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Butterfly communities track climatic variation over space but not time in the Iberian Peninsula

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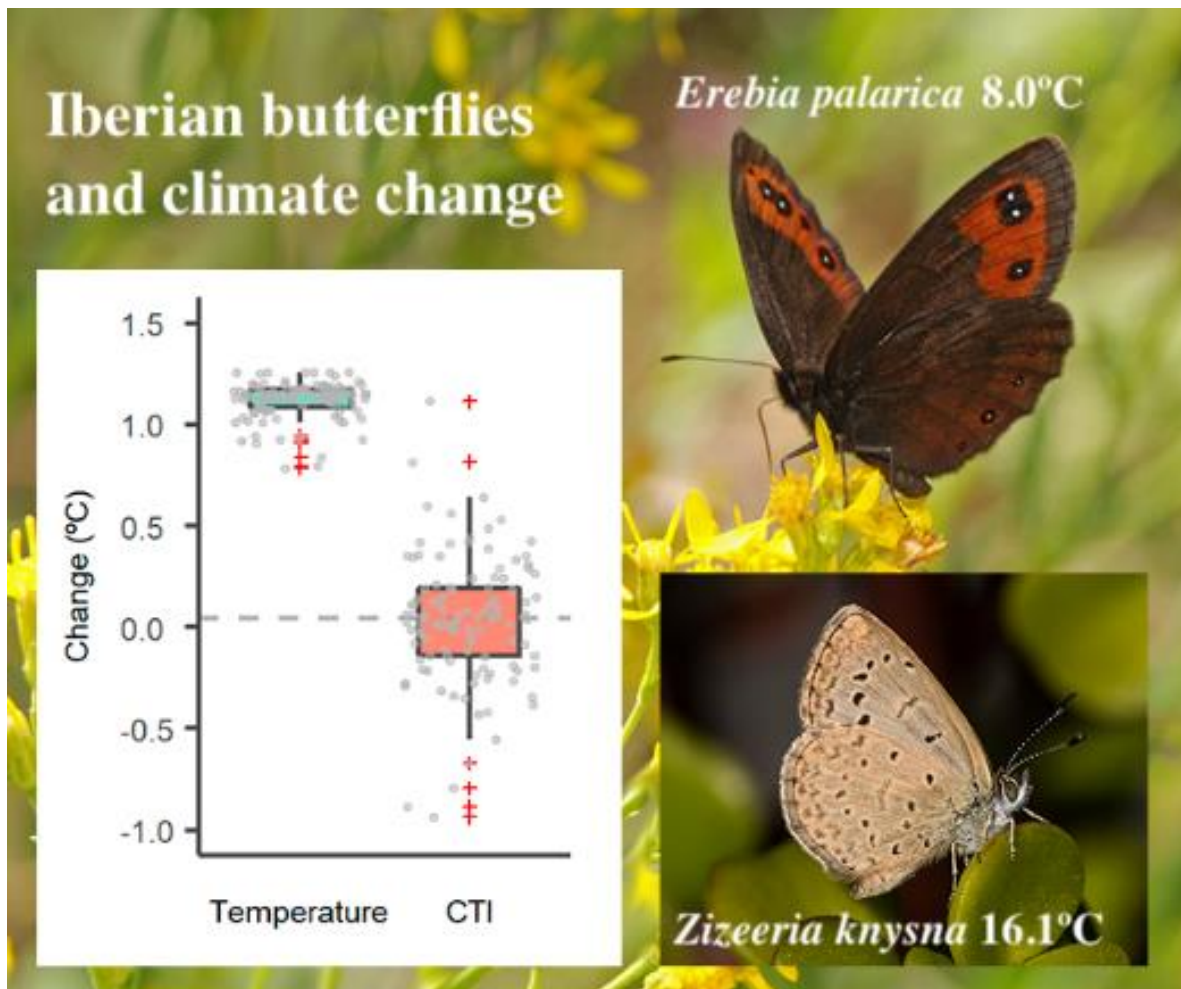
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Running title: Iberian butterflies and climate change

Graphical Abstract



Highlights

1. We tested indices of community environmental associations based on occurrence records to infer how butterflies responded to climatic and land cover changes in the Iberian Peninsula from 1901 to 2016.
2. Community Temperature Index and Community Precipitation Index responded to spatial variation in the climate, but did not change significantly over time. Instead, butterfly communities became more associated with closed vegetation.
3. Local variation in climatic conditions and elevation dampened butterfly community responses to heating and drying, suggesting that topographic heterogeneity could shield regional butterfly faunas from the impacts of climate change.

Abstract

1. Indices of environmental associations such as the Community Temperature Index (CTI) and Community Precipitation Index (CPI) can be derived from occurrence data to extend the geographic scope or time frame of evidence for responses of insect diversity to global change.
2. We tested whether occurrence records from 1901 to 2016 from the Iberian Peninsula could shed light on butterfly community responses to changes over space and time in the climate; and whether local climatic variation caused by topographic heterogeneity could buffer communities against the effects of climate change.
3. CTI and CPI were closely related to variation in temperature and precipitation across 115 well-sampled 10 km grid squares. However, whereas temperature and precipitation changed systematically from 1901-1979 to 1980-2016, and these changes were positively related to changes in CTI and CPI, community climatic associations did not change significantly over time. Butterfly communities became more associated with closed vegetation, suggesting that land cover changes overshadowed the effects of climate change.
4. Local (1 km) climatic variation generally exceeded change over time at 10 km resolution, and heterogeneity in elevation slowed rates of warming. In turn, spatial variation in climatic conditions dampened butterfly community responses to heating and drying.
5. Occurrence data are limited by their spatial resolution but can inform understanding of insect community responses to global change for regions lacking long-term monitoring data. Our results suggest that local climatic variation accompanying topographic heterogeneity can shield regional butterfly faunas from the impacts of climate change.

Key words

Climatic debt, Community Precipitation Index (CPI), Community Temperature Index (CTI), land abandonment, climate change, refugia, TAO Index

Introduction

Insect abundance and diversity are affected globally by threats including climate change, habitat degradation and pollution, whose intensity varies geographically and over time (Montgomery et al., 2020; Wagner, 2020). Geographic variation in insect trends therefore offers pointers regarding the drivers of changing insect biodiversity, and the resilience of different insect communities to these respective drivers (Wagner et al., 2021). Existing evidence for changes to insect communities is biased towards a few temperate regions where landscapes have undergone long-lasting and intensive human exploitation, potentially concealing or exacerbating the effects of recent climate change (Dirzo et al., 2014; van Klink

et al., 2020). Therefore, to determine how insect diversity responds to climate change there is a need to examine changes to insect communities for as wide a range of environments as possible, even in regions where data are limited. Long-term evidence from regions not yet subject to extensive habitat degradation, or from gradients of land-use intensity, could be especially useful to detect the potential for intact habitats or topographic variation to shield biodiversity against the negative impacts of climate change (Halsch et al., 2021).

Opportunistic historical records from museum specimens and publications often represent the only evidence of species distributions and community composition before pronounced climate warming in the late twentieth century (Kharouba et al., 2019; Montgomery et al., 2020). In some cases, these historical data have been used to provide evidence of changes to insect distributions or diversity over the past century or more (Eskildsen et al., 2015; Habel et al., 2016, 2019; Lewthwaite et al., 2017; Van Dooren, 2019; van Strien et al., 2019). Historical data are subject to possible effects of sampling bias, including spatial or temporal variation in recorder activity, which complicates interpretation of changes to species distributions, abundance, or richness (Ries et al., 2019; Didham et al., 2020). Nevertheless, even with incomplete data for a location, indices based on the environmental associations of species can provide information on changes to communities and their environmental drivers. Indices such as the Community Temperature Index (CTI) or Community Precipitation Index (CPI) can be calculated based on the climatic associations of constituent species over their geographic ranges (Devictor et al., 2008; Schweiger et al., 2014). CTI and CPI have been shown to vary over space or time consistent with spatial or temporal variation in climatic conditions (Nieto-Sánchez et al., 2015; Herrando et al., 2019). In turn, comparison of rates of change in these indices between different regions, habitats or taxonomic groups can offer clues to the factors influencing vulnerability to climate change, and hence help to identify priorities for conservation (Devictor et al., 2012).

The insect communities of Mediterranean systems exemplify these challenges. In the past century, Mediterranean regions have been exposed to rapid rates of climate change (Serrano-Notivoli et al., 2018, 2019), as well as to contrasting pressures of rural depopulation and land abandonment, versus urbanisation, infrastructure development and agricultural intensification (Debussche et al., 1999; Rescia et al., 2010; Serra et al., 2014; Herrando et al., 2016). Over recent decades, Mediterranean butterfly communities have responded to climatic warming (Zografou et al., 2014; Nieto-Sánchez et al., 2015) and drying (Herrando et al., 2019), as well as vegetation encroachment (Ubach et al., 2020) and changing agricultural practices (Lee et al., 2020). Some evidence from these regional studies suggests that topographic variation or vegetation cover may counteract effects of climate change on insects (Nieto-Sánchez et al., 2015; Herrando et al., 2019), as has been observed for Mediterranean bird communities (Clavero et al., 2011; Barnagaud et al., 2013; Tellería 2019, 2020). However, wider geographic tests of the scope for topography or vegetation to offset the impacts of climate change are

limited by availability of longer-term or larger-scale evidence of changes to Mediterranean insect communities (Lobo et al., 2018).

Here, we derive species-climatic associations and community indices from butterfly distribution records in the Iberian Peninsula over the course of 116 years, and test whether variation in the community indices is consistent with climatic variation over space and time. We calculate CTI and CPI independently for a set of well-sampled 10 km squares by estimating species-climatic associations using occurrence information from the remaining grid squares in the Iberian Peninsula. We then test i) whether the indices for the well-sampled squares are related to geographic variation in temperature and precipitation; and ii) whether changes over time in the community indices (1901-1979 versus 1980-2016) are related to the magnitude of temperature or precipitation change over the same period. We use our analysis of change in CTI and CPI, and of an index representing the associations of component butterfly species with open versus closed vegetation (“TAO”; Ubach et al., 2020), to assess whether regional butterfly faunas show evidence of buffering effects against climate change from topographic variation; or of direct responses to changes in vegetation cover, as has been inferred from monitoring data in the north-eastern Iberian Peninsula (Herrando et al., 2016, 2019; Ubach et al., 2020). We assess in particular whether topographic variation can increase the resilience of insect communities to environmental change through its effects on spatial and temporal variation in climatic conditions, and consider the implications of our results for adapting the conservation of insect communities to climate change.

Materials and methods

Butterfly distribution data

We used atlas data for the Papilionoidea and Hesperioidea of the Iberian Peninsula (García-Barros et al., 2004) updated to 2016. The database includes 380,214 distribution records at a resolution of 10 x 10 km Universal Transverse Mercator (UTM) squares from publications, public and private collections, and field surveys, which we updated and verified to ensure that identifications and locations were reliable. We analysed occurrence records from 10 km squares for 225 species, representing >95% of Iberian species for which there are reliable distribution data. Species nomenclature follows Wiemers et al. (2018). Where species identifications are uncertain (for a few cryptic species pairs; Platania et al., 2020), we assign records to the more widespread of the two taxa in the Iberian Peninsula, and if unequivocal records are not available for one of the species, we calculate species-climatic associations just for one taxon (see Table S1 for the full species list, climatic associations, and notes).

