Long-term change and spatial variation in butterfly communities over an elevation gradient: driven by climate, buffered by habitat.

Susana Nieto-Sánchez[1*], David Gutiérrez[1] and Robert J. Wilson[2]

1 Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, 28933 Móstoles, Madrid, Spain

*e-mail: susana.nieto87@gmail.com

2 College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, UK

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(A) Abstract

(B) Aim

Efforts to adapt conservation to climate change are hampered by a scarcity of studies of community-level ecological responses. We examined temporal (40 years) and spatial (1700 m elevation gradient) variation in butterfly communities, aiming to test whether the composition of communities in terms of species' thermal envelopes tracked regional warming, and whether local habitat influenced community responses to climate variation.

(B) Location

Sierra de Guadarrama (central Spain).

(B) Methods

Butterfly assemblages were sampled at sites between 550 m and 2250 m elevation, in 1967-1973 and 2006-2012. Changes in community composition over time and space were evaluated using the community temperature index, or CTI, which reflects for local assemblages the balance between species whose geographic ranges occupy regions of low versus high temperatures. We used multiple regressions and an information-theoretic approach to test: 1) whether relationships of CTI with elevation or temperature remained consistent after an estimated 1.78 °C regional warming; and 2) how spatial variation in CTI was related to air temperature and land cover.

(B) Results

CTI decreased consistently with increasing elevation, and increased after 40 years of warming, as communities were increasingly composed by species with warmer geographic ranges. Long-term CTI change represented a *c*. 160 m uphill shift in community thermal composition, whereas isotherms shifted 307 m upwards. In 2006-2012, CTI was influenced positively by temperature, and negatively by forest and meadow cover.

(B) Main Conclusions

Variation in community composition over space and time suggested a role of climate in structuring butterfly assemblages. Despite this, changing spatial patterns of community composition (CTI) did not appear to keep pace with climate change. In addition, lower values of CTI recorded for sites with greater forest and meadow/pasture cover suggested a role for local habitat in buffering the effects of climate change on community composition.

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(A) Keywords

Altitude gradient; climate change indicator; community composition change; Lepidoptera; mountain biodiversity; Species Temperature Index.

(A) Introduction

Climate change is a driving force of biodiversity decline (Mace *et al.,* 2005; Parmesan, 2006), whose effects on biodiversity are expected to worsen (Rosenzweig *et al.*, 2007; Scholes & Settele, 2014). Species can deal with climate change by adapting to new conditions, or by latitudinal or elevational range shifts (Walther *et al.*, 2002; Parmesan, 2006; Chen *et al.*, 2011). These changes and associated alterations in species interactions modify community composition, potentially influencing functional diversity (Thuiller *et al.*, 2006). However, most studies of how traits affect ecological responses to climate change have focused on species rather than communities (e.g. Pearson *et al.*, 2014), and knowledge of the recent responses of entire assemblages to climate change remains scarce (Lindström *et al.*, 2013).

As ectotherms, insects are expected to be sensitive to climate warming, because environmental temperature has direct effects on their thermoregulation, activity and development rates (Kingsolver, 1989). Short generation times mean that insect populations respond rapidly to weather variation (Roy *et al.*, 2001), and may undergo fast evolutionary responses to selective pressures induced by climate change (Van Asch *et al.*, 2007). The effects of climatic conditions on insect population dynamics are also modified by microclimatic variation caused by topography (Bennie *et al.*, 2013) and habitat structure (Suggitt *et al.*, 2011). As a result, fine-resolution patterns in landscape-level distributions of insects and other ectotherms can reflect the thermal limitations of those species' wider geographic ranges (Thomas *et al.*, 1999; Gillingham *et al.*, 2012; Suggitt *et al.*, 2012).

