and Butterfly Sampling

Many butterflies are restricted to mountain ranges in the Iberian Peninsula, where they reach their warm range limits and are threatened by climate change (Romo, Munguira, and García-Barros 2007; Romo et al. 2023). We sampled four mountain ranges in Central Spain, taking advantage of historical butterfly data recorded between 1984 and 2005 (Figure 2, Table S1). Our 75 field sites occur at a similar latitude (40°04′ to 41°00′ N) but differ in longitude (1°00′ to 5°50′ W): 13 sites in Sierra de Gredos (395 to 1955 m above sea level), 32 sites in Sierra de Guadarrama (928–2252 m); 20 sites in Sistema Ibérico Meridional (1066–1622 m) and 10 sites in Sierra de Javalambre (1114–2010 m). Vegetation changes similarly over elevation in the four regions, with scrub or evergreen woodland (mainly *Quercus rotundifolia*, or *Juniperus thurifera*) at low elevations, deciduous woodland (mainly *Quercus pyrenaica* or *Q. faginea*) around 1000–1500 m, and pine forests (mainly *Pinus sylvestris*) and rocky grassland at higher elevations. The Sierras de Gredos and Guadarrama are mainly composed by granitoids and have steep elevation gradients; while the Sistema Ibérico Meridional and Javalambre have gentler landscapes with more topographic diversity, formed by limestones. Temperature recorded at meteorological stations declines by 5.9°C per 1 km increase in elevation (Wilson et al. 2005), and has risen across all study regions by an average of 0.056°C/year in the last four decades (Table S2). Fine-scale rates of climatic change differ depending on prevailing weather and local topography (Gómez-Vadillo et al. 2022). Precipitation increases with elevation, but trends in precipitation are regionally variable (Serrano-Notivoli et al. 2018).

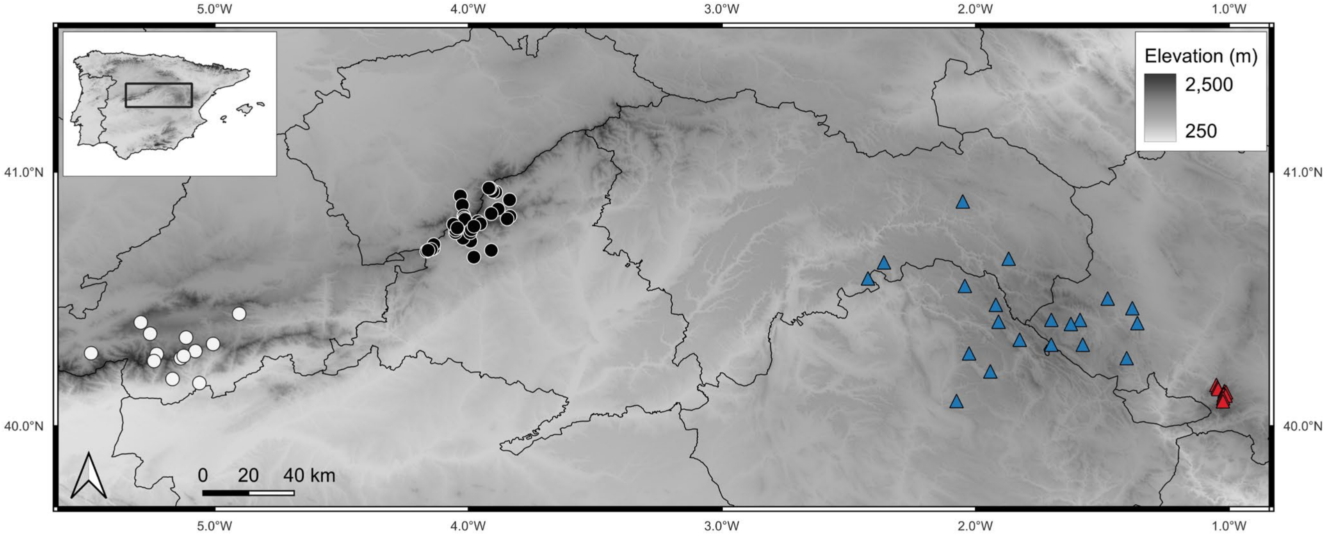

FIGURE 2 | Map of the four study areas: From west to east, study sites in Sierra de Gredos (white circles), Sierra de Guadarrama (black circles), Sistema Ibérico Meridional (blue triangles) and Javalambre (red triangles). Inset map shows location in central Spain. Digital Elevation Map downloaded from Centro Nacional de Información Geográfica (CNIG). Solid lines show boundaries of Spanish administrative provinces.

In all regions, sample sites were open areas across the elevations and habitat types available (e.g., meadows, woodland clearings, openings in scrub). Historical surveys for three regions (Gredos, Sistema Ibérico Meridional and Javalambre) were conducted by capturing any butterfly encountered during site visits, in different years between 1984 and 1991 (Supporting Information: Methods 1.1, Table S1). In the fourth region (Sierra de Guadarrama), 500 m long transects were conducted every 3 weeks between May and August either in 2004 (21 sites, four visits) or 2005 (11 sites, five visits) (Gutiérrez-Illán, Gutiérrez, and Wilson 2010). Butterflies were sampled by walking at a constant speed, counting all individuals observed 5 m in front and 2.5 m to each side, during sunny, not overly windy conditions between 09:30 and 17:30 CET. Recent data were collected between 2017 and 2022 in all regions following the same sampling regime as for 2004 and 2005 in Sierra de Guadarrama. We established 500 m transects where historical surveys had been conducted, after consulting authors of the original studies. During recent surveys, sites in each region were sampled for at least 2 years to reduce possible effects of interannual variation on inferred changes to communities over time (Stuble et al. 2021) (Supporting Information: Methods 1.2, Table S1). All butterflies were identified to species level except the genera *Pyrgus* and *Carcharodus*, because of concern about reliability of field identification to species level, which were excluded from analyses.

Analyses use surveys grouped into two time periods by combining visits per site for each period: 1984–2005 (historical) and 2017–2022 (recent). For analyses, species were considered present at a site in each period if at least one individual was recorded. We took this approach to reduce effects on communities of annual stochasticity in climate and population dynamics.

2.2 | Local Climate Modelling

To characterise fine-scale climatic conditions in each period, and how these changed over time, we modelled local climate temperatures at 30 m resolution using the packages *Microclima* (Maclean, Mosedale, and Bennie 2019) and *NicheMapR* (Kearney et al. 2020) in *R 4.2.2* (R Core Team 2022). Based on digital elevation models and freely available high temporal resolution climate data, *NicheMapR* models vertical air flow and soil microclimate, and *Microclima* uses the outputs to model hourly temperatures near the ground. We used the *runauto* function in *Microclima* to model temperature 10 cm from the ground for the habitat type open shrubland (H = 7) (see Maclean, Mosedale, and Bennie 2019) for the geographic centroid of each transect. These specifications were selected as most transects were located in open areas with scattered trees, to approximate the conditions experienced by juvenile stages of butterflies near the ground, or of nectaring butterflies in open habitats.