To test changes in the climatic associations of butterfly communities over time, we split the data into two periods (Fig. 1). Recording intensity has increased over time, so for the first

period we selected a longer time span, from 1901 to 1979, to achieve sufficient occurrence records (97,838 unique records of 218 species). The second period, from 1980 to 2016, had an average of more than five times as many records per year (259,803 records of 225 species) and corresponded to the period previously used to estimate butterfly species-climate associations for Europe (1981-2000; Schweiger et al., 2014). In the Iberian Peninsula, mean annual temperature increased by an equivalent amount over each period (Fig. 1c) and conditions also tended to be drier in 1980-2016 (Fig. 1d). A species was considered present in either period where there had been at least one confirmed record in each 10 km square.

To minimise bias from spatial and temporal variation in recording, we restricted our analyses of geographic patterns and temporal changes in butterfly communities to grid squares with the most complete sampling in both periods. We used KnowBR software (Lobo et al., 2018) to estimate inventory completeness for each 10 km square in each period. Inventory completeness is estimated using the number of species recorded divided by the expected species richness, based on rates of species accumulation per distribution record. We used the following criteria to select adequately sampled 10 km squares: i) a minimum of 300 total occurrence records; ii) a minimum of 50 records in each period (1901-1979 and 1980-2016); and iii) a minimum inventory completeness computed by KnowBR of 50% in each period. A total of 115 grid squares exceeded this threshold sampling intensity (Fig. 1), representing *c.* 2.5% of 10 km squares with any occurrence records, and *c.* 1.8% of squares in the entire Iberian Peninsula.

Climatic data and community indices

We used the dataset CHELSAcruts (Climatologies at high resolution for the earth's land surface areas: Karger et al., 2017) to obtain monthly maximum and minimum temperatures and precipitation sums over the period 1901-2016 at a resolution of 1 km. We used these data to calculate the mean annual temperature (°C) and precipitation (mm) for each period (1901-1979 and 1980-2016) in each 10 km square. This allowed us to compute for each species at 10 km resolution in the Iberian Peninsula the same metrics that have been calculated in the CLIMBER database (Climatic niche characteristics of the butterflies in Europe) using butterfly records at 50 km resolution for 1981-2000 (Schweiger et al., 2014; Platania et al., 2020). For each species, we calculate the Species Temperature Index (STI) as the mean temperature (°C), and the Species Precipitation Index (SPI) as the mean precipitation (mm), in 10 km squares where the species was recorded in 1980-2016, the period when distributions were sampled more completely. We tested whether our measures of STI and SPI for the Iberian Peninsula were consistent with those calculated across Europe for 222 species (Platania et al., 2020) and with a previous calculation for 63 species in the Iberian Peninsula based on atlas data from 1998-2005 (Herrando et al., 2019) using Spearman rank correlations because most variables were not normally distributed (Table S2).

To ensure our measures of Community Temperature Index (CTI) and Community Precipitation Index (CPI) were independent from (and could therefore be compared to) these measures of STI and SPI, we excluded the 115 best-sampled grid squares from the data and re-calculated STI and SPI for each species based on all remaining 10 km grid squares with occurrence records in 1980-2016 ($n = 4390$). We used these re-calculated indices to calculate CTI and CPI, for all squares except those that underpinned our species-level indices. We checked the revised species indices by correlating them with the STI and SPI values from all squares (Table S2). For the 115 well-sampled squares, we computed community indices based on the presence of species in 1901-1979 and 1980-2016 respectively. For each square, the Community Temperature Index (CTI) was the mean STI value of species recorded in the square during each respective period, and the Community Precipitation Index (CPI) was the mean SPI. We treated each species equally in the calculations because the occurrence records were not collected in a sufficiently systematic way to measure relative species abundances. Then for each 10 km square we calculated change over time in Community Temperature Index (Δ CTI) and Community Precipitation Index (Δ CPI) by subtracting the square's 1901-1979 index from its 1980-2016 index.

We obtained environmental data for the 115 well-sampled 10 km squares to test for factors influencing geographic variation and change over time in butterfly communities. The changes in mean annual temperature and precipitation from 1901-1979 to 1980-2016 were calculated for each square as a measure of the magnitude of climatic changes expected to have influenced butterfly communities. Temperature, rainfall and vegetation vary over elevation gradients (Körner, 2007); while topographic variation can influence rates of climatic change, as well as providing microclimatic variation that protects species from climatic change by allowing localised changes to species distributions (Scherrer & Körner, 2011). We used the 25 m resolution European Digital elevation model (EU-DEM, 2016) to compute mean elevation (m) and standard deviation in elevation (as a measure of topographic variability) per 10 km square; and we also computed the standard deviation of annual mean temperature and precipitation across the 100 constituent 1 km cells in each square as measures of local climatic variation. We recorded longitude, latitude and distance from the coast for each square because of their potential influences on butterfly faunas (Romo & García-Barros, 2010; Pulido-Pastor et al., 2018), and on climatic conditions and rates of change (Serrano-Notivoli et al., 2018, 2019).

Community associations with vegetation cover

The composition of insect communities in Mediterranean Europe has responded to recent land abandonment (Stefanescu et al., 2011; Dantas de Miranda et al., 2019; Wölfling et al., 2019; Ubach et al., 2020). To test whether increased vegetation cover had influenced Iberian butterfly communities, or modified their responses to climate change, we used an index (TAO) for the association of species with open or closed vegetation (Ubach et al., 2020). TAO represents a value between +1 (species associated with entirely open habitats) and -1 (species associated

with entirely closed habitats) and has been calculated for butterflies in North East Spain based on habitat associations in the Catalan Butterfly Monitoring Scheme. Thus, in common with STI and SPI, TAO was calculated for each species independently of its occurrence in the 115 well-sampled squares. However, whereas we used atlas data to calculate STI and SPI, we applied the published TAO values based on monitoring data for 145 species for which the index has been calculated (Ubach et al., 2020) (Table S1). We computed the community TAO index (TAOc) for each of the 115 well-sampled 10 km squares for 1901-1979 and 1980-2016 as the average TAO for species that were recorded in the respective period. As for calculation of CTI and CPI, we treated each species equally (i.e., species presence rather than relative abundance). We measured change in TAOc over time (Δ TAOc) in the same way as for CTI and CPI, as the index for the first period subtracted from the index for the second.

Data analysis

Relating community indices to climatic and geographic variables

To test whether butterfly community indices in the 115 squares in 1980-2016 reflected spatial variation in climatic conditions, we ran linear models of CTI and CPI against observed mean temperature and precipitation (the respective climatic predictors). We included elevation, latitude, longitude and distance to the coast as explanatory variables, as well as standard deviation (SD) in elevation (at 25 m resolution in each 10 km square) and standard deviation in the climatic predictor (at 1 km resolution), to test for effects of variation in topography or local climate within each grid square. We tested the interaction between SD climatic variation and the climatic variable, to assess whether spatial variation in climatic conditions could influence butterfly community responses to the average climate. To understand geographic variation in temperature and precipitation across the 115 squares, and the climatic gradients that butterfly communities were responding to, we also modelled temperature and precipitation against elevation, SD elevation, latitude, longitude, and distance from the coast. We used the same approach to model the effects of these geographic variables on TAOc (the association of the butterfly community with open or closed vegetation). We also correlated CTI, CPI and TAOc to test whether butterfly community associations with the climatic variables and land cover were linked.

We used R version 3.6 for all analyses (R Core Team, 2018). For model selection we used the dredge function in the MuMIn package (Bartoń, 2020). We standardised all explanatory variables to compare variable effect sizes in the models (Schielzeth, 2010), and used an information theoretic approach, comparing candidate models using the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). The most parsimonious model for each test was that with the lowest AICc, and we constructed a confidence model set including all candidate models whose AICc differed by 6 or less from

the most parsimonious model ($\Delta\text{AIC} \leq 6$) (Richards, 2008). We consider a parameter to have strong support if it was included in all models of the confidence set (Richards, 2015).

Change in community indices

To test whether climatic conditions or butterfly community associations changed from 1901-1979 to 1980-2016, we used non-parametric Wilcoxon tests paired by the 115 grid squares, since not all datasets were normally distributed.

To test whether communities had changed to a greater extent where climatic conditions had changed more, we modelled change in the community indices against change in the respective climatic variable (i.e., CTI change against change in mean temperature; CPI change against change in annual precipitation). Again, we tested for possible effects of elevation, latitude, longitude and distance from the coast, and for standard deviation in the climatic variable and elevation. As a test for the possible buffering effect of local variation in climatic conditions, we included an interaction between the magnitude of temperature or precipitation change with standard deviation in temperature or precipitation in each grid square in 1980-2016. For all analyses, we used model selection based on AICc in MuMIn as above.

To understand the factors influencing exposure to climatic change, we modelled rates of temperature or precipitation change across the 115 squares against the same set of environmental variables (elevation, latitude, longitude, distance from the coast), including SD elevation to test whether topographic variation influenced temperature or precipitation change. We tested interaction terms for mean and SD elevation with distance from the coast, given the importance of elevation and coastal proximity for climatic variation in the Iberian Peninsula (Serrano-Notivoli et al., 2019). We also compared changes to mean annual temperature and precipitation in the 10 km squares with the overall estimated variation in temperature and precipitation over the constituent 1 km squares, to understand whether localised displacements by butterflies might allow them to cope with observed rates of climatic change.

For the 1980-2016 community indices and change in these indices over time, we tested for spatial autocorrelation, which can cause overfitting in model selection (Diniz-Filho et al., 2008). We calculated global Moran's I in each index and its associated climatic variable for a distance of 248 km, at which each of the 115 squares had at least one nearest neighbour, and tested whether autocorrelation was reduced in the residuals of the best model for each variable analysed. We also calculated variance inflation factors to assess collinearity amongst all predictors in the models (Zuur et al., 2010).

Results

Values of Species Temperature Index (STI) and Species Precipitation Index (SPI) calculated from the 10 km atlas data for 1980-2016 were strongly positively correlated with previous calculations of STI and SPI for the species in Europe and the Iberian Peninsula (Table S2).

The 115 well-sampled 10 km squares were widely distributed, including locations from coastal and inland, low, and high elevation, and a wide range of longitudes and latitudes (Fig. 1, Table 1). Across these squares, the main geographic gradients in the climate were lower mean temperature at higher elevation (effect size in the top-ranked model: $-0.85 \pm \text{SE } 0.01$) and latitude (-0.26 ± 0.01), and greater precipitation at higher latitude (0.67 ± 0.07). In addition, temperature was lower but annual precipitation was greater in squares with greater standard deviation in elevation, nearer the coast, and further west (Table 2a).