Given an expected link between the geographic ranges of species and local responses to climate variation, effects of warming on ecological communities are expected to include increased abundance of species whose geographic ranges occupy warmer parts of the world, and decreased abundance of species whose ranges occupy cooler regions (Devictor *et al.*, 2008). Based on this framework, the community temperature index (CTI) has been proposed

as a simple measure of community response to climate change (Van Swaay *et al.*, 2008; Devictor *et al.*, 2008, 2012). CTI summarises ecological community composition in terms of the geographic thermal envelopes of the component species, and is measured in the same unit as climate warming (temperature). Specifically, CTI is the abundance-weighted average of the

5   species temperature indices (STI, the long-term average temperature experienced by individuals of a species over its range) of the assemblage. Recent positive temporal trends in CTI for a number of taxa and regions (Godet *et al.*, 2011; Devictor *et al.*, 2012; Lindström *et al.*, 2013) suggest changes to community composition consistent with the effects of climate warming. Nevertheless, variation in land cover and terrain (e.g. vegetation, shading,

10   topography or orientation) has been shown to attenuate local effects of climate change on community composition (Stefanescu *et al.*, 2011; Scherrer & Körner, 2011; Kampichler *et al.*, 2012; Roth *et al.*, 2014). For example, shaded habitats such as forests may limit effects of warming on community composition by providing cool microclimates (De Frenne *et al.*, 2013). In this respect, quantifying the effects of topography, elevation (Roth *et al.*, 2014) and

15   land use type (Zografou *et al.*, 2014) on community responses to climate change could yield valuable information on the capacity of local habitats to buffer ecological communities against effects of climate change. In the absence of long-term data on community change for different habitats (e.g. Kampichler *et al.*, 2012), research on relationships between habitat and species' thermal envelopes has provided important insights into the responses of communities

20   to the different components of global change (Clavero *et al.*, 2011; Barnagaud *et al.*, 2013).

Here, we examined spatial variation in community composition for mountain butterfly assemblages, in relation to long-term changes in regional temperatures, and local variation in habitat and climate. We tested whether changes in butterfly communities, quantified using CTI, were consistent with the effects of climate variation over space and time, by assessing:

25   1) whether CTI declined with increasing elevation, as expected from regional temperature

lapse rates (i.e., decrease in temperature with respect to increasing elevation, usually ranging

5.5-6.5°C for each 1000 m of ascent; MacArthur, 1972); 2) whether CTI increased following

a *c.* 40-year period of warming; and 3) whether land cover modified the effects of

environmental temperature on community composition, with the expectation that habitats

5　such as forests might maintain lower-CTI communities relative to more open habitats, by

providing locally shady or cool conditions.

(A) Methods

(B) Study system

The study area was the Sierra de Guadarrama (Madrid, Spain), a mountain range running

10　from 40º 30' N 4º 20' W in the south-west to 41º 10' N 3º 30' W in the north-east (Fig. 1)

identified as a prime butterfly area in Europe (Munguira *et al.*, 2003), and representing the

lower latitudinal and elevational boundary for several butterfly species (García-Barros *et al.*,

2013). Approximately 9% of species identified in the present study reach their southern range

limit in the Sierra de Guadarrama; many other species are restricted to mountain ranges where

15　they occur further south in the Iberian Peninsula; and no species reach their northern limit

here (distribution ranges based on García-Barros *et al.*, 2004; Tolman & Lewington, 2011).

This mountain range, with a maximum elevation of 2430 m, is bordered by two plains, the

northern one with a minimum elevation of 700 m and the southern one with a minimum of

400 m. The region's climate is influenced by its elevation and topography; dominant

20　vegetation types are *Quercus rotundifolia* woodlands below 1000 m, *Quercus pyrenaica*

woodlands at 1000-1500 m and *Pinus sylvestris* woodlands at 1500-2000 m; scrub and open

grassland are present at all elevations (Rivas-Martínez *et al.*, 1987).

(B) Butterfly data

We compare historical butterfly assemblages sampled in 1967-1973 (Monserrat, 1976), and data recorded in 2006-2012. Sampling was carried out in natural and semi-natural habitats (pastures, woodland clearings and alpine meadows) stratified across a representative sample of elevations in the region; site selection was also subject to accessibility criteria.

1967-1973 records include data from 44 sites visited 928 times, when a sample of individuals of all observed species during each visit was recorded, but the dates, number and duration of visits to each site varied (Monserrat, 1976). To ensure that coverage of the flight periods of butterfly communities was complete for sites included in analysis, we selected 17 sites (elevation range 620-1860 m; average elevation 1122 m; see Fig. 1) whose earliest annual visit was no later than May 8 and whose last annual visit was no earlier than August 19. Sampling effort was also quantified by computing species accumulation curves for each site, and all 17 selected sites had final rates of species accumulation of 0.005-0.086 species per individual sampled (for further details on site selection, see Wilson *et al.*, 2007). Based on these criteria, we ensured that presence-absence data were comparable for sites in 1967-1973 and those sampled under standardised methods in 2006-2012.