We modelled monthly temperature maxima (monthly mean of daily maxima) for two different 10-year periods covering, respectively, the beginning and end of the period over which historical and recent butterfly surveys took place. To summarise historical local climate, we used 1980 to 1989, and for recent conditions we used 2013 to 2022. Despite the differences in survey years between regions (Gredos: 1985–87 and 2021–22; Guadarrama: 2004–05, 2017 and 2021; Meridional: 1986 and 2020–22; Javalambre: 1991 and 2020–22), temperatures during the 10-year periods were representative of survey years temperatures (Figure S1). We used mean monthly maxima (hereafter T_{max}) because in temperate environments daily maximum temperature gives an estimate of conditions for activity by diurnal ectotherms (Greiser et al. 2022), and is the most closely related temperature variable to vital rates across all butterfly life stages (Kiekebusch et al. 2024). Ground-truthing of *Microclima* versus temperature loggers suggests that the model gives accurate estimates of temperature maxima (Gómez-Vadillo et al. 2022). We then computed the change in T_{max} over time (ΔT_{max}) as the difference between recent and historical T_{max}.

2.3 | Community Composition Indices

2.3.1 | Community Temperature Index (CTI)

To quantify community thermal associations, we calculated community temperature index (Devictor et al. 2008) as the average species temperature index (STI) for all species present at each site in each period (historical or recent), using incidence data. STI for each species was extracted from Mingarro et al. (2021), as the mean temperature in 10 × 10 km squares where it was recorded in the Iberian Peninsula from 1980 to 2016, based on 1 km resolution CHELSA climate data (Karger et al. 2017). To check the consistency of our results, we also calculated CTI based on STI across the entire European range of each species in 1981–2000 (Platania et al. 2020) (Supporting Information: Methods 1.3). Results based on European CTI were largely consistent with those for Iberian CTI (Supporting Information: Results 2.1).

Several methodologies were used to collect butterfly data, so we re-sampled the field data to estimate CTI based on equivalent sample effort across sites and time periods. We conducted 100 randomisations with four visits to each site in both the historical and recent periods (four was set as the minimum number of visits per site in either period in order to keep as many sites as possible in the analysis). One site from Gredos had only three historical sampling visits and was therefore removed from all analyses involving CTI. We summarised historical and recent CTI for each site as the median from the 100 randomisations. To quantify changes in thermal affinity for communities over time, we calculated change in CTI (ΔCTI) as the median difference between recent and historical CTI in each site: positive values of ΔCTI indicate community thermophilisation.

2.3.2 | Community Range in Thermal Affinities (CTI_{SD})

Changes in time to community composition depend on the balance between colonisation and local extinction (Figure 1). To assess the roles of each process we employed two approaches: first, we analysed change over time in the range of thermal affinities of species in each community (CTI_{SD}, following Gaget et al. 2021). CTI_{SD} is the standard deviation across STI values of all species present. If CTI rises alongside increases in CTI_{SD}, it implies that thermophilisation has resulted mainly from colonisation by species with warm thermal affinities. In contrast, increases in CTI accompanying decreases in CTI_{SD} suggest greater effects from extinction of species with cool affinities (Figure 1). We calculated CTI_{SD} using incidence data based on the 100 randomisations of equal sample effort across sites and periods; and change in CTI_{SD} as the difference between median recent and historical CTI_{SD} for each study site ($\Delta\mathrm{CTI}_{SD}$).

2.3.3 | Species Richness

Our second approach to estimate the relative roles of colonisation and extinction in community change used species richness. Species richness will increase if colonisation exceeds local extinction, but decrease in the opposite case (Figure 1). Because of the changes in butterfly sampling over time, we used a standard and robust approach to estimate species richness across sites and periods based on equivalent sample effort (Roswell, Dushoff, and Winfree 2021). We quantified sample coverage (SC) using all data for each site and period using the *iNEXT* function in *R* (Hsieh, Ma, and Chao 2016). In *iNEXT*, species richness is computed against abundance (sample size), leading to rarefacted estimates of species richness (below observed sample size), observed estimates or extrapolated estimates (above observed sample size). To estimate sample coverage (SC) we computed species richness curves based on observed abundance for the Hill number of order $q=0$ (species richness) (Chao and Jost 2015). SC is calculated by dividing observed richness by the asymptotic estimate of richness. We used 300 knots (equally spaced increments of sample size) to estimate species richness and sample coverage up to double the total number of sampled individuals, the maximum recommended to avoid over-extrapolation (Colwell et al. 2012). Species richness and sample coverage are estimated at each knot, together with their 95% lower and upper confidence limits.

We used paired tests (t-test for normal, or Wilcoxon test for non-normal data) to check for changes to observed sample coverage or species richness between historical and recent periods. As we detected significant changes in both variables (Table 1), we followed Roswell, Dushoff, and Winfree's (2021) recommendation to equalise SC in our comparisons of richness over time. We used the sample size-based output from *iNEXT* to extract estimates for species richness (diversity estimate of order $q=0$, hereafter qD to refer to equal-coverage *estimates* rather than *observed* richness). We used several filters to equalise SC across sites and surveys (Supporting Information: Methods 1.4), minimising the number of sites at which species richness was extrapolated but maximising the number of sites included. Here, we report results for qD estimated for the second lowest maximum SC of sites in the historical survey ($\mathrm{SC}\geq0.75$). Employing this filter meant that one site in Sistema Ibérico Meridional had to be excluded as its maximum historical SC (extrapolated to double the observed sample size) was below the threshold. Using $\mathrm{SC}\geq0.75$, qD values were rarefacted for 61 sites historically and all sites in the recent survey ($N=74$), and extrapolated for 13 sites in the historical survey (see example in Figure S2). All sites were included in analyses with a filter based on the minimum historical sampling coverage ($\mathrm{SC}\ \geq0.66$): these results, and those for a more conservative filter ($\mathrm{SC}\geq0.93$) are detailed in Supporting Information: Results 2.2.

TABLE 1 | Species number, total species abundance, mean observed sample coverage (SC) and species richness (both from *iNEXT*) for each mountain region and period (Historical and Recent).