The mean annual temperature was higher in all 115 squares in 1980-2016 than in 1901-1979 (median change $+1.14$ °C; range 0.8 - 1.3 °C). Annual precipitation was lower in 111 (97%) of the grid squares in 1980-2016 (median change -48 mm; maximum reduction 80 mm) (Paired Wilcoxon tests for changes in both climatic variables, $n = 115$, $P < 0.001$) (Table 1, Fig. 2c, d). The mean estimated range in annual temperature across 1 km cells in a 10 km square was 5.2 °C in 1980-2016: in 105 squares (91%), this spatial variation in temperature was greater than the change from 1901-1979 to 1980-2016 (the ten exceptions were all lowland squares below 655 m average elevation). The mean range in annual precipitation across 1 km cells per 10 km square was 432 mm (minimum 69 mm, maximum 890 mm), and this spatial variation was greater than the change in precipitation between the two periods for all 115 squares.

Temperature increases from 1901-1979 to 1980-2016 were lower in grid squares with greater standard deviation in elevation (effect size: -0.50 ± 0.10). Temperature increases were greater at higher latitudes and longitudes (further north and east), at higher elevations, and further from the coast (Table 2b). Precipitation change showed less clear geographic patterns, although declines appeared to be greater at higher elevation, further east, and further inland. Precipitation also decreased where elevation was more variable, although a positive interaction between distance to the coast and standard deviation in elevation gave a weak indication that topographic variation at inland sites had maintained higher precipitation than in locations with more uniform elevation (Table 2b).

Geographic variation in community indices

Community Temperature Index (CTI) and Community Precipitation Index (CPI) for the 115 squares in 1980-2016 were respectively positively related to mean temperature (effect size: 1.47 ± 0.10) and precipitation (0.25 ± 0.05) (Fig. 2a, b). CTI in 1980-2016 varied by 0.22 °C per 1 °C geographic difference in mean temperature, and CPI varied by 13.87 mm per 100 mm difference in annual precipitation. Mean temperature was the only variable included in all

models in the confidence set for CTI (Table 3a). All models in the confidence set for CPI included positive effects of precipitation, elevation and latitude, and negative effects of distance to the coast (i.e., CPI was greater at higher elevation and in the north, and nearer the coast, in addition to the effects of precipitation; Fig. 3b). The top-ranked (lowest AICc) models for both community indices included negative interactions between the climatic term and its standard deviation among 1 km cells in the 10 km squares, suggesting that CTI or CPI did not respond so strongly to temperature or precipitation where there was greater local climatic variation. CTI and CPI were negatively correlated with one another ($n = 115$, $r_s = -0.94$, $P < 0.001$).

For individual species, the TAO index of association with open or closed vegetation was not significantly related to STI or SPI (Table S2). Community TAO (TAOc) in the 115 squares in 1980-2016 was also not related to CTI ($r_s = 0.12$, $P = 0.21$) or CPI ($r_s = -0.15$, $P = 0.11$). The best model for TAOc included a negative effect of elevation (-0.31 ± 0.10), and a negative interaction between elevation and distance from the coast (-0.40 ± 0.10) (Table 4). This model indicates that communities were more associated with closed vegetation at low elevations near the coast and at high elevations inland, and were more associated with open habitats at relatively high elevations nearer the coast but low elevations inland (possibly related to geographic patterns in the vegetation of the Iberian Peninsula, e.g., see Loidi, 2017).

Changes to community indices over time

In contrast to observed changes in temperature and precipitation, CTI and CPI did not change systematically across the focal squares between 1901-1979 and 1980-2016 (Table 1, Fig. 2). CTI increased in 69 and decreased in 46 squares (Wilcoxon test, $P = 0.12$), whilst CPI increased in 58 and decreased in 57 squares ($P = 0.95$). The most parsimonious models explained only a small amount of variation in changes to CTI and CPI over time (adjusted r^2 0.09 and 0.07 respectively; Fig. 4), but showed that changes to the community indices were related to rates of climatic change, because positive effects of temperature change (effect size: 0.26 ± 0.13) and precipitation change (0.26 ± 0.10) were included in the top-ranked models for CTI and CPI respectively (Table 3b).

A negative effect of distance to the coast was the only variable included in all models in the confidence set for CTI change, indicating that CTI increased least in squares that were further inland (Fig. 3). CTI also increased less at higher latitudes. These effects contrast with the greater observed increases in temperature further inland and further north (Table 2b). Models for CPI change were weakly supported, with maximum $\Delta AICc$ from the null model of only 4.02. The top-ranked model suggested that CPI remained relatively high (despite reductions in precipitation) in squares that were further inland (positive effect of distance to the coast) and where there was greater local variation in precipitation (positive effect of SD precipitation; positive interaction between precipitation change and SD precipitation).

Community TAOc decreased in 71 grid cells and increased in 44 (Wilcoxon test, $V = 4357$, $P = 0.004$), showing that butterfly communities in 1980-2016 were associated with more closed vegetation than in 1901-1979. All candidate models for change in TAOc were weakly supported (no variables included in all models of the candidate set, maximum $\Delta AICc$ from null model = 1.17; Table 4), suggesting that changes to vegetation associations were occurring throughout the Iberian Peninsula. Whereas respective changes to CTI and CPI were negatively correlated ($r_s = -0.76$, $P < 0.001$), change to TAOc was not correlated with change in CTI ($r_s = -0.12$, $P = 0.21$) or CPI ($r_s = -0.07$, $P = 0.42$).

Spatial autocorrelation in CTI, CPI and change in these indices was reduced by the fitted models (Table S3). There was no significant spatial autocorrelation in TAOc or $\Delta TAOc$. Variance Inflation Factors ranged from 1.1 to 2.7 for variables included in the models, suggesting that results were robust to multicollinearity.

Discussion

We used indices based on occurrence records from the Iberian Peninsula to assess butterfly community variation over space and time in response to climate and land cover. The climatic associations of butterfly communities, quantified by Community Temperature Index (CTI) and Community Precipitation Index (CPI), were correlated with geographic variation in mean temperature and precipitation, respectively. Between 1901-1979 and 1980-2016, greater rates of warming and drying were associated with greater increases in CTI and reductions in CPI. However, whereas temperature and precipitation changed significantly over time, the community climatic indices did not show significant change. Topographic variation may have buffered communities against the effects of warming and drying, because rates of warming were reduced by greater variation in elevation, and we found evidence that local climatic variation dampened community responses to climate over space and time. The most widespread change to butterfly communities over time was an increased association with more closed vegetation. Thus, our results suggest that the Iberian butterfly fauna at 10 km spatial resolution has not yet shown generalised responses to climate change. Instead, local climatic variation related to topography, and the capacity of butterflies for behavioural thermoregulation, may have buffered communities against the effects of climate change; or climate-driven changes may have been overshadowed by factors such as land cover change.

Climatic associations of butterfly communities

We separated atlas data for the butterflies of the Iberian Peninsula into 115 well-sampled 10 km squares, and the remaining squares from which we calculated species temperature and precipitation indices. For the well-sampled squares, we found strong evidence that butterfly CTI was correlated with temperature, and CPI with precipitation. Evidence that these indices of community composition vary over geographic gradients in the climate (e.g., Nieto-Sánchez et al., 2015), combined with widespread recent observations of range shifts by species in

response to warming (Lenoir et al., 2020), suggest that space-for-time substitutions in biogeographic patterns will occur as communities are increasingly composed of warm- or dry-adapted species (Devictor et al., 2008, 2012). Our results do not demonstrate recent space-for-time substitutions in the butterfly fauna of the Iberian Peninsula, because whilst conditions became significantly hotter and drier between 1901-1979 and 1980-2016, the butterfly faunas showed no generalised increases in CTI or decreases in CPI.

Previous studies at finer resolution in different parts of the Iberian Peninsula have shown inconsistent recent changes to the climatic associations of butterfly communities. For example, CTI increased between 1967-1973 and 2006-2012 at sites between 580 m and 2250 m elevation in the Sierra de Guadarrama in central Spain (Nieto-Sánchez et al., 2015). In contrast, CTI in monitored sites showed non-significant decreases in north-eastern Spain (Stefanescu et al., 2011; Devictor et al., 2012), where butterfly and bird communities appear to be responding more to changes in precipitation (Herrando et al., 2019). We found that (accounting for geographic variation), CTI increased more where there was greater warming, and CPI reduced more where precipitation declined more, and therefore that the previously recorded geographic differences could partly be explained by different rates of warming and drying in different regions. Conditions heated most further from the coast, such as where Nieto-Sánchez et al. (2015) found increases in CTI, whereas precipitation reduced more in the east, where Herrando et al.'s (2019) study was focused.

Changes to the climatic variables themselves were more pronounced than changes to butterfly communities, with several possible methodological and biological explanations. We sought to control for sampling effort by restricting analyses to the most comprehensively sampled grid squares over both periods. However, documented faunas are likely to be incomplete for most grid squares, particularly in the 1901-1979 baseline period used to calculate change in CTI and CPI. Uncertainty in baseline data imposes noise on observed insect trends (Didham et al., 2020), which in this case might obscure responses of CTI and CPI to climatic change. In this respect, it is reassuring that we did detect albeit weak effects of warming on the rate of CTI change, and of drying on the rate of CPI change (Fig. 4).

Our results could also be explained by time lags in community responses to climate change (“climatic debt”; Devictor et al., 2012), or time lags in extirpations resulting from global change more generally (“extinction debt”; Kuussaari et al. 2009). Following postglacial recolonizations from ice age refugia (Schmitt, 2007), faunal composition in the Iberian Peninsula in the baseline period (1901-1979) is likely to have been associated largely with climatic conditions (Hawkins & Porter, 2003). In the Iberian Peninsula, butterfly species richness generally declines to the south and west associated with increasing water stress (Stefanescu et al., 2004; see also Penado et al., 2016 for bumblebee species richness and temperature). Hence, if species requiring cooler or wetter environments are lost from a location, relatively few species associated with warmer or drier conditions may be available to colonise,

and the chances of specialists doing so is limited by isolated habitat distributions (Wilson et al., 2007). CTI increased less both inland and at higher latitudes, despite high rates of warming in these locations: in both cases, few thermophilic species may be present nearby (Romo & García-Barros, 2010; Pulido-Pastor et al., 2018) and would need to travel long distances across inhospitable habitats for colonization. Nevertheless, there is evidence that species formerly restricted to southern or coastal regions, such as *Zizeeria knysna* (Trimen, 1862; Lycaenidae) or *Charaxes jasius* (Linnaeus, 1767; Nymphalidae), have begun to colonise inland and at higher elevations (Munguira, *pers. obs.*; Cancela & Vasconcelos, 2019).