From 2006 onwards, standardised 500 m-long x 5 m-wide transects were walked every 2 weeks during suitable conditions for butterfly activity (sunshine and no intense wind, between 10:00 and 17:00 h Central European Summer Time; Pollard & Yates, 1993), from April to October in 2006 and from March to October since 2007, when recording began earlier to ensure that all flight periods were recorded from initial emergence at low elevation sites. Butterflies were counted at 34 sites in 2006, 40 sites in 2007-2008, and 24 sites in 2009-2012. The 24 sites visited every year over 2006-2012 (elevation range 589-2251 m; average elevation 1441 m) were compared with 1967-1973 data to determine temporal changes in

community composition; 2006-2008 sites were used to examine the effects of temperature and land cover on community composition.

Individuals from the genera *Carcharodus*, *Melitaea* (*M. parthenoides*, *M. deione*, *M. celadussa*), *Pyrgus* and *Satyrium* (*S. esculi* and *S. ilicis*) were not practical to identify in the field, so were identified to genus level but not included in analyses of community composition (other species from the genera *Melitaea* and *Satyrium*, not listed here, were identified to species level and included in analysis). Nomenclature follows García-Barros *et al.* (2013).

(C) Community temperature index

The community temperature index is based on the Species Temperature Index, or STI, of the individual species composing an assemblage (Devictor *et al.*, 2008). For a given species, the STI (measured in ºC) is the long-term average temperature experienced by individuals of a species over its range (Devictor *et al.*, 2008). As climate warming is expected to favour high-STI species, causing increases in community CTI, comparing CTI and temperature changes can reveal whether community composition is tracking climate change.

STIs for European butterfly species have been calculated by averaging annual mean temperature (calculated from monthly interpolated temperature data for the period 1971-2000 from the ALARM project; available on-line at *http://www.alarmproject.net/climate/climate*) over occupied 50 x 50 km grid squares in Europe. STIs are available from Schweiger *et al.* (2014). For a given site *j*, the CTI, measured in ºC, is calculated as the average of the STI of each species *i* occurring in the site (STI_i), weighted by species abundance (a_{ij}):

$$CTI_j = \frac{\sum a_{ij} \cdot STI_i}{\sum a_{ij}} \qquad (1)$$

CTI can also be calculated by substituting a_{ij} in equation 1 by 1/0 for species presence/absence (e.g. Devictor *et al.*, 2012), to test whether changes in CTI are related to

shifts in species distributions rather than variation in the dominance structure of species. Given the differences in sampling regimes between 1967-1973 and 2006-2012, we analysed results for long-term change using species presence-absence data, which based on our site selection criteria are more likely than abundance data to be consistent between periods.

5   For CTI calculations, we excluded specimens identified to genera level (see above) and *Favonius quercus*, a canopy-dwelling species whose occurrence and abundance is probably underestimated by the transect method. Excluded individuals represented *c.* 0.80% and 1.4% of total records for 1967-1973 and 2006-2012, respectively.

(B) Environmental data

10   Universal Transverse Mercator (UTM) coordinates were recorded to the nearest metre at least every 100 m along each transect, using a handheld Garmin GPS unit. The coordinates were used to plot each transect in ArcGIS 8.1 (ESRI, 2001). The average elevation of 100 m cells intercepted by transects was determined using a digital elevation model interpolated from the original *c.* 80 m resolution (Farr *et al.*, 2007).

15   **(C) Long-term changes in temperature**

We examined climatic change in the Sierra de Guadarrama by comparing 1967-1973 and 2006-2012 temperatures. As no temperature records for sites in 1967-1973 were available, temperatures were estimated based on lapse rates. Selected meteorological stations (data from the Spanish Agencia Estatal de Meteorología, AEMET) had: (1) complete records for

20   monthly mean temperatures for each period and (2) similar elevation range to the study sites (10 stations for 1967-1973 and 7 stations for 2006-2012; stations differed between periods, in some cases due to slight location changes, so they were considered independent points in statistical analysis; Fig. 1). Mean annual temperature was regressed against elevation separately for each period to obtain lapse rates.