			Species number				Total spp. abundance	Mean obs. SC[a]	Obs. species richness[b]
Region	**N_{sites}**	**Survey**	**Total**	**Shared**	**Gained**	**Lost**			
Sierra de Gredos	13	Historical	90	87	13	3	2511	0.931 ± 0.04	35.5 ± 13.3
		Recent	100				10,042	0.982 ± 0.01	47.5 ± 15.5
Sierra de Guadarrama	32	Historical	90	86	8	4	7250	0.942 ± 0.06	28 ± 7.62
		Recent	94				17,338	0.978 ± 0.02	38.6 ± 9.64
Sistema Ibérico Meridional	20	Historical	84	81	32	3	726	0.700 ± 0.12	19.5 ± 4.61
		Recent	113				15,622	0.982 ± 0.01	55.4 ± 9.07
Javalambre	10	Historical	93	90	20	3	2047	0.931 ± 0.02	41.6 ± 9.57
		Recent	110				10,326	0.983 ± 0.01	62.3 ± 17
Overall	75	Historical	126	121	3	5	12,534[c]	0.874 ± 0.13	28.8 ± 11.1
		Recent	124				53,328[c]	0.981 ± 0.01	47.8 ± 14.6

Note: Standard deviation (SD) is shown for mean observed sample coverage and richness. Total species number is broken down into those shared, gained and lost comparing historical and recent surveys.

[a] Wilcoxon paired test observed SC: Overall: $V=2833.5$, $p=1.04\times10^{-13}$; Sierra de Guadarrama: $V=518.5$, $p=2.04\times10^{-6}$. Paired t-test observed SC: Sierra de Gredos: $t(12)=4.76$, $p=4.6\times10^{-4}$; Ibérico Meridional: $t(19)=10.98$, $p=1.15\times10^{-9}$; Javalambre: $t(9)=9.46$, $p=5.67\times10^{-6}$.

[b] Wilcoxon paired test observed species richness: Overall: $V=2818$, $p=1.91\times10^{-13}$. Paired t-test observed species richness: Sierra de Gredos: $t(12)=2.73$, $p=0.02$; Sierra de Guadarrama: $t(31)=10.44$, $p=1.13\times10^{-11}$; Ibérico Meridional: $t(19)=14.74$, $p=7.5\times10^{-12}$; Javalambre: $t(9)=6.27$, $p=1.4\times10^{-4}$.

[c] Total count without including *Pyrgus* or *Carcharodus* species which account for 1.04% of total abundance in historical surveys (132 out of 12,666) and 1.12% in recent surveys (604 out of 53,932).

2.3.4 | Species Persistence and Occupancy Over Time

To test whether site CTI increased over time because colonising species had warmer thermal affinities than extinct species, we determined the thermal affinities of species in three persistence categories per site (Colonising, Extinct or Persisting). We classified species as follows: present in both historical and recent survey periods (persisting); present historically but not in the recent period (extinct); or present in the recent but not the historical period (colonising). To quantify thermal affinity for species in each group, we again used STI, calculating an average CTI value for each group at each site in each randomisation of equal survey effort, using the median values of the 100 randomisations for our analyses.

To understand factors influencing CTI for each persistence category, we also calculated the median number of sites where each species was present in historical and recent surveys (N_{sites}), based on the 100 randomisations of equal survey effort. We then tested whether the change in occupancy of species over time (ΔN_{sites}) was explained by two features of species' thermal tolerance. First, we used STI as the thermal affinity for each species (hereafter STI_{mean}). Second, we extracted from Mingarro et al. (2021) the standard deviation of temperature in 10 × 10 km squares where each species had been recorded in the Iberian Peninsula from 1980 to 2016 (STI_{SD}) to estimate thermal niche breadth.

2.4 | Data Analysis

We used *R 4.2.2* (R Core Team 2022) for all analyses. To test for change over time we conducted tests paired by site, comparing historical and recent local climate (annual T_{max}) and community variables (SC, CTI, CTI_{SD} and qD). We used t-tests for normally distributed data and Wilcoxon tests for non-normal data.

To examine relationships of response variables (CTI, CTI_{SD}, qD and N_{sites}) with the local climate (T_{max} and ΔT_{max}) or species traits (STI and STI_{SD}) we conducted general linear models (GLM) using *glm* function from package *stats* (R Core Team 2022). We used a Gaussian error term because all response variables were normally distributed, and standardised explanatory variables to compare effect sizes based on model coefficients (Schielzeth 2010). We used multi-model inference based on an information theoretic approach, ordering all possible models by their Akaike Information Criterion corrected for small sample size (AIC_c) via the *dredge* function in *MuMin* (Bartoń 2023). We selected only models with $\Delta AIC_c < 2$ (Burnham and Anderson 2002) and calculated an averaged model using *model.avg* (Bartoń 2023). Collinearity was analysed beforehand to avoid effects on parameter estimation, and spatial autocorrelation was analysed for the residuals of all models conducted (Supporting Information: Methods 1.5, Table S3). Finally, we used the *predict* function from package *stats* to estimate response variables from the averaged model over the range of explanatory variables.

To test how site CTI was related to local climate in each period and region, we conducted GLMs of historical CTI against historical T_{max}, and recent CTI against recent T_{max}, including region (Gredos, Guadarrama, Sistema Ibérico Meridional and Javalambre) as a fixed factor, and its interaction with T_{max}. We followed the same approach for CTI_{SD} and species richness. For richness we used historical and recent qD based on equal Sample Coverage against historical and recent T_{max}, respectively, including the fixed effect and interaction with region, and a quadratic effect of T_{max} to test for a humped relationship with temperature.

To test whether CTI change depended on historical local climate and rates of local climatic change, we tested ΔCTI for each site against historical T_{max} and change over time in T_{max} (ΔT_{max}), including possible interactions between historical T_{max}, ΔT_{max} and region. We conducted GLMs for change in CTI_{SD} and qD in the same way.

To answer whether colonisers had warmer thermal affinities than extinct species, and if this was consistent over the climatic gradient, we conducted a linear mixed effects model using CTI for each persistence category at each site as the response variable (i.e., three values per site: Colonising, Extinct or Persisting). We included a random effect of site identity nested in region. We used explanatory variables of persistence category, historical T_{max} and their interaction to test for differences in thermal affinity for each category depending on site local climate. We used functions *lmer* from package *lme4* (Bates et al. 2015) and *predictSE* from *AICcmodavg* (Mazerolle 2023) to predict values from the model. To test for differences among persistence categories, we used the package *emmeans* (Lenth et al. 2024) for pairwise comparisons (Tukey test) on estimated marginal means.

We also analysed how the temporal change in occupancy by species (ΔN_{sites}) and historical occupancy (historical N_{sites}) were explained by their thermal affinity (STI_{mean}) and thermal niche breadth (STI_{SD}). Since traits of related taxa may not be statistically independent because of common ancestry, we used the Phylogenetic Generalised Least Squares (PGLS) analysis from *caper* package in *R* (Orme et al. 2023) based on the ultrametric phylogenetic tree from Wiemers et al. (2019) (Figure S3). We used PGLS models with maximum likelihood to estimate the lambda parameter of the phylogenetic signal, and again selected models based on $\Delta AIC_c < 2$.

See Table S4 for a schematic representation of all analyses conducted.