A second possible biological explanation for the discrepancy in rates of climatic and community change is that other changes to vegetation or land cover have obscured changes driven by the climate (González-Megías et al., 2008). We found that an index of the vegetation associations of communities (TAOc) showed a significant shift towards species more associated with closed vegetation. Equivalent changes have been observed in butterfly monitoring data from Catalonia (north east Spain) since the 1990s (Stefanescu et al., 2011; Herrando et al., 2016; Ubach et al., 2020), driven at least partly by extirpations of species using open habitats. Our results suggest that these changes have occurred across the Iberian Peninsula for a longer period of time (since 1980 or before), likely associated with habitat abandonment as rural to urban migration occurred during the twentieth century (Rescia et al., 2010; Serra et al., 2014). There was little evidence for geographic variation in changes to TAOc, suggesting a widespread trend. Faunal changes towards insects and birds using more closed vegetation have been observed in several parts of Mediterranean Europe (Clavero et al., 2011; Barnagaud et al., 2013; Herrando et al., 2016; Dantas de Miranda et al., 2019; Wölfling et al., 2019; Tellería 2019, 2020), and their consequences for functional and taxonomic diversity merit research.

It is possible that changes to climatic conditions have not yet been sufficient to cause systematic changes in the butterflies recorded at 10 km resolution. For most grid squares, changes to temperature or precipitation over time were exceeded by spatial variation among 1 km cells in 1980-2016. Hence, it is likely that species would have been able, if needed, to shift their distributions locally within 10 km squares to maintain associations with favourable climatic conditions (Roth et al., 2014; Colom et al., 2020). Local range shifts could occur via movements to higher elevations (Wilson et al., 2007; Geppert et al., 2020; Marshall et al., 2020), or to cooler microclimates on north-facing slopes or in narrow valleys (Scherrer & Körner, 2011), which could provide locally cooler or moister conditions. Butterflies can also respond *in situ* to climatic variability through changes to behaviours such as egg-site selection (Bennett et al., 2015), basking (Barton et al., 2014) and aestivation (García-Barros, 1988), and through plasticity in physiology and morphology (e.g., de Jong et al., 2010; Gibbs et al., 2011). Variation within and among species in phenological responses to climate change could also buffer populations and communities against changes to prevailing climatic conditions during flight periods (e.g., Stefanescu et al., 2003; Gutiérrez & Wilson, 2021). Nevertheless, climatic

unpredictability may limit the scope of phenotypic plasticity to buffer populations against climate change (Kingsolver & Huey, 1998; Kingsolver & Buckley, 2018). As a result, although the geographic distributions of butterflies may be closely related to variation in the climate, there are likely to be delays in climate-driven range shifts resulting from colonizations or local extinctions (Rapacciuolo et al., 2011), with accompanying delays in community responses (Devictor et al., 2012).

Environmental buffers against climatic change

Greater variation in elevation or topography could shield ecological communities from the impacts of global change for several reasons. Steeper slopes lead to a wider range of habitats and abiotic conditions (including microclimates). Landscapes with steeper slopes experience reduced rates of conversion to intensive uses but are subject to abandonment if extensive agriculture or livestock rearing become economically unsustainable (Debussche et al., 1999). In Catalonia, sites with greater topographic heterogeneity support butterfly populations with less variable population dynamics (Oliver et al., 2014) and reduced local extinction risk (Fernández-Chacón et al., 2013). The ability of topographic variation to provide a wider range of microclimatic conditions and hence to reduce rates of extirpation from 10 km cells has been observed for insects and plants that are sensitive to warming in England (Suggitt et al., 2018). In our study we show that 10 km squares with greater variation in elevation (e.g., in mountainous regions) experienced reduced warming from 1901-1979 to 1980-2016, decreasing the exposure of mountain butterfly communities to hotter conditions. These observations reinforce the importance of topographic or microclimatic heterogeneity in models of ecological responses to climate change and highlight the vulnerability of insects in flat landscapes to climate change (Luoto & Heikkinen, 2008; Roth et al., 2014; Penado et al., 2016). Nevertheless, warming rates and reductions in precipitation tended to be greater at high elevations: observed community responses to climate change over gradients of elevation and land use will reflect these combined changes to temperature, precipitation, and weather patterns (Halsch et al., 2021), and their effects on insects and interacting species such as host plants (Gutiérrez et al., 2016).

Land abandonment or changed forestry practices have led to increased tree cover in southern Europe (Debussche et al., 1999; Rescia et al., 2010; Marshall et al., 2020). Apart from promoting population recovery in woodland butterflies (Stefanescu et al., 2011) greater vegetation cover could counteract the ecological effects of climate change by providing cooler microclimates (Barnagaud et al., 2012; De Frenne et al., 2019). Mountain bird communities in the Iberian Peninsula have recently become increasingly dominated by forest species, in some cases with evidence that forest species have expanded downhill to take advantage of increasing habitat availability (Tellería 2019) and reducing Community Temperature Index despite climatic warming (Clavero et al., 2011; Stefanescu et al., 2011). However, in our study there was little evidence that changes to the TAOc index for butterfly communities were correlated

with changes to climatic associations, or that increasing contributions by species of closed habitats would act either antagonistically or synergistically to the community changes expected from climate change.

Adapting conservation to climate change

Topographic variation can reduce rates of climate warming and provide a range of microclimatic conditions and habitats, helping species to shift their distributions on a local scale (Roth et al., 2014). The need to protect sufficient abiotic variation to facilitate ecological and evolutionary responses to global change (“conserving nature’s stage”; Lawler et al., 2015) demands that habitats are protected, connected and managed across geographic and climatic gradients, permitting communities to track ongoing changes to climate and land cover (Mingarro et al., 2020).

We demonstrate that occurrence data can be valuable for identifying long-term or large-scale changes to a fauna, and for suggesting the reasons behind apparent differences in trends between regions or at different spatial scales. We were able to use atlas data from throughout the Iberian Peninsula to calculate Species Temperature and Species Precipitation Indices that were closely correlated with STI and SPI for Europe (Platania et al., 2020), even though most 10 km squares have incomplete faunal information for butterflies (García-Barros et al., 2004), as is the case for other insects in the Iberian Peninsula (Penado et al., 2016; Lobo et al., 2018) and for butterflies in much of the world (Girardello et al., 2019). A limited number of relatively well-sampled 10 km squares could then be used to detect changes in communities over time from before 1980, and to infer the factors driving these changes.

We suggest that the identification of potential refugia from climate change in regions where there are geographic or historical gaps in species distribution data will benefit from: a) geographic information on climatic variation over space and time (Serrano-Notivoli et al., 2018, 2019); b) comprehensive evidence of past distributions from the ongoing cataloguing of natural history collections (Kharouba et al., 2019; Montgomery et al., 2020); and c) up-to-date surveys of species distributions and abundance (e.g., Stefanescu et al., 2004, 2011). Our study shows how the complementary use of such data can provide information on changes to butterfly communities and their drivers for one region of Mediterranean Europe.

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Conflict of interest

The authors declare no conflict of interest.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Species Temperature Index (STI) and Species Precipitation Index (SPI) for 225 butterfly species based on confirmed 10 km distribution records in the Iberian Peninsula from 1980 to 2016. The total number of squares where each species was recorded is shown, with the number of 115 well-sampled 10 km squares in parenthesis and superscript. STI and SPI calculated excluding these 115 well-sampled squares (to permit independent analyses of CTI and CPI) also shown in superscript. Species are shown in alphabetical order within families.

Table S2. Spearman correlation coefficients (r_s) of Species Temperature Index (STI) and Species Precipitation Index (SPI) from 10 km atlas data in the Iberian Peninsula (1980-2016) against published calculations of STI and SPI for Europe and the Iberian Peninsula, and the TAO open/closed vegetation index from Ubach et al. (2020). Spatial resolution and sampling period of data used to derive the indices are shown.

Table S3. Spatial autocorrelation in community indices, their climatic explanatory variables and in the residuals of the top-ranked models. Results show Moran's I calculated for a 148 km interval, the minimum distance at which all 115 grid squares have at least one neighbour.

Data S1. Geographic, temperature, precipitation, and community indices (CTI, CPI, TAOc) in 1901-1979 and 1980-2016, and change over time in these variables, for the 115 well-sampled 10 km squares.

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Table 1. Environmental and butterfly community variation in the 115 grid squares which met criteria for completeness of sampling in both 1901-1979 and 1980-2016. Community associations are summarised as the Community Temperature Index (CTI), Community Precipitation Index (CPI) and TAOc Index of species associations with vegetation cover (-1: closed; +1: open; Ubach et al., 2020). Temperature and precipitation are average values per 10 km square, sourced at 1 km resolution (Karger et al., 2017).

	Minimum	Maximum	Median
Latitude (°N)	36.17	43.49	42.05
Longitude (°E)	-9.40	2.70	-1.76
Elevation (m)	12.68	2348.16	1065.32
Distance to the coast (km)	0.46	329.50	149.24
1901-1979			
Mean annual temperature (°C)	0.54	17.88	9.31
Annual precipitation (mm)	317.91	1753.28	875.02
CTI	9.13	13.43	11.48
CPI	715.21	957.05	821.44
TAOc	0.28	0.45	0.35
1980-2016			
Mean annual temperature (°C)	1.64	18.68	10.45
Annual precipitation (mm)	299.12	1720.22	812.13
CTI	9.07	13.61	11.49
CPI	706.75	942.86	819.69
TAOc	0.27	0.41	0.34

Table 2. Models for climatic variation among the 115 focal grid squares. a) Mean annual temperature (°C) and precipitation (mm) in 1980-2016; b) Changes to temperature and precipitation from 1901-1979 to 1980-2016. Standard deviation (SD) represents variation across 1 km cells in the 10 km grid squares for elevation. Interaction terms of elevation and SD elevation with distance from the coast were tested. Coefficients (\pm SE) are shown for the top-ranking model based on AICc; variables in bold selected in all models within the confidence set (Δ AICc $<$ 6 of the top model). Variable importance shows the sum of weights of models containing the variable in the confidence set. †Denotes terms included in all models under a less conservative criterion of Δ AICc $<$ 2 (Burnham & Anderson, 2002).