(C) Spatial determinants of CTI

CTI is expected to be influenced mainly by temperature, but may be associated with factors including land cover (e.g. Clavero *et al.*, 2011; Barnagaud *et al.*, 2013). We tested the effects of temperature and land cover on CTI in the 40 sites with butterfly data for 2006-2008 (34

5 sites were sampled in 2006-2008 and 6 additional sites in 2007-2008; see above), and mean CTI values for the three years (two years in six sites) were used. For the period 2006-2012, hourly air temperature was recorded by HOBO H8 Pro HR/Temp and U23 HR/Temp loggers in semi-shaded conditions at each of the 40 sampling sites; 20 data loggers were started in spring 2004, and the remainder in spring 2006. Mechanical failure or damage to some loggers

10 generated gaps of variable duration in the data, with daily temperature data completeness averaging 91% per logger (range 69-100%). Therefore, daily average temperatures were interpolated for missing logger periods using linear regressions of temperature data from the site in question against data from the site with the most quantitatively consistent temperature time series (for further details, see Gutiérrez & Wilson, 2014).

15   Land cover was determined from regional vectorial land cover maps at 1:50,000 scale, for which only patches of at least 2.25 ha in area were mapped (Ministerio de Medio Ambiente, 2000, 2002a, 2002b, 2003). Land covers from maps showed good agreement for all study sites with our field observations on general vegetation type (Gutiérrez Illán *et al*., 2010a). These vector data were used to determine the proportional contribution of each cover type to

20 each 100-m grid cell. Environmental variables were measured for each transect as the average for 100-m grid squares intercepted by the transect (Gutiérrez Illán *et al.*, 2010a).

    The main land cover classes present in our study area were: forest (sum of woodlands and juniper), shrubland, meadows/pasture, bare rock, artificial and crops. From these cover classes, those present on fewer than 10% of transect were discarded from further analysis

25 (Gutiérrez Illán *et al.*, 2010b), leaving forest, shrubland, and meadows/pasture.

(B) Data analyses

(C) Long-term changes in CTI

To study long-term CTI variation (1967-1973 vs. 2006-2012), we calculated CTI values per site and period based on presence-absence. Because historical (1967-1973) and modern (2006-2012) site locations differed, we used an unpaired-site model (Tingley & Beissinger, 2009) to infer any elevational CTI shift. This approach can be used when historical locations are not described well enough to enable a paired-site (or matched pair) analysis, and requires the response variable to be related to a defining covariate affecting range (e.g. elevation, latitude) and time. We performed linear regression models with CTI as the response variable, and elevation, time period and their interaction as predictors. The interaction term allowed us to test whether the change in CTI between periods varied along the elevation gradient. For model selection, we followed the information-theoretic approach based on Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham & Anderson, 2002). We fitted all possible models with combinations of linear terms for elevation, period and their interaction, and they were then ranked by their AIC$_c$. The model confidence set (or 'best model set') is the set of the best model(s) selected from the total collection of possible models, where 'best' is defined as models fulfilling the user-specified criteria (Burnham & Anderson, 2002). In our case, the criteria were: (1) models within six ΔAIC$_c$ units of the top-ranked (lowest AIC$_c$) model (Richards, 2005); (2) within this set, we selected only those models which did not have simpler, higher-ranking variants (i.e. including a smaller number of the same explanatory variables), thus avoiding over-parameterised models whilst maintaining a high probability of selecting the true best model (Richards, 2008).

Following model selection we used model-averaging to obtain model coefficients based on the confidence sets, thus incorporating model selection uncertainty whilst weighting the influence of each model by the strength of its supporting evidence (Burnham & Anderson,

2002). Model-averaged coefficients were derived by weighting using Akaike weights (AIC$_c$w) and averaging coefficients over all models in the confidence set. Averaging over all models means that in cases in which a variable was not in a particular model, its coefficient value was set to zero. Variable importance (the sum of model weights over all models that

5   include a given variable) was calculated to quantify the relative importance of each variable in the context of the set of models considered (see Burnham & Anderson, 2002). Model selection and averaging were performed with 'MuMIn' package version 1.9.13 (R Development Core Team, 2012; Bartoń, 2012).