3 | Results

We recorded 126 species in historical surveys (1984–2005) and 124 species in recent surveys (2017–2022), with total counts of 12,534 and 53,328 individuals, respectively (Table 1). Of 129 species overall, 121 were shared between surveys, with three gained and five lost between historical and recent periods (Table S5). In all four regions, observed sample coverage (SC) of recent surveys was significantly higher (mean 0.981 ± SD 0.01) than historical surveys (0.874 ± SD 0.13), especially in the Sistema Ibérico Meridional (Table 1). Reflecting the increase

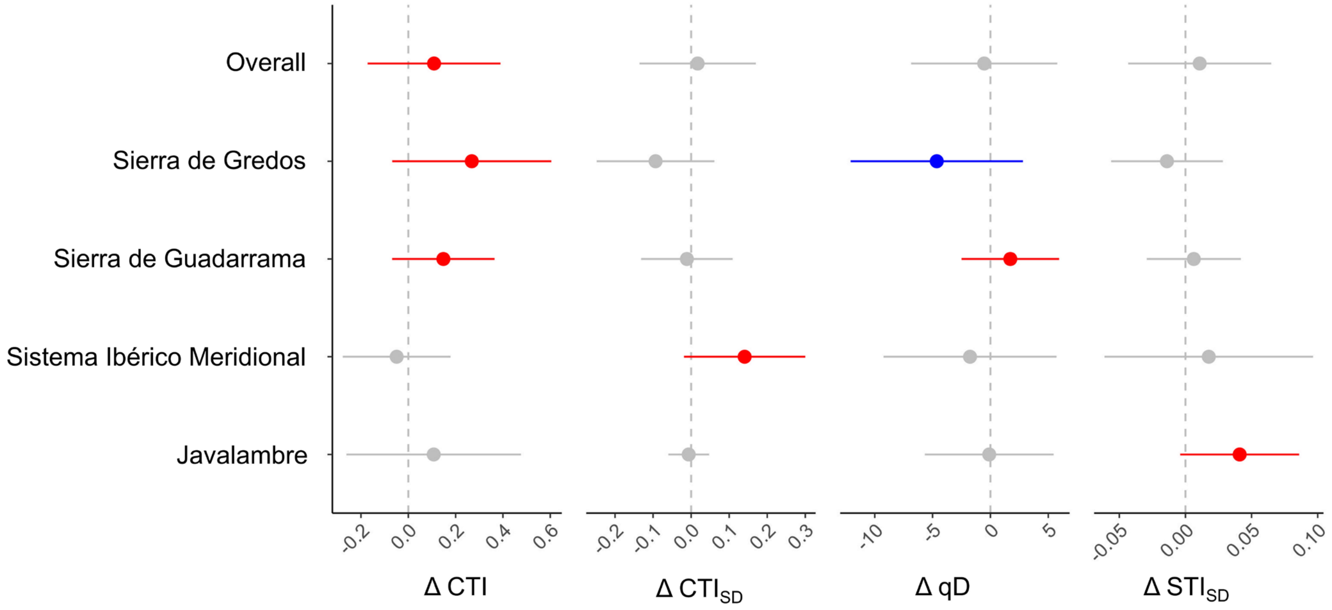

FIGURE 3 | Change over time (Δ) in community temperature index (CTI), standard deviation of community temperature index (CTI_{SD}), estimated species richness (qD based on equal sample coverage of 0.75) and species temperature index standard deviation (STI_{SD}, a measure of the thermal niche breadth of species in each community). Rows show results overall and per region. Symbols show mean change ± standard deviation based on equal effort sampling. Blue shows significant decrease, red significant increase and grey non-significant change, based on tests paired by site (Table S6). Grey vertical dashed lines represent no change over time.

in sampling coverage, recent observed species richness was significantly higher than historical richness in all regions (Table 1).

3.1 | Temporal Change in Local Climate and Community Composition

Overall, local temperature near the ground (T_{max}) decreased from 1980–1989 to 2013–2022 by an average of −0.43°C ($V = 124$, $p < 0.001$) (Table S6, Figure S4). Temperature decreased most in Sistema Ibérico Meridional (−0.916°C) and Javalambre (−0.805°C) (Figure S4). Temperature increased only at 11 sites (15%), six in Gredos and five in Guadarrama. There was no relationship between local temperature change and historical temperature (Spearman correlation: $r_S = -0.162$, $n = 74$, $p = 0.167$).

CTI increased at 50 sites (68%), by an average of +0.109 overall ($t = 3.333$, $p < 0.01$). Across sites, there were significant increases in CTI in Gredos (+0.268) and Guadarrama (+0.148) (Figure 3, Table S6). CTI_{SD} did not change in any regions except for Sistema Ibérico Meridional (+0.141, $t = 3.951$, $p < 0.001$) (Figure 3, Table S6) suggesting that, overall, sites experienced similar numbers of colonisations and extinctions (Figure 1). Species richness corrected for sample coverage (qD) also did not change overall, but there was a significant decrease in Gredos (−4.638) and an increase in Guadarrama (+1.721) (Figure 3, Table S6). Average standard deviation in STI (a measure of the thermal niche breadth of species) did not change over time in any region except for Javalambre (+0.041).

3.2 | Relationship Between Community Composition and Climate

CTI was positively related to T_{max} in both periods and all regions (Figure 4A, Table 2, Table S7). However, butterfly communities at historically cold sites appeared to increase CTI most, with 15 sites out of 74 showing a lower CTI in the historical period than the overall minimum CTI in recent data (Figure 4A). Estimated species richness (qD) at equal Sample Coverage ($SC \geq 0.75$) showed a positive relationship with T_{max} for the historical period, but a humped relationship in the recent data (Figure 4B, Table 2, Table S7), resulting from a reduction over time in qD at the hottest sites. Regional differences were maintained, with qD ranked Javalambre>Sistema Ibérico Meridional>Sierra de Gredos>Sierra de Guadarrama in both periods (Figure 4B). These results were consistent using alternative Sample Coverage filters ($SC \geq 0.66$ and $SC \geq 0.93$) (Figure S5, Table S7).

Change over time in Community Temperature Index (ΔCTI) was positively correlated with temperature change (ΔT_{max}) ($r_S = 0.364$, $n = 74$, $p = 0.001$). However, the best model for ΔCTI included historical T_{max}, region and their interaction (Table 2). Communities occupying sites with colder conditions historically increased CTI most, although only in Gredos and Javalambre (Figure 5). We note that the best model for ΔCTI based on STI from European distributions included a positive effect of temperature change (Figure S6, Table S8).