Climate term	Intercept	Elevation	SD elevation	Latitude	Longitude	Distance to coast	Interaction elevation: distance to coast	Interaction SD elevation: distance to coast	Adj. r ²	AICc
a) 1980-2016 climatic conditions										
Temperature	-0.00 (\pm 0.01)	-0.85 (\pm 0.01)	-0.06 (\pm 0.01)	-0.26 (\pm 0.01)	+0.03† (\pm 0.01)	+0.12 (\pm 0.01)		-0.03 (\pm 0.01)	0.99	-215.0
Importance		0.97	0.97	0.97	0.91	0.97	0.28	0.89		
Precipitation	+0.00 (\pm 0.05)		+0.39 (\pm 0.06)	+0.67 (\pm 0.07)	-0.38 (\pm 0.06)	-0.26 (\pm 0.05)			0.67	207.1
Importance		0.55	1.00	1.00	1.00	1.00	0.14	0.26		
b) Change in climatic conditions										
Temperature	-0.01 (\pm 0.06)	+0.27† (\pm 0.10)	-0.50 (\pm 0.10)	+0.50 (\pm 0.07)	+0.12 (\pm 0.07)	+0.39 (\pm 0.07)		-0.14 (\pm 0.07)	0.61	227.3
Importance		0.97	0.99	0.99	0.60	0.99	0.36	0.62		
Precipitation	+0.01 (\pm 0.07)	-0.33† (\pm 0.12)	-0.22 (\pm 0.12)		-0.20† (\pm 0.08)	-0.08 (\pm 0.09)		+0.13 (\pm 0.08)	0.40	276.1
Importance		0.95	0.67	0.29	0.90	0.73	0.27	0.27		

Table 3. Models for community climatic associations in the 115 focal grid squares. a) Community Temperature Index (CTI) and Community Precipitation Index (CPI) in 1980-2016; b) Changes to CTI and CPI from 1901-1979 to 1980-2016. *Independent climate terms were a) mean annual temperature (°C) for CTI and mean annual precipitation (mm) for CPI; or b) change in these variables over time. Standard deviation (SD) represents variation across 1 km cells in the 10 km grid squares for the respective climate terms and elevation. Coefficients (\pm SE) are shown for the top-ranking model based on AICc; variables in bold selected in all models within the confidence set (Δ AICc $<$ 6 of the top model). Variable importance shows the sum of weights of models containing the variable in the confidence set. †Denotes terms included in all models under a less conservative criterion of Δ AICc $<$ 2 (Burnham & Anderson, 2002).

Index	Intercept	Climate term*	SD climate term	Interaction climate:SD	Elevation	SD elevation	Latitude	Longitude	Distance to coast	Adj. r ²	AICc
a) 1980-2016 community associations											
CTI	-0.04 (\pm 0.03)	+1.47 (\pm 0.10)	+0.40 (\pm 0.29)	-0.06 (\pm 0.02)	+0.64 (\pm 0.09)	-0.47 (\pm 0.30)		-0.08† (\pm 0.03)	-0.11 (\pm 0.03)	0.94	7.4
Importance		0.97	0.69	0.45	0.62	0.53	0.69	0.76	0.58		
CPI	+0.07 (\pm 0.04)	+0.25 (\pm 0.05)	+0.09† (\pm 0.06)	-0.08† (\pm 0.03)	+0.36 (\pm 0.05)	+0.14† (\pm 0.05)	+0.37 (\pm 0.04)		-0.10 (\pm 0.03)	0.91	44.5
Importance		0.96	0.84	0.77	0.96	0.92	0.96	0.31	0.96		
b) Change in community associations											
ΔCTI	+1.0 e ⁻¹⁶ (\pm 0.09)	+0.26 (\pm 0.13)					-0.22 (\pm 0.11)		-0.41 (\pm 0.11)	0.09	321.7
Importance		0.54	0.29	0.03	0.23	0.26	0.42	0.32	0.93		
ΔCPI	+0.07 (\pm 0.10)	+0.26† (\pm 0.10)	+0.17† (\pm 0.10)	+0.18 (\pm 0.09)					+0.21† (\pm 0.10)	0.07	325.4
Importance		0.68	0.58	0.41	0.26	0.21	0.19	0.31	0.76		

Table 4. Models for community associations with open or closed vegetation in the 115 focal grid squares. Models for a) the community TAOc index (Ubach et al., 2020) based on species presence /absence in 1980-2016, and b) changes to TAOc from 1901-1979 to 1980-2016. TAOc varies from +1 (species associated with entirely open habitats) to -1 (species associated with entirely closed habitats). Standard deviation (SD) represents variation across 1 km cells in the 10 km grid squares for elevation. Interaction terms of elevation and SD elevation with distance from the coast were tested. Coefficients (\pm SE) are shown for the top-ranking model based on AICc; variables in bold selected in all models within the confidence set (Δ AICc $<$ 6 of the top model). Variable importance shows the sum of weights of models containing the variable in the confidence set.

Response	Intercept	Elevation	SD elevation	Latitude	Longitude	Distance to coast	Interaction elevation: distance to coast	Interaction SD elevation: distance to coast	Adj. r ²	AICc
a) TAOc	+0.07 (\pm 0.09)	-0.31 (\pm 0.10)				+0.01 (\pm 0.10)	-0.40 (\pm 0.10)		0.14	316.0
Importance		0.92	0.25	0.23	0.22	0.92	0.92	0.05		
b) ΔTAOc	+0.00 (\pm 0.09)			+0.16 (\pm 0.09)		+0.15 (\pm 0.09)			0.05	328.3
Importance		0.44	0.53	0.55	0.32	0.69	0.19	0.21		

Figure legends

Fig. 1. Variation in climatic conditions over space and time in the Iberian Peninsula. a, b) 1 km resolution mean annual temperature ($^{\circ}\text{C}$, a) and precipitation (mm, b) in 1980-2016 (data from Karger et al., 2017); c) mean annual temperature ($^{\circ}\text{C}$) and d) precipitation (mm) across all grid squares from 1901 to 2016; lines smoothed according to loess method (local polynomial regression fitting) with 95% confidence intervals. In a and b, the 115 well-sampled 10 km grid squares are outlined in black.

Fig. 2. The relationship between community indices and climatic variables in the 115 well-sampled grid squares. Scatter plots for 1980-2016 of a) Community Temperature Index (CTI) against mean annual temperature; b) Community Precipitation Index (CPI) against mean annual precipitation. Boxplots show changes to the climatic variables (dark) and community indices (light) from 1901-1979 to 1980-2016 for c) temperature/CTI, and d) precipitation/CPI. Dotted lines in c and d show no change in indices or climatic variables.

Fig. 3. Butterfly Community Temperature Index (CTI – a, c) and Community Precipitation Index (CPI – b, d) for 115 well-sampled 10 km grid squares in 1980-2016 (a, b) and their change since 1901-1979 (c, d). Units are equivalent to $^{\circ}\text{C}$ for CTI and mm for CPI.

Fig. 4. Observed against modelled changes in a) CTI and b) CPI from 1901-1979 to 1980-2016, based on the top-ranking models in Table 3b. Units are equivalent to a) $^{\circ}\text{C}$ and b) mm. Dashed line shows best fit, with shaded area showing 95% confidence intervals of the model. Symbols are shaded based on observed changes to a) Temperature and b) Precipitation in the 115 grid squares. Note that observed and modelled changes to CTI and CPI were both positive and negative, whereas temperature increased in all squares, and precipitation decreased in 111 grid squares.

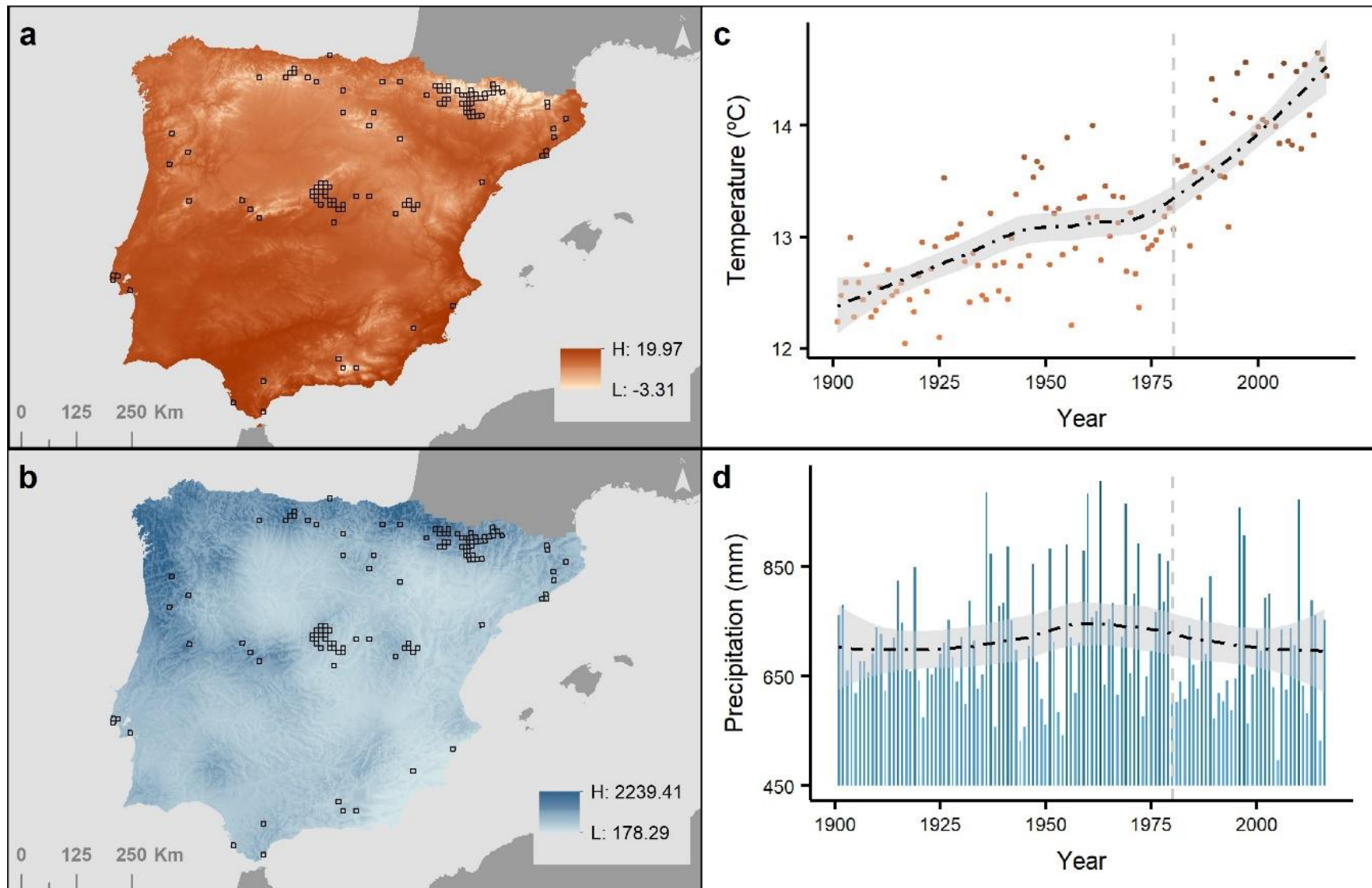


Figure 1.