The long-term change in temperature was examined following the same rationale as for

10   CTI-elevation regressions. This allowed testing of whether a significant warming had occurred, and whether lapse rates were similar between periods.

To test the ability of butterfly community composition to track temperature change, we compared the magnitude of isotherm and CTI elevation shifts (Devictor *et al.*, 2008). CTI would be expected to change at the same rate as temperature if species were exclusively

15   influenced by temperature change and they could respond instantaneously and linearly to temperature (Devictor *et al.*, 2008, 2012; Lindström *et al.*, 2012). This is not likely to be the case for most species, as other abiotic variables than temperature, species interactions and dispersal limitations affect species distributions, and in turn community composition. Hence, the shift in km in CTI relative to that in isotherms was estimated to reveal the extent to which

20   communities are tracking climate change (Devictor *et al.*, 2008). Assuming no change in temperature lapse rates (i.e. no interaction with period), then the long-term elevation shift for isotherms is the ratio between the temporal change in mean temperature (the negative of the coefficient for 'Period') and the lapse rate (the coefficient for 'Elevation', Table 1). Likewise, if the gradient of CTI against elevation is consistent over time, then the elevational

displacement of communities with the same CTI can be calculated by dividing the negative of the coefficient for 'Period' by the coefficient for 'Elevation' (Table 1).

As an additional test of butterfly community tracking of temperature change, we regressed site CTI against temperature for each period using the same methodology as for the CTI-elevation relationship. Site temperatures were based on elevation and lapse rates for each period. No significant effect of period is expected in the CTI-temperature relationship if butterfly communities are keeping pace with thermal change (Table 1).

(C) Spatial determinants of CTI

To test the effects of temperature and land cover variables (site proportional cover of forest, shrubland and meadows/pasture) on CTI, multiple regression models were performed using the 40 site data from 2006-2008, including CTI based on abundance and presence-absence as response variables. Site temperatures (°C) were calculated from HOBO field data as the average of annual mean temperature in 2006-2008. Shrub cover was removed from the initial set of independent variables because of high collinearity with forest and meadow/pasture cover; all other pairs of variables had Spearman pairwise correlation values lower than 0.7 (Dormann *et al.*, 2013) and were retained for analysis. The effect of these selected independent variables on CTI was examined following the information-theoretic approach using the same rationale as for the assessment of long-term changes, with all possible models fitted with combinations of linear terms for the selected independent variables (excluding interaction terms in this case) and then ranked by AIC_c.

(C) Spatial Autocorrelation

When using information theory criteria, existence of autocorrelation in the data may affect AIC_c selection, as autocorrelated data will tend to generate more complicated (i.e. with more explanatory variables) models (Diniz-Filho *et al.*, 2008). Consequently, we checked for

spatial autocorrelation in the CTI dataset by calculating Moran's *I* coefficient (Iriondo *et al.*, 2008). Moran's *I* calculation and testing for significance were performed using 9999 Monte Carlo permutations in Excel add-in Rookcase (Sawada, 1999). Spatial autocorrelation was significant for some distance classes (Table 2); however, the correlograms became non-significant using residuals from models, suggesting that the spatial autocorrelation was accounted for by the environmental variables.

(A) Results

(B) Long-term changes in CTI

Mean annual temperature decreased with elevation in both study periods. Lapse rates were *c.* 6 °C km^{-1} for 1967-1973 (Temperature(°C) = -0.00598 (±4.4e-4)·Elevation (m) + 16.85 (±0.42), R^2 = 0.96, p < 0.001, n = 10) and 5.6 °C km^{-1} for 2006-2012 (Temperature(°C) = -0.00563 (±7.0e-4) ·Elevation (m) + 18.26 (±0.72), R^2= 0.93, p < 0.001, n = 7). The previous equations, showing the relationship between temperature and elevation for both study periods, allowed us to estimate site annual mean temperatures based on elevation. The model confidence set for annual mean temperature at meteorological stations in 1967-1973 and 2006-2012 consisted of one model, including elevation and time period as explanatory variables. Therefore, lapse rates were similar between periods, but 2006-2012 was *c.* 1.78 °C warmer than 1967-1973 (Table 1; Fig. 2): this temperature increment was equivalent to a *c.* 307 m upward shift in isotherms.