Change in CTI_{SD} was negatively correlated with ΔT_{max} ($r_S = -0.388$, $p < 0.001$), but the best model for ΔCTI_{SD} included only an effect of region (Table 2). Three GLMs were selected for

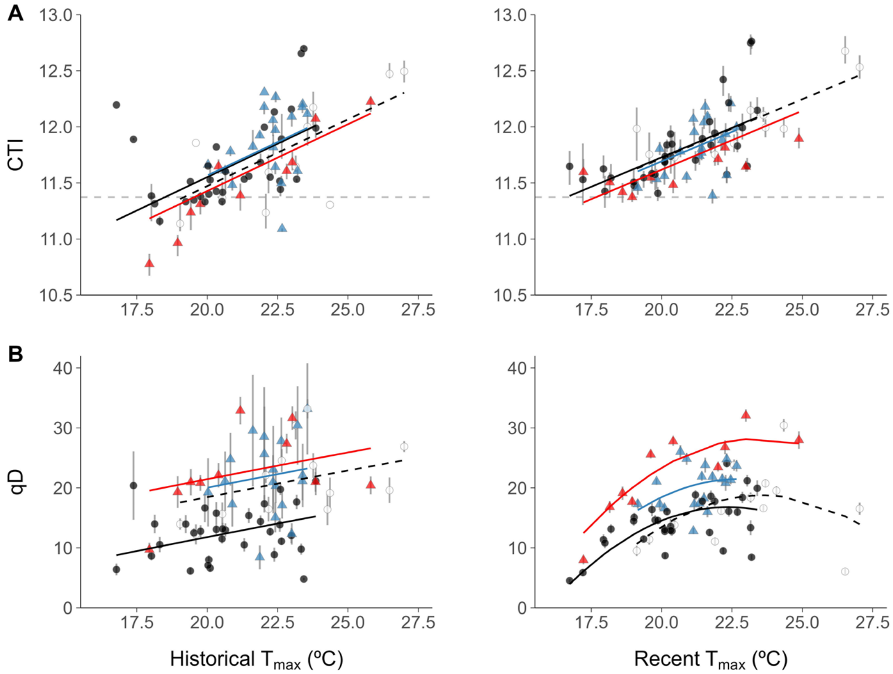

FIGURE 4 | Historical and recent relationships of butterfly communities with local climate temperature. (A) Community temperature index (CTI) and (B) Estimated species richness (qD based on equal sample coverage of 0.75) against historical (left column) and recent (right column) local temperature (T_{max}). White dots and black dashed line correspond to Sierra de Gredos, black dots and black solid line Sierra de Guadarrama, blue triangles and blue solid line Sistema Ibérico Meridional, and red triangles and red solid line Javalambre. In panel A, symbols represent the median CTI value across the 100 randomisations for each site and grey bars around symbols are 25% and 75% percentiles. Grey dashed line represents the minimum median CTI value for the recent period (CTI = 11.37) to highlight that CTI increased for communities with historically cold affinities. In panel B, symbols represent qD and grey bars are the 95% lower and upper confidence limits extracted from *iNEXT* function in *R* (Hsieh, Ma, and Chao 2016).

change over time in qD (Table 2), suggesting that changes to species richness mainly differed among regions rather than related to local climatic conditions (Figure S7, Table S7).

3.3 | Thermal Affinities in Species Persistence Categories

Thermal affinities of species differed depending on persistence category (Colonising, Extinct and Persisting) and site historical T_{max} (Table 2, Table S7). Colonising species had warmer thermal affinities than species that became extinct at the same sites (contrast analysis: model estimate = 0.334, $df = 152$, $t.ratio = 5.423$, $p < 0.001$) (Figure 6A, Table S9), throughout the climatic gradient. A positive relationship between CTI of persisting species and historical T_{max} (Model coefficient = 0.209 ± SD 0.061) shows persistence of warm-affinity species at historically hot sites and cool-affinity species at cold sites (Figure 6A, Table S7).

Change over time in occupancy (ΔN_{sites}) was related both to species' thermal affinity and thermal niche breadth (Table 2). Occupancy for species with a cold thermal affinity ($STI_{mean} < 10°C$) decreased, whereas occupancy increased for those with an intermediate affinity (STI 10°C–14°C), independently of their thermal niche breadth (STI_{SD}) (Figure 6B). Species with narrow thermal niche breadths but warm thermal affinities (> 14°C) tended to decrease. Species with broad thermal niches showed the greatest increases in occupancy, as long as their STI was greater than 10°C (Figure 6B).

The number of sites occupied historically by a species was also related to STI and STI_{SD} (Figure S8, Table 2). Species with a warm thermal affinity (high STI) and broad thermal niche (high STI_{SD}) occupied the largest number of sites. Species with a cool thermal affinity (low STI) occupied few sites, irrespective of their thermal niche breadth. Warm-adapted thermal specialists (high STI and low STI_{SD}) also occupied few sites.

4 | Discussion

We investigated how butterfly communities responded to local climate in four mountain landscapes. Changes in temperature near the ground varied between regions, with cooling observed at many sites. Both historical and recent community temperature index (CTI) were positively related to local temperature, but CTI generally increased (community thermophilisation), especially in regions experiencing warming in some sites. CTI also increased more in historically colder sites, leading to a narrower range of community thermal affinities. A lack of change in species richness and CTI_{SD} showed that there were similar rates of colonisation and local extinction overall. Colonising species had warmer thermal affinities than locally extinct species;

TABLE 2 | (A) General linear models (GLM) selected for historical and recent community temperature index (CTI), estimated species richness (qD based on equal Sample Coverage of 0.75), CTI among persistence categories and change over time in CTI, $\mathrm{CTI}_{\mathrm{SD}}$ and qD. (B) Phylogenetic generalised least squares (PGLS) models to explain historical occupancy ($\mathrm{N}_{\mathrm{sites}}$) and change over time in occupancy ($\Delta\mathrm{N}_{\mathrm{sites}}$) for each species. In this case, lambda is shown instead of model weight, which is a measure of the effect of phylogeny in the model. Only models with $\Delta\mathrm{AIC}_{\mathrm{c}} < 2$ are shown and were used for model averaging (see Table S7 for model coefficients).

(A)