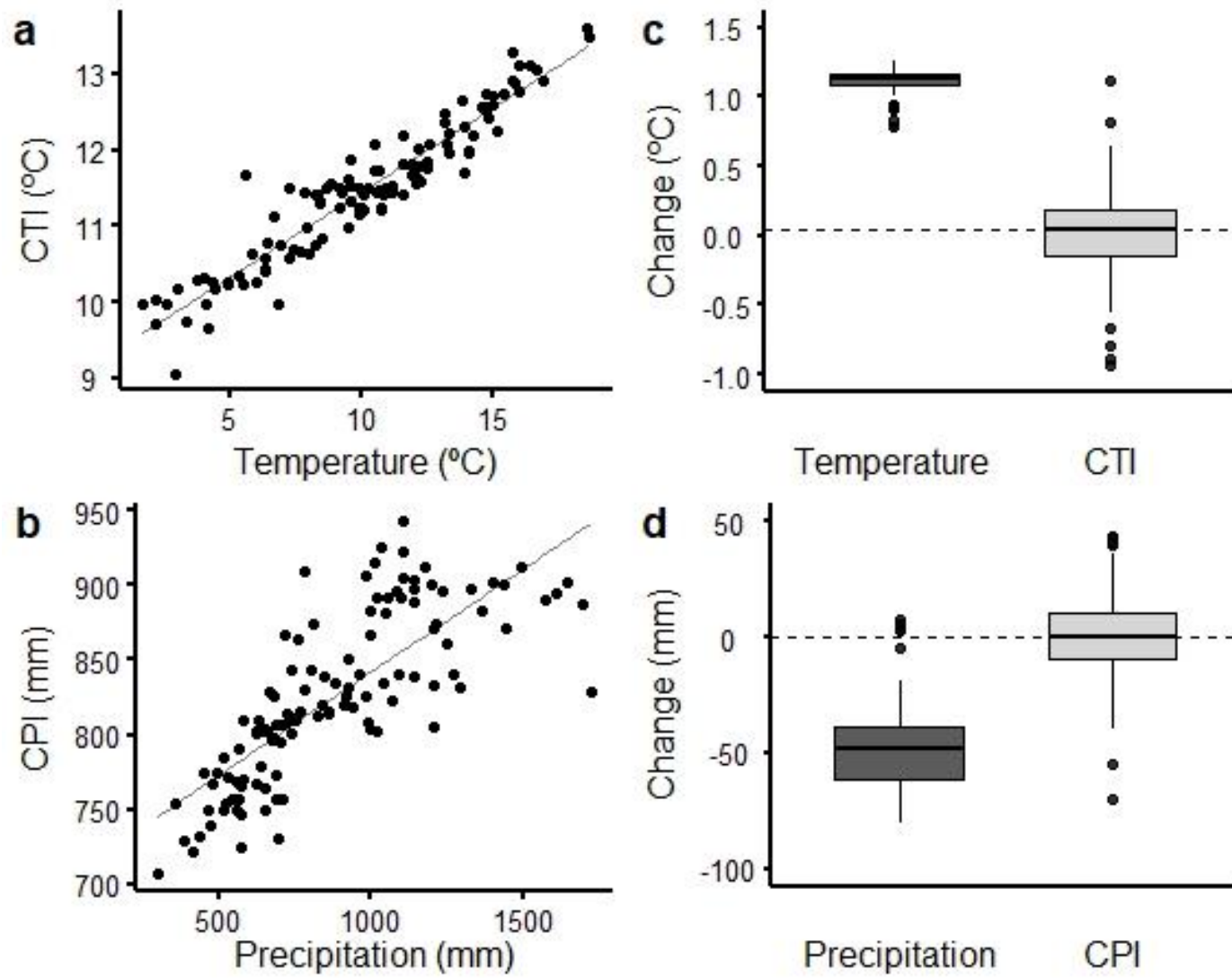


Figure 2

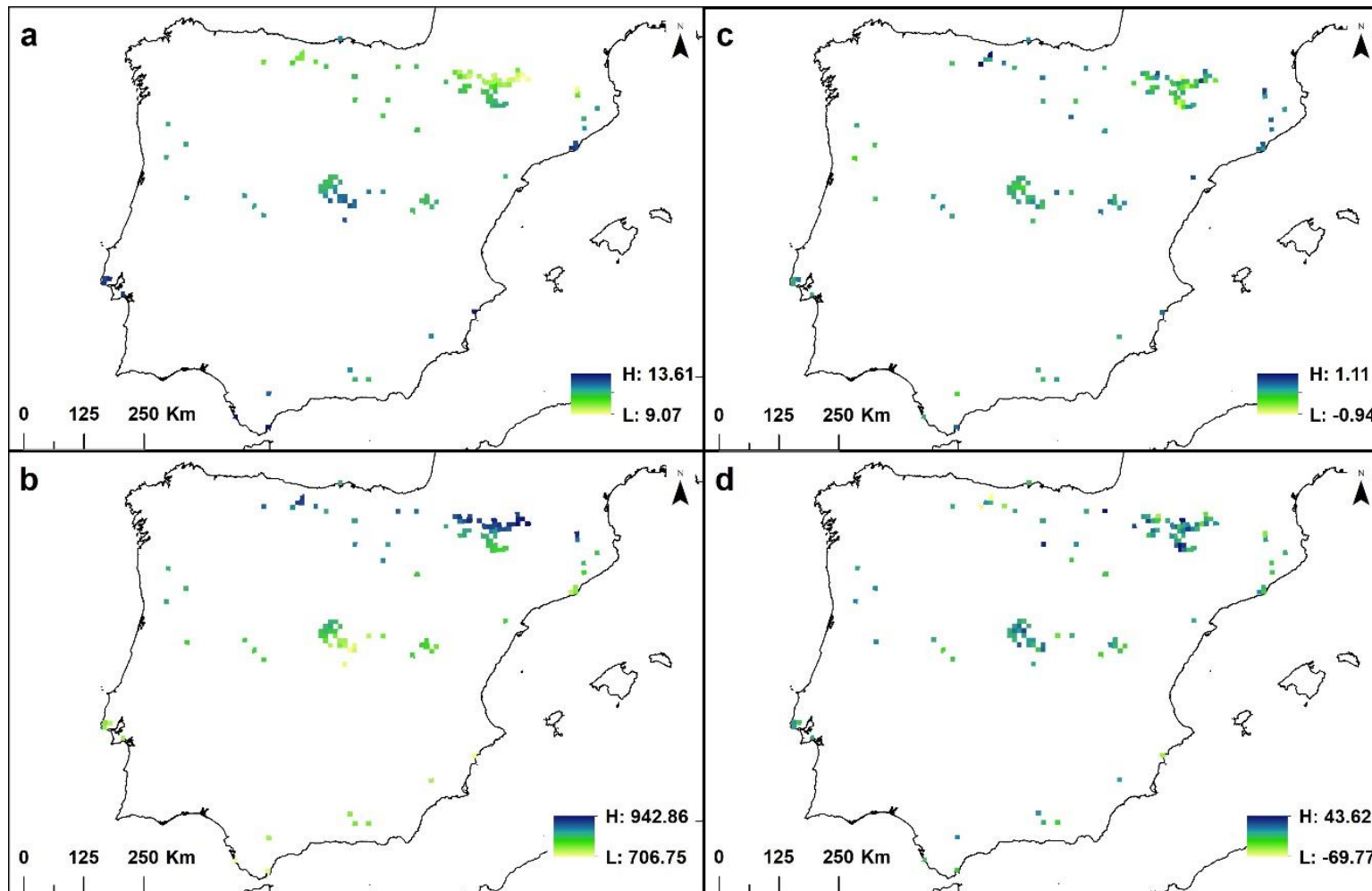


Figure 3.

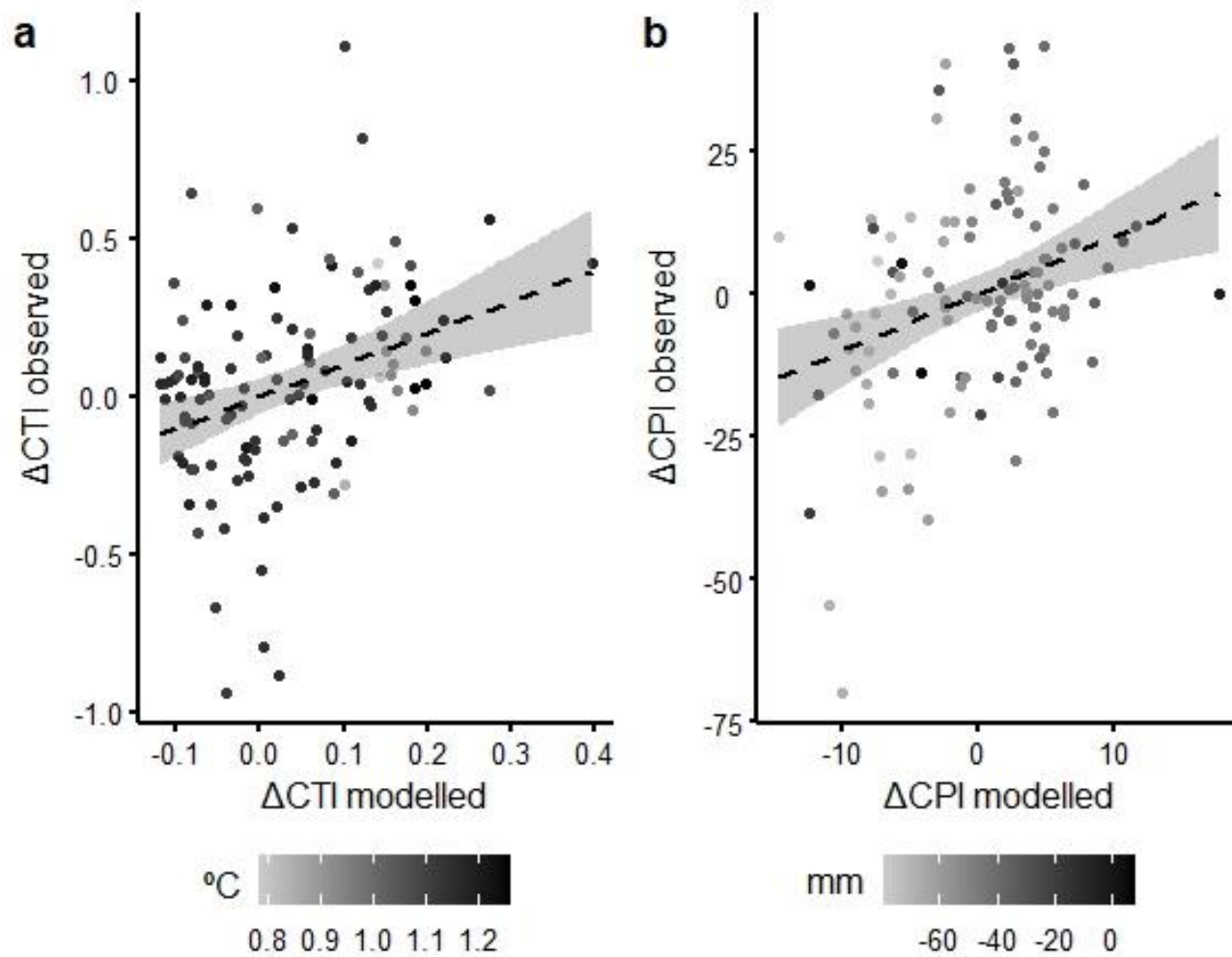


Figure 4

Supplementary Tables

Table S1. Species Temperature Index (STI) and Species Precipitation Index (SPI) for 225 butterfly species based on confirmed 10 km records in the Iberian Peninsula from 1980 to 2016. The total number of squares where each species was recorded is shown, with the number of 115 well-sampled 10 km squares in parenthesis and superscript. STI and SPI calculated excluding these 115 well-sampled squares (to permit independent analyses of CTI and CPI) also shown in superscript. Species are shown in alphabetical order within families. For 145 species shown in bold the TAO open/closed vegetation index was used from Ubach et al. (2020).