Variable	**Model**	R^2	R^2_{adj}	**df**	**logLik**	$\mathbf{AIC_c}$	$\mathbf{\Delta AIC_c}$	**weight**
$\mathrm{CTI}_{\mathrm{hist}}$	Historical $\mathrm{T}_{\mathrm{max}}$ + Region	0.406	0.645	6	−17.452	48.157	0	0.492
	Historical $\mathrm{T}_{\mathrm{max}}$	0.346	0.550	3	−20.972	48.288	0.131	0.461
$\mathrm{CTI}_{\mathrm{rec}}$	Recent $\mathrm{T}_{\mathrm{max}}$ + Region	0.521	1.359	6	9.353	−5.451	0	0.479
	Recent $\mathrm{T}_{\mathrm{max}}$	0.472	1.232	3	5.757	−5.171	0.280	0.416
$\mathrm{qD}_{\mathrm{hist}}$	Historical $\mathrm{T}_{\mathrm{max}}$ + Region	0.479	0.479	6	−226.598	466.450	0	0.399
	Historical $\mathrm{T}_{\mathrm{max}}^{2}$ + Region	0.477	0.477	6	−226.749	466.752	0.302	0.343
	Historical $\mathrm{T}_{\mathrm{max}}$ + Region + Historical $\mathrm{T}_{\mathrm{max}}^{2}$	0.482	0.483	7	−226.348	468.394	1.944	0.151
$\mathrm{qD}_{\mathrm{rec}}$	Recent $\mathrm{T}_{\mathrm{max}}$ × Region + Recent $\mathrm{T}_{\mathrm{max}}^{2}$	0.623	0.624	10	−199.231	421.954	0	0.559
	Recent $\mathrm{T}_{\mathrm{max}}$ + Region + Recent $\mathrm{T}_{\mathrm{max}}^{2}$	0.578	0.579	7	−203.367	422.432	0.477	0.440
ΔCTI	Historical $\mathrm{T}_{\mathrm{max}}$ × Region	0.329	1.372	9	4.611	11.591	0	0.482
$\Delta\mathrm{CTI}_{\mathrm{SD}}$	Region	0.277	−0.179	5	46.654	−82.425	0	0.371
ΔqD	Region	0.141	0.142	5	−235.271	481.424	0	0.303
	Historical $\mathrm{T}_{\mathrm{max}}$ + Region	0.160	0.160	6	−234.474	482.202	0.778	0.205
	$\Delta\mathrm{T}_{\mathrm{max}}$ + Region	0.148	0.148	6	−234.979	483.211	1.787	0.124
CTI	Historical $\mathrm{T}_{\mathrm{max}}$ × Species persistence category	0.289	0.399	9	−105.504	229.858	0	0.982

(B)

Variable	**Model**	R^2	R^2_{adj}	**df**	**logLik**	$\mathbf{AIC_c}$	$\mathbf{\Delta AIC_c}$	**Lambda**
Historical $\mathrm{N}_{\mathrm{sites}}$	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{SD}} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.099	0.077	4	−514.950	1038.222	0	0.234
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2} + \mathrm{STI}_{\mathrm{SD}} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.101	0.072	5	−514.775	1040.038	1.816	0.229
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.069	0.054	3	−516.961	1040.114	1.892	0.216
	$\mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.053	0.046	2	−518.028	1040.151	1.929	0.210
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.084	0.062	4	−515.917	1040.157	1.935	0.214
$\Delta\mathrm{N}_{\mathrm{sites}}$	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2}$	0.127	0.113	3	−429.249	864.690	0	0.056
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.136	0.115	4	−428.652	865.626	0.935	0.060
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{SD}} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.128	0.107	4	−428.712	865.746	1.056	0.022
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2} + \mathrm{STI}_{\mathrm{SD}} + \mathrm{STI}_{\mathrm{mean}}{:}\mathrm{STI}_{\mathrm{SD}}$	0.148	0.120	5	−427.631	865.749	1.059	0.051
	$\mathrm{STI}_{\mathrm{mean}} + \mathrm{STI}_{\mathrm{mean}}^{2} + \mathrm{STI}_{\mathrm{SD}}$	0.133	0.112	4	−428.872	866.068	1.377	0.060

and species with warm affinities and broader thermal niches increased occupancy most over time. These results suggest an overall shift in the composition of mountain butterfly communities towards species with warm thermal affinities and broad thermal tolerance. Historically, cold conditions were not in themselves sufficient to protect against the community-level effects of climate change. Instead, a regional perspective to identifying refugia for conservation may help to spread the risk of climate change by ensuring a wide range of local conditions and rates of climatic change.

4.1 | Community Responses to Local Climate Over Time

Previous studies have demonstrated relationships of CTI with latitude or elevation as climate proxies. We used a fine-scale climate model to show positive relationships between CTI and temperature in two time periods (1984–2005 and 2017–2022) (Figure 4A, Table 2A). CTI increased over time, but particularly in historically cold locations, causing thermal affinities to become more similar across communities (Figure 4A). A

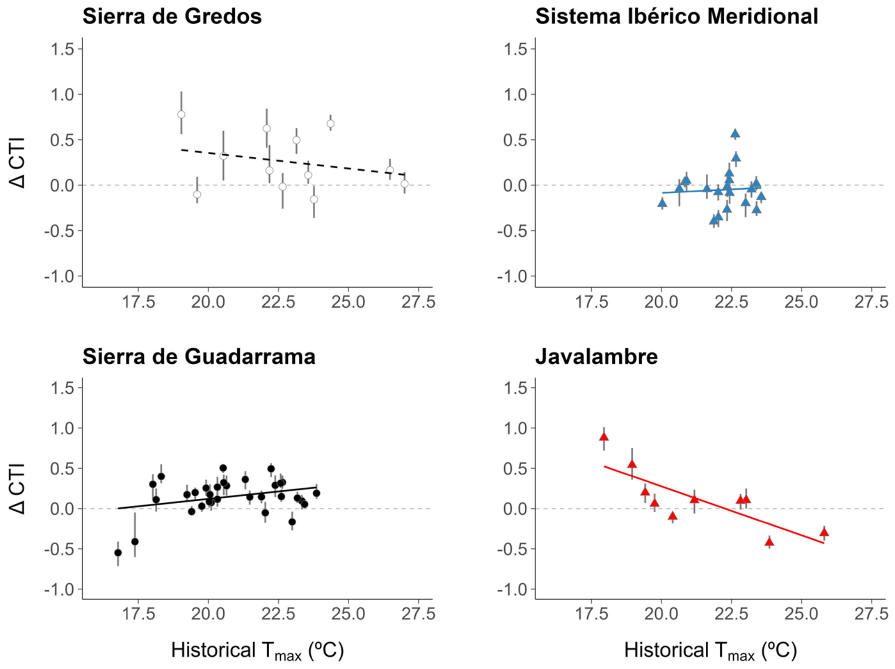

FIGURE 5 | Change in community temperature index (ΔCTI) explained by historical T_{max}. Horizontal grey dashed line shows no change in CTI over time (ΔCTI = 0). Communities inhabiting historically cold sites in Gredos and Javalambre increased CTI most over time.

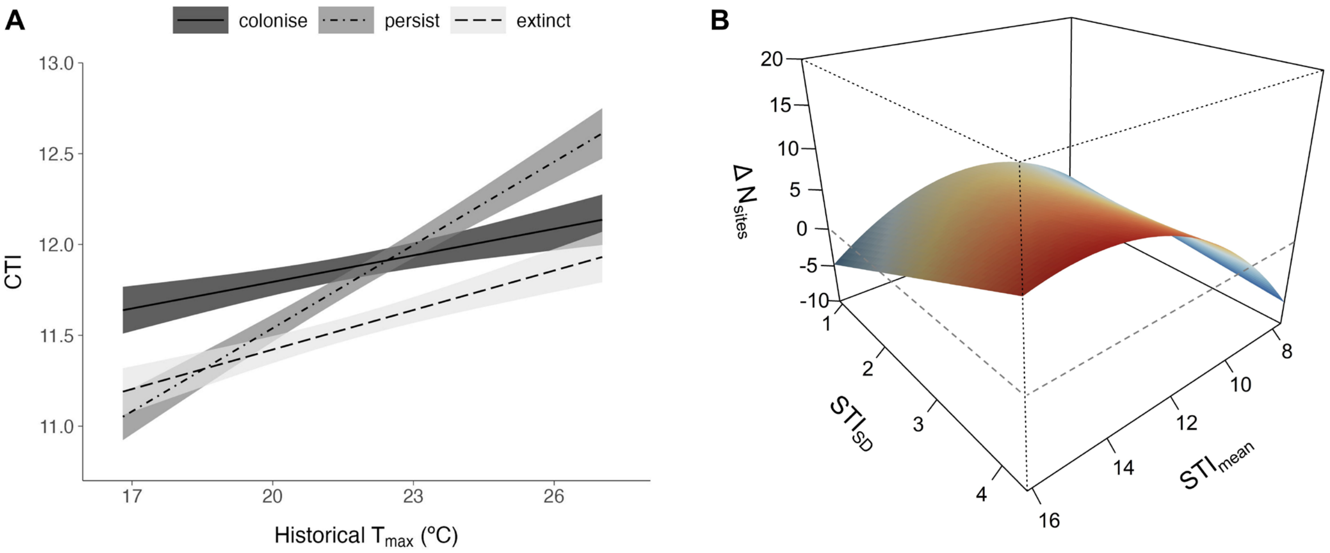

FIGURE 6 | Relationships between thermal affinity and species persistence over time. (A) Community temperature index (CTI) for each persistence category against historical local temperature: Lines of best fit and standard error plotted for model coefficients in Table S7. (B) Change in number of sites where each species was found (recent sites vs. historical sites) against thermal affinity (mean species temperature index) and thermal niche breadth (standard deviation in species temperature index). Plotted surface refers to predicted values from model averaging across selected PGLS (Table 2). Grey dashed lines show no change in number of sites over time.

tendency of communities with lower baseline temperatures to show faster thermophilisation has been observed in a wide range of terrestrial, freshwater and marine assemblages (Antão et al. 2020; Bertrand et al. 2016; Khaliq et al. 2024) along with homogenisation in community thermal affinities (e.g., Savage and Vellend 2015; Thorn et al. 2022). We also found an indication that rates of thermophilisation were positively related to rates of local temperature change, in common with other studies (Gaüzère, Jiguet, and Devictor 2015; Khaliq et al. 2024; Zellweger et al. 2020). However, in our case, the community effects of both baseline temperature and local climate change were obscured to some extent by differences between regions, because CTI did not increase in the two regions where local temperatures cooled at all sample sites (Figures 3 and S4).

One challenge to uncovering the climatic factors driving community change is that the thermal conditions experienced by small ectotherms are unlikely to be captured by coarse resolution climate data, especially in mountains (Pincebourde et al. 2016). We incorporated effects of topography on local climate near the ground using *Microclima* (Maclean, Mosedale, and Bennie 2019), which can provide accurate temperature estimates in topographically heterogeneous environments (Baker et al. 2021; Brusse et al. 2024; Gómez-Vadillo et al. 2022). The modelled declines in temperature we found at many sites (Figures S1 and S4) could result from the following weather system effects: a reduction in snow cover, as recorded in central Spain (González-Flórez, González-Cervera, and Durán 2022), might influence incoming solar radiation and surface maximum temperatures by increasing evapotranspiration and, in consequence, cloud cover (García-Valdecasas Ojeda et al. 2020). Increased cloudiness decreases insolation and hence maximum surface temperatures on south-facing slopes, also reducing topographically driven differences among sites (Maclean et al. 2017; Maclean, Mosedale, and Bennie 2019). Nevertheless, estimating historical temperatures in remote regions remains challenging, and sensitive to the data used to drive microclimate models. The National Centers for Environmental Prediction (NCEP) data used by *Microclima* (Kearney et al. 2020) estimate relatively high temperatures in the mid-1980s and conservative warming rates compared with other climate data sources, both in Europe (Krauskopf and Huth 2020) and South America (Balmaceda-Huarte et al. 2021), so our data may underestimate possible warming between the historical and recent surveys.

4.2 | Importance of Colonisation and Extinction in Community Change

We inferred similar rates of colonisation and extinction overall, because neither variation in community thermal affinities (CTI_{SD}) nor species richness changed over time (Figure 3). Both observations are consistent with community thermophilisation caused by the substitution of locally extinct species with cool thermal affinities by colonising warm-affinity species (Figure 1). The same pattern has been inferred for butterflies both in mountain sites in Italy (Bonelli et al. 2022), and using Global Biodiversity Information Facility (GBIF) data more broadly for North America and Europe (Lajeunesse and Fourcade 2023). Community thermophilisation despite estimated cooling in many sites may appear paradoxical. However, we note that the effects of broad environmental changes on plant communities (including thermophilisation) can outweigh effects of fine-scale climate treatments (Govaert et al. 2021; Lorer et al. 2024). In the same way, it is possible that the mountain butterfly communities we studied were influenced by responses to climatic or other environmental variation in the surrounding landscapes (e.g., because of land cover change, or colonisation by butterflies from more lowland sites). In addition, estimates of species temperature index (STI) based on Iberian versus European species distributions gave slightly different results, with a stronger positive correlation between change in CTI and local temperature when using European CTI (Figure S6, Table S7). STI is an estimate of thermal affinity and is unlikely to represent all components of the thermal niche that determine population responses to climatic change, and there is a need for greater understanding of these responses based on more direct measurements of species' thermal physiology and ability to behaviourally thermoregulate (Williamson et al. 2025).

The relationship of species richness with temperature was positive in historical data but humped in recent surveys (Figure 4B). This change mainly resulted from reductions in species richness at the hottest sites, as found for mountain bumblebee communities in Norway between the 1960s and 2012 (Fourcade, Åström, and Öckinger 2019). Reductions in species richness suggest that community changes at the hottest sites arose principally by extinctions (i.e., biotic attrition at the warm limits of the gradient; Colwell et al. 2008; Guo, Lenoir, and Bonebrake 2018). CTI_{SD} is also expected to decline if extinctions are the main cause of thermophilisation (Gaget et al. 2021). Whilst CTI_{SD} did not change overall (Figure 3), its decline in some sites in Sierra de Gredos is consistent with CTI change driven mainly by local extinctions, as also suggested by a decline in species richness in this region (Figure 1).

Species colonising sites had warmer thermal affinities than those experiencing local extinction, a difference underlying community thermophilisation observed in several taxa (Hemberger and Williams 2024; Khaliq et al. 2024; Lajeunesse and Fourcade 2023; Tayleur et al. 2016). Compared with persisting species, colonisers had warmer affinities at cold locations, but cooler affinities at hot locations (Figure 6A). Consistent with this observation, lower rates of thermophilisation in historically warm sites could result partly from a lack of colonising species adapted to warmer conditions (Bertrand et al. 2011; Khaliq et al. 2024). In our system, thermal specialists adapted to the warmest conditions occupied few sites historically (Figure S8), potentially hampering their ability to colonise additional sites (see Wilson et al. 2007).