Species name	N 10 km		STI (°C)		SPI (mm)	
	squares					
Papilionidae						
<i>Iphiclides feisthamelii</i>	1801	(104)	12.79	12.94	777	771
<i>Papilio machaon</i>	1697	(100)	13.34	13.56	730	720
<i>Parnassius apollo</i>	351	(61)	8.38	8.61	906	885
<i>Parnassius mnemosyne</i>	41	(23)	4.67	4.33	1169	1123
<i>Zerynthia rumina</i>	1196	(59)	13.90	14.00	689	687
Hesperiidae						
<i>Borbo borbonica</i>	5	(1)	18.20	18.13	652	645
<i>Carcharodus alceae</i>	1015	(65)	13.17	13.33	750	746
<i>Carcharodus baeticus</i>	459	(30)	13.67	13.74	629	629
<i>Carcharodus floccifera</i>	150	(26)	9.87	10.24	926	912
<i>Carcharodus lavatherae</i>	200	(37)	10.64	11.22	823	788
<i>Carcharodus tripolinus</i>	22	(3)	16.88	17.10	592	600
<i>Carterocephalus palaemon</i>	41	(4)	9.15	9.52	1159	1165
<i>Erynnis tages</i>	651	(64)	11.05	11.29	920	911
<i>Gegenes nostradamus</i>	155	(12)	16.12	16.16	534	536
<i>Hesperia comma</i>	563	(85)	9.94	10.14	881	869
<i>Heteropterus morpheus</i>	99	(5)	11.94	12.07	1186	1180
<i>Muschampia proto</i>	522	(31)	13.66	13.76	597	594
<i>Ochlodes sylvanus</i>	659	(70)	10.64	10.92	991	986
<i>Pyrgus alveus</i>	253	(49)	9.19	9.59	977	957
<i>Pyrgus andromedae</i>	19	(11)	4.57	5.24	1036	845

<i>Pyrgus armoricanus</i>	297	(35)	10.54	10.68	849	847
<i>Pyrgus cacaliae</i>	7	(5)	2.85	3.16	1030	1025
<i>Pyrgus carthami</i>	315	(48)	9.76	9.94	879	868
<i>Pyrgus cinarae</i>	7	(1)	9.97	9.89	699	692
<i>Pyrgus cirsii</i>	174	(36)	10.05	10.33	791	760
<i>Pyrgus foulquieri</i>	24	(5)	10.39	10.66	921	888
<i>Pyrgus malvoides</i>	560	(71)	10.52	10.70	934	929
<i>Pyrgus onopordi</i>	297	(34)	11.81	11.92	722	715
<i>Pyrgus serratulae</i>	324	(55)	9.24	9.50	946	940
<i>Pyrgus sidae</i>	6	(1)	9.89	9.17	985	981
<i>Spialia sertorius</i>	1125	(87)	12.36	12.56	777	768
<i>Thymelicus acteon</i>	1271	(80)	12.90	13.08	780	771
<i>Thymelicus lineola</i>	601	(67)	11.38	11.59	776	762
<i>Thymelicus sylvestris</i>	1281	(97)	12.04	12.24	805	796
Pieridae						
<i>Anthocharis cardamines</i>	1144	(102)	11.58	11.77	879	876
<i>Anthocharis euphenoides</i>	880	(81)	12.12	12.30	695	685
<i>Aporia crataegi</i>	1082	(98)	11.10	11.28	804	793
<i>Colias alfacariensis</i>	845	(90)	11.22	11.42	743	726
<i>Colias crocea</i>	2555	(114)	13.15	13.30	772	766
<i>Colias phicomone</i>	96	(30)	5.76	6.06	1140	1120
<i>Colotis evagore</i>	79	(4)	16.41	16.58	441	437
<i>Euchloe bazae</i> [†]	9	(0)	15.21	15.21	410	410
<i>Euchloe belemia</i>	615	(12)	16.05	16.06	589	589
<i>Euchloe crameri</i>	1551	(89)	13.66	13.87	687	677
<i>Euchloe simplonia</i>	2	(1)	3.11	2.16	1174	841
<i>Euchloe tagis</i>	179	(10)	14.69	14.72	579	580
<i>Gonepteryx cleopatra</i>	1281	(98)	13.29	13.54	740	728
<i>Gonepteryx rhamni</i>	1278	(99)	11.63	11.79	892	890
<i>Leptidea reali</i> [‡]	37	(4)	9.23	9.40	828	801
<i>Leptidea sinapis</i>	1317	(96)	11.98	12.18	882	878
<i>Pieris brassicae</i>	1932	(110)	13.50	13.70	806	802
<i>Pieris ergane</i>	61	(14)	8.67	9.21	891	847

<i>Pieris mannii</i>	110	(24)	11.53	12.25	690	659
<i>Pieris napi</i>	1227	(103)	11.72	11.91	862	858
<i>Pieris rapae</i>	2710	(114)	13.33	13.47	773	768
<i>Pontia callidice</i>	59	(22)	4.36	4.36	1056	988
<i>Pontia daplidice</i>	1722	(100)	13.49	13.69	690	678
<i>Zegris eupheme</i>	257	(18)	13.86	13.87	482	478
Riodinidae						
<i>Hamearis lucina</i>	248	(41)	9.26	9.59	973	955
Lycaenidae						
<i>Agriades glandon</i>	36	(19)	4.19	3.70	1178	1161
<i>Agriades pyrenaicus</i>	31	(6)	6.81	7.31	1299	1264
<i>Agriades zullichi</i>	7	(2)	6.34	6.35	533	523
<i>Aricia cramera</i>	1522	(85)	13.53	13.71	705	698
<i>Aricia montensis</i>	488	(65)	10.01	10.29	904	892
<i>Aricia morronensis</i>	116	(17)	8.94	9.03	841	837
<i>Aricia nicias</i>	16	(4)	4.57	4.70	951	911
<i>Azanus jesous</i> [‡]	2	(1)	18.28	18.05	678	667
<i>Cacyreus marshalli</i>	513	(20)	14.65	14.71	753	753
<i>Callophrys avis</i>	122	(9)	13.91	13.91	820	827
<i>Callophrys rubi</i>	1267	(81)	12.82	12.98	760	752
<i>Celastrina argiolus</i>	1287	(78)	12.78	12.95	837	833
<i>Cupido alcetas</i>	89	(12)	10.27	10.41	871	849
<i>Cupido argiades</i>	380	(27)	11.13	11.27	985	983
<i>Cupido lorquini</i> [‡]	95	(8)	14.56	14.73	644	646
<i>Cupido minimus</i>	496	(66)	10.11	10.41	847	828
<i>Cupido osiris</i>	281	(46)	10.06	10.53	841	807
<i>Cyaniris semiargus</i>	461	(65)	9.66	9.92	873	858
<i>Eumedonia eumedon</i>	69	(12)	7.62	8.12	952	930
<i>Favonius quercus</i>	537	(56)	12.23	12.37	784	778
<i>Glaucopsyche alexis</i>	749	(70)	11.63	11.78	750	741
<i>Glaucopsyche melanops</i>	1075	(69)	13.31	13.49	728	720
<i>Iolana debilitata</i>	82	(18)	12.37	12.76	587	573
<i>Kretania hesperica</i>	61	(11)	12.62	12.82	493	491

<i>Laeosopis roboris</i>	464	(46)	11.66	11.92	847	840
<i>Lampides boeticus</i>	1373	(101)	12.85	13.07	770	763
<i>Leptotes pirithous</i>	1480	(56)	13.71	13.78	818	820
<i>Lycaena alciphron</i>	504	(64)	10.21	10.48	886	873
<i>Lycaena bleusei</i>	197	(22)	12.70	12.87	780	788
<i>Lycaena helle</i>	4	(1)	4.42	5.42	906	838
<i>Lycaena hippothoe</i>	141	(28)	6.85	7.18	1042	1012
<i>Lycaena phlaeas</i>	1772	(96)	13.39	13.58	730	721
<i>Lycaena tityrus</i>	360	(32)	10.31	10.65	1113	1107
<i>Lycaena virgaureae</i>	291	(46)	8.18	8.41	986	972
<i>Lysandra albicans</i>	580	(57)	11.71	11.94	671	651
<i>Lysandra bellargus</i>	946	(85)	12.26	12.52	736	720
<i>Lysandra caelestissima</i>	10	(4)	9.31	9.40	665	673
<i>Lysandra coridon</i>	471	(58)	9.48	9.75	951	935
<i>Phengaris alcon</i>	109	(13)	9.63	10.20	1099	1093
<i>Phengaris arion</i>	198	(39)	9.19	9.77	953	922
<i>Phengaris nausithous</i>	23	(3)	7.87	7.92	1018	1002
<i>Plebejus argus</i>	751	(77)	10.64	10.86	876	866
<i>Plebejus idas</i>	266	(52)	8.73	9.00	953	934
<i>Polyommatus amandus</i>	200	(37)	9.35	9.78	892	857
<i>Polyommatus celina</i> ^{†‡}	90	(0)	15.66	15.66	617	617
<i>Polyommatus damon</i>	152	(25)	9.37	9.77	863	833
<i>Polyommatus daphnis</i>	78	(8)	11.06	10.99	686	688
<i>Polyommatus dorylas</i>	400	(51)	9.41	9.73	914	898
<i>Polyommatus eros</i>	38	(20)	4.75	5.19	1133	1051
<i>Polyommatus escheri</i>	414	(63)	10.66	10.99	784	764
<i>Polyommatus fabressei</i>	80	(7)	10.87	11.05	563	560
<i>Polyommatus fulgens</i>	197	(27)	10.56	10.77	834	814
<i>Polyommatus golgus</i>	12	(2)	8.35	8.74	579	582
<i>Polyommatus icarus</i>	2077	(113)	12.86	13.02	756	748
<i>Polyommatus nivescens</i>	118	(16)	11.76	12.13	567	546
<i>Polyommatus ripartii</i>	197	(25)	10.60	10.75	829	803
<i>Polyommatus thersites</i>	513	(63)	11.14	11.40	751	736