The species that increased occupancy most over time had intermediate thermal affinity (STI around 10°C–14°C) and broad thermal niche (STI_{SD}) (Figure 6B). Tolerance of a wider range of climatic conditions may confer two advantages in this respect: reduced risk of local extinction caused by local climate variability; and greater chances of colonisation if species have wider distributions because of a broader niche breadth. In the former case, specialists for hot conditions (high STI and low STI_{SD}) may have gone extinct from sites where conditions cooled. The loss of hot-adapted species may have contributed to the reduction in species richness and the lower rate of CTI increase at the hottest sites (Figure 4B, Figure 5). In terms of regional distribution size, species with both warm affinities and broad thermal niches occupied more sites historically (Figure S8). The result concurs with evidence that greater geographic range size and proximity to climatically suitable regions positively influence rates of colonisation in Canadian butterflies (Lewthwaite and Mooers 2022) and European birds (Howard et al. 2023). In Finland, somewhat in agreement with our findings, butterflies with wider moisture niche breadth have extended their ranges further north; however, unlike our results, narrow tolerance for warmer conditions has favoured northward range shifts in moths (Hällfors et al. 2023). Community change is therefore likely to depend not only on species' climatic niches, but also on other traits influencing their likelihood of colonisation and extinction (e.g., mobility), and on the geographic or landscape context (Engelhardt et al. 2022; Fourcade et al. 2021).

4.3 | Mountains as Climate Change Refugia

Based on their roles as historical refugia, mountains have been proposed as important sites to protect cool-adapted taxa against climate change (Ashcroft et al. 2012; Dobrowski 2011). However, local ecological responses to climate change are complex to predict, and are influenced by human effects on land cover, vegetation structure and biogeochemistry. In mountains, topographic heterogeneity can reduce rates of community thermophilisation (Mingarro et al. 2021) by providing a wide range of local climates that reduce extinction risk for warming-sensitive species (Suggitt et al. 2018). Localised mountain environments that warm more slowly might also be vital to protect cool-adapted taxa (Stark and Fridley 2022). Our results suggest that communities in initially cool sites experienced greater thermophilisation (Figure 5). Limitations of sampling in the historical data made it difficult to assess the effects of extreme climatic conditions at different times of year, which may be important in butterfly population dynamics (McDermott Long et al. 2017). However, the effects of local climatic conditions on CTI were influenced by regional differences. CTI increased most in regions where some sites had warmed (Sierras de Gredos and Guadarrama), and did not change in the region where conditions cooled the most (Sistema Ibérico Meridional) (Figure 3).

These results suggest the importance of a regional perspective in conserving mountain biodiversity. Regional differences in warming resulting from localised weather (Maclean et al. 2017) or regional topography (Gómez-Vadillo et al. 2022), influence the rates at which communities change (Becker-Scarpitta, Vissault, and Vellend 2019). Monitoring and conservation across several mountain ranges may therefore be important to spread climatic risk for cool-adapted species. In Mediterranean mountains the capacity of communities to 'track' warming is constrained because most species reach their warm range limits (Romo, Munguira, and García-Barros 2007). Therefore, there needs to be a focus on protecting cool-adapted species in situ (Jones et al. 2023), rather than on facilitating colonisations from elsewhere.

We focused on local climatic variation resulting from topography, but insect communities also respond to changing land cover through its effects on both microclimate and other aspects of habitat quality (e.g., host plant cover and growth form). Shading from forest cover can reduce rates of warming and delay CTI increases (Borderieux, Gégout, and Serra-Diaz 2023; Richard et al. 2021). In the Sierra de Guadarrama, greater forest cover and vegetation heterogeneity have reduced butterfly CTI increase over time (Álvarez et al. 2024; Nieto-Sánchez, Gutiérrez, and Wilson 2015). Afforestation in the Iberian Peninsula due to land abandonment (Palmero-Iniesta et al. 2021), rather than favouring species with cool thermal affinities, appears mainly to benefit species associated with closed versus open habitats (Caro-Miralles and Gutiérrez 2023; Mora, Wilby, and Menéndez 2023). Cold-adapted, alpine species needing open habitats above tree lines may depend critically on topographic microrefugia that warm slowly (Graae et al. 2018). The conservation of cool-adapted species requiring open habitats in subalpine areas thus may require sustainable land use like traditional grazing by transhumance (Ubach et al. 2023). Warming-sensitive species need large, high-quality habitats to persist (Fourcade et al. 2021), so it will be necessary to manage and monitor their responses over large habitat areas providing persistent cool conditions.

Applying local climate models to mountain environments that lack fine-scale meteorological information can be valuable in understanding changes to ectotherm communities. We show that mountain butterfly communities in central Spain are becoming increasingly dominated by species with warm thermal affinities and broader thermal niches. Mountains are a vital focus as climate change refugia because they provide a wide variety of local climates and rates of climatic change. In this context, ongoing monitoring of ecological responses and modelling of local climate across mountain environments represent a key focus for adapting conservation to climate change.

Author Contributions

G.U., H.R. and R.J.W. conceptualised the study and designed the methodology. G.U., M.M., S.C.-C., J.P.C. and R.J.W. conducted data collection and curation. M.M. led the software and validation process for the climatic data. G.U. performed data analysis and visualisation. Funding acquisition was provided by R.J.W. G.U., H.R. and R.J.W. wrote the first draft of the manuscript, with G.U. and R.J.W. leading its revision. All authors contributed to reviewing and editing the manuscript and approved the final manuscript.

Acknowledgements

David Gutiérrez, Javier Gutiérrez Illán, Ana Burón, Adrián Sánchez, Xel Ha Martínez Castaneira, Marta Goded, Lee Bassett, Heidi Buck, Oscar Moreno, David Martínez, Rosa Agudo, Irene Martínez, Miriam Jiménez and Juan Sánchez Rodríguez conducted fieldwork. Elia Guariento provided comments on the text. Hugo Alejandro Álvarez and Ilya Maclean assisted with analysis. Jose Luís Viejo, José Martín, Arturo Baz, Miguel L. Munguira and Enrique García-Barros provided guidance regarding historical data. Research permits were provided by Comunidades Autónomas of Castilla y León, Castilla-La Mancha, Aragón and Madrid. Funding was provided by MCI/AEI/FEDER EU (projects RTI2018-096739-B-C21, PID2021-126293OB-I00 and PRE2019-091025), Biodiversa+ PCI2022-135061-2 project funded by MCIN/AEI/10.13039/501100011033 and the European Union "NextGenerationEU"/PRTR. Open Access funding was provided thanks to the CRUE-CSIC agreement with Wiley.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings on this study are openly available in Dryad at http://doi.org/10.5061/dryad.2z34tmptv.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13967.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.