<i>Polyommatus violeatae</i> [†]	22	(0)	11.95	11.95	572	572
<i>Pseudophilotes abencerragus</i>	109	(8)	14.81	15.00	551	554
<i>Pseudophilotes panoptes</i>	777	(65)	12.42	12.58	669	657
<i>Satyrium acaciae</i>	258	(47)	9.74	10.01	886	881
<i>Satyrium esculi</i>	1105	(72)	13.19	13.33	741	735
<i>Satyrium ilicis</i>	367	(56)	10.51	10.80	924	916
<i>Satyrium pruni</i> [†]	10	(0)	11.50	11.50	1063	1063
<i>Satyrium spini</i>	579	(73)	11.83	12.09	796	779
<i>Satyrium w-album</i>	104	(24)	9.36	10.06	964	913
<i>Scolitantides orion</i>	81	(13)	10.97	11.21	686	677
<i>Tarucus theophrastus</i> [†]	26	(0)	18.25	18.25	276	276
<i>Thecla betulae</i>	233	(20)	10.33	10.51	1063	1055
<i>Tomares ballus</i>	424	(31)	14.79	14.85	605	604
<i>Zizeeria knysna</i>	188	(16)	16.12	16.34	616	614
Nymphalidae						
<i>Aglais io</i>	949	(89)	11.29	11.49	925	926
<i>Aglais urticae</i>	900	(81)	10.61	10.79	908	902
<i>Apatura ilia</i>	176	(16)	10.84	11.07	958	955
<i>Apatura iris</i>	151	(21)	9.88	10.29	1174	1182
<i>Aphantopus hyperantus</i>	308	(22)	9.72	9.95	1049	1043
<i>Araschnia levana</i>	76	(8)	11.58	11.77	1015	1021
<i>Arethusana arethusa</i>	283	(30)	10.65	10.82	872	868
<i>Argynnis pandora</i>	1071	(64)	12.67	12.75	725	722
<i>Argynnis paphia</i>	674	(81)	10.36	10.59	971	968
<i>Boloria dia</i>	544	(52)	10.36	10.59	944	933
<i>Boloria eunomia</i>	22	(3)	6.12	5.84	987	966
<i>Boloria euphrosyne</i>	341	(46)	8.61	8.92	1028	1010
<i>Boloria napaea</i>	8	(3)	3.81	4.34	869	787
<i>Boloria pales</i>	73	(27)	5.63	6.14	1180	1171
<i>Boloria selene</i>	464	(39)	9.99	10.18	1074	1079
<i>Brenthis daphne</i>	443	(59)	9.72	9.95	953	942
<i>Brenthis hecate</i>	243	(23)	10.61	10.73	789	782
<i>Brenthis ino</i>	270	(31)	9.21	9.46	966	947

<i>Brintesia circe</i>	1222	(80)	11.52	11.62	757	748
<i>Charaxes jasius</i>	422	(20)	14.80	14.88	728	725
<i>Chazara briseis</i>	325	(38)	11.48	11.54	676	667
<i>Chazara priouri</i>	28	(5)	11.64	11.92	475	465
<i>Coenonympha arcania</i>	700	(78)	10.01	10.19	957	952
<i>Coenonympha dorus</i>	714	(59)	12.20	12.43	733	717
<i>Coenonympha glycerion</i>	502	(48)	9.76	9.83	878	876
<i>Coenonympha pamphilus</i>	1862	(98)	12.85	13.04	788	781
<i>Danaus chrysippus</i>	106	(7)	16.52	16.65	473	467
<i>Danaus plexippus</i>	71	(2)	16.80	16.80	742	744
<i>Erebia arvernensis</i> ‡	74	(22)	5.74	6.10	1176	1153
<i>Erebia epiphron</i>	110	(27)	6.34	6.75	1137	1118
<i>Erebia epistygne</i>	98	(9)	10.61	10.66	615	615
<i>Erebia euryale</i>	90	(26)	6.30	6.80	1147	1133
<i>Erebia gorge</i>	43	(19)	5.81	6.76	1204	1192
<i>Erebia gorgone</i>	34	(22)	4.20	3.27	1200	1165
<i>Erebia hispania</i>	11	(2)	7.81	8.13	526	518
<i>Erebia lefebvrei</i>	63	(27)	5.51	5.87	1152	1130
<i>Erebia manto</i>	17	(10)	5.07	5.77	1177	1208
<i>Erebia meolans</i>	349	(63)	8.86	9.09	1044	1048
<i>Erebia neoridas</i>	106	(30)	7.57	8.09	991	942
<i>Erebia oeme</i>	18	(8)	3.60	3.41	995	971
<i>Erebia palarica</i>	92	(6)	7.98	8.07	1131	1122
<i>Erebia pandrose</i> ¥	37	(16)	4.22	4.11	1119	1055
<i>Erebia pronoe</i>	25	(16)	4.78	5.41	1247	1351
<i>Erebia rondoui</i>	45	(19)	4.74	5.11	1068	1031
<i>Erebia triarius</i>	318	(56)	8.88	9.12	953	945
<i>Erebia zapateri</i>	53	(6)	9.67	9.71	594	593
<i>Euphydryas aurinia</i>	929	(84)	11.80	12.00	876	873
<i>Euphydryas desfontainii</i>	314	(37)	12.25	12.52	708	686
<i>Fabriciana adippe</i>	622	(78)	10.34	10.52	928	922
<i>Fabriciana niobe</i>	338	(41)	10.65	10.79	796	791
<i>Hipparchia fagi</i>	130	(23)	10.47	10.74	863	847

<i>Hipparchia fidia</i>	473	(46)	13.00	13.17	695	685
<i>Hipparchia hermione</i>	865	(84)	10.94	11.12	862	855
<i>Hipparchia semele</i>	978	(81)	11.59	11.69	770	763
<i>Hipparchia statilinus</i>	1206	(74)	12.45	12.56	743	739
<i>Hyponephele lupina</i>	339	(29)	12.74	12.79	600	595
<i>Hyponephele lycaon</i>	482	(61)	10.39	10.51	813	799
<i>Issoria lathonia</i>	1247	(98)	11.89	12.09	793	785
<i>Lasiommata maera</i>	755	(85)	10.91	11.19	917	913
<i>Lasiommata megera</i>	1958	(107)	13.11	13.28	739	731
<i>Lasiommata petropolitana</i>	12	(9)	4.53	3.18	1095	1116
<i>Libythea celtis</i>	236	(31)	12.71	12.85	765	763
<i>Limenitis camilla</i>	198	(20)	10.71	11.09	1079	1074
<i>Limenitis reducta</i>	533	(74)	10.82	11.05	861	849
<i>Lopinga achine</i>	9	(1)	8.98	9.30	1228	1204
<i>Maniola jurtina</i>	2148	(104)	13.05	13.20	757	750
<i>Melanargia galathea</i>	533	(53)	10.68	11.01	1045	1040
<i>Melanargia ines</i>	606	(28)	14.85	14.92	602	600
<i>Melanargia lachesis</i>	1283	(80)	11.68	11.75	740	737
<i>Melanargia occitanica</i>	515	(31)	13.31	13.38	611	602
<i>Melanargia russiae</i>	392	(57)	9.50	9.64	908	898
<i>Melitaea aetherie</i>	65	(1)	16.65	16.63	611	610
<i>Melitaea celadussa</i>	517	(69)	9.90	10.12	960	953
<i>Melitaea cinxia</i>	534	(63)	10.40	10.50	831	824
<i>Melitaea deione</i>	523	(64)	11.09	11.37	922	920
<i>Melitaea diamina</i>	106	(29)	7.13	7.58	1119	1087
<i>Melitaea didyma</i>	605	(78)	11.19	11.54	758	732
<i>Melitaea parthenoides</i>	512	(69)	9.74	9.96	979	973
<i>Melitaea phoebe</i>	1228	(98)	11.79	11.97	753	742
<i>Melitaea trivia</i>	260	(28)	10.84	10.86	859	861
<i>Minois dryas</i>	37	(1)	12.80	12.89	1311	1309
<i>Nymphalis antiopa</i>	349	(47)	9.77	10.08	1038	1028
<i>Nymphalis polychloros</i>	781	(68)	12.40	12.54	786	781
<i>Pararge aegeria</i>	1949	(99)	13.31	13.46	821	818

<i>Polygonia c-album</i>	827	(83)	11.54	11.74	857	849
<i>Pseudochazara mercurius</i> [‡]	22	(3)	9.84	9.97	488	488
<i>Pyronia bathseba</i>	1163	(76)	12.70	12.81	673	664
<i>Pyronia cecilia</i>	1234	(56)	14.23	14.32	650	647
<i>Pyronia tithonus</i>	1362	(96)	11.68	11.84	824	817
<i>Satyrus actaea</i>	409	(44)	10.82	11.00	737	721
<i>Satyrus ferula</i>	27	(13)	6.54	7.32	1022	959
<i>Speyeria aglaja</i>	602	(79)	9.73	9.90	925	915
<i>Vanessa atalanta</i>	1472	(100)	13.12	13.34	802	796
<i>Vanessa cardui</i>	1870	(106)	13.16	13.34	739	730
<i>Vanessa virginiensis</i>	38	(2)	14.99	15.31	826	820

Notes: † Five species not recorded in the 115 well-sampled squares. ‡ Three species for which European STI and SPI were not calculated by Platania et al. (2020). ¥ Cryptic species: confirmed records of *Leptidea reali* and *Poloyommatus celina* under-estimate the distribution size compared with *L. sinapis* and *P. icarus* respectively (see Platania et al., 2020); *Cupido lorquinii* under-estimates the distribution based on new evidence the species is conspecific with *Cupido carswelli* (Hinojosa et al., 2020); data for *Erebia pandrose* and *E. sthenno* were combined, as in García-Barros et al. (2013).

Supplementary references

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Table S2. Spearman correlation coefficients (r_s) of Species Temperature Index (STI) and Species Precipitation Index (SPI) from 10 km atlas data in the Iberian Peninsula (1980-2016) against published calculations of STI and SPI for Europe and the Iberian Peninsula, and the TAO open/closed vegetation index from Ubach et al. (2020). Spatial resolution and sampling period of data used to derive the indices are shown. Significance of Spearman correlations: *** $P < 0.0001$; ^{NS} $P > 0.1$.

Comparison	Data	Years	n	Species	Species
index	resolution		species	Temperature	Precipitation
				Index (STI)	Index (SPI)
Excluding 115 focal squares	10 km	1980-2016	225	0.998***	0.990***
Europe (Platania et al., 2020)	50 km	1981-2000	222	0.710***	0.665***
Iberian Peninsula (Herrando et al., 2019)	10 km	1998-2005	63	0.992***	0.954***
TAO vegetation index (Ubach et al., 2020)	≤1 km (transect sections)	1997-2017	145	-0.121 ^{NS}	-0.103 ^{NS}

Table S3. Spatial autocorrelation in community indices, their climatic explanatory variables and in the residuals of the top-ranked models. Results show Moran’s I calculated for a 148 km interval, the minimum distance at which all 115 grid squares have at least one neighbour. The climate terms for CTI and CPI respectively are mean annual temperature and mean annual precipitation in 1980-2016, and for Δ CTI and Δ CPI respectively change in these variables since 1901-1979. Residuals are calculated from the models shown in Table 3; residuals for TAOc and Δ TAOc from the models in Table 4.

Moran’s I	Community index	Climate term	Residual variation
for:			
CTI	0.551	0.409	-0.024
Δ CTI	0.217	0.267	0.141
CPI	0.548	0.472	0.017
Δ CPI	0.068	0.145	0.034
TAOc	-0.010	-	-0.030
Δ TAOc	0.025	-	-0.008