The confidence set for presence-absence CTI over the elevation gradient consisted of two models, one including elevation and period, and the other one just elevation (Table 1). CTI decreased with elevation (Fig. 3), showing that butterfly communities at higher elevations were on average composed by species associated with cooler temperatures than communities at lower elevations. The inclusion of the parameter for period indicates that, for a given

elevation, butterfly communities in 2006-2012 consisted of species occupying warmer geographic ranges than in 1967-1973. Based on Elevation and Period parameters obtained by model averaging, a *c.* 160 m upward shift was estimated for butterfly communities of equivalent composition (CTI).

5 The confidence set for presence-absence CTI against temperature in each period was composed by two models, one including temperature and period, and the other just temperature (Table 1). There was a positive relationship between CTI and temperature (Fig. 3), showing that communities on warmer sites were on average composed by species with higher STI values. The negative term for period indicates that, for a given temperature,

10 communities in 2006-2012 were on average composed by species occupying cooler geographic ranges than those in 1967-1973.

(B) Spatial determinants of CTI

The confidence set for abundance CTI in 2006-2008 consisted of one model including mean temperature; however, the model set for presence-absence CTI consisted of two models: one

15 including mean temperature, forest and pasture cover and the other including mean temperature and forest (Table 3). Accordingly, communities at cooler sites with higher forest and pasture covers were composed by species occupying cooler geographic ranges.

(A) Discussion

We found evidence that the composition of butterfly assemblages in a Mediterranean

20 mountain range tracked temperature temporally (40-years) and spatially (1700 m elevation gradient). However, temporal changes to communities occurred at a lower rate than regional warming, and spatial variation in community structure was influenced by habitat type.

(B) Long-term change in community composition

Changes over time and space to the Community Temperature Index (CTI) were consistent with temporal warming and spatial temperature gradients. CTI decreased with elevation in both periods, but no long-term differences were found in the slope of the CTI relationship with elevation, suggesting consistency 40 years apart in the rate at which individuals of species whose geographic ranges occupy cooler regions ("cool thermal envelopes") replaced individuals of species with warmer thermal envelopes as elevation increased. However, the intercepts of the regression lines differed between periods, indicating that butterfly communities in 2006-2012 were composed on average by species with warmer thermal envelopes than in 1967-1973.

A 1.78 ℃ increase in annual mean temperature was estimated between study periods (equivalent to a 0.046°C year^{-1} increase), with no evidence for differential warming along the elevation gradient. The magnitude of warming was consistent with previously published estimates for the same area using different time frames (1.3 ℃ increase between 1967-1973 and 1997-2003, equivalent to 0.043°C year^{-1} increase; Wilson *et al.*, 2005). Changes to butterfly communities were also consistent with previous results in the study area (Wilson *et al.*, 2007).

Geographic-scale climate associations are known to influence species' local climatic or microclimatic affiliations (Gillingham *et al.*, 2012), and the combined responses of multiple species to local or regional temperature variation hence modify CTI along gradients of latitude (Devictor *et al.*, 2008, 2012), elevation (Roth *et al.*, 2014), and between habitat types (Clavero *et al.*, 2011; Barnagaud *et al.*, 2013). Our results are consistent with recent temporal increases in CTI reported for several bird and butterfly communities (Godet *et al.*, 2011; Filz *et al.*, 2013; Lindström *et al.*, 2013; Reif *et al.*, 2013; Zografou *et al.*, 2014), but contrast with the declines in CTI reported in a previous study of Iberian butterflies (Stefanescu *et al.*, 2011).

In addition, the 40-year consistency in the rate CTI decreases with elevation in the Sierra de Guadarrama contrasts with temporal changes reported in Switzerland, where the slope of the elevation gradient in butterfly CTI became steeper over eight years, so that CTI only increased over time at low elevations (Roth *et al.*, 2014).

5 **(B) Spatial determinants of community composition**

Community thermal associations derived from species data collected at a geographical scale (STI) were strongly related to regional temperature gradients, but also to land cover. Specifically, resources or conditions in forests and meadows may have favoured butterfly assemblages of low-STI species. A pattern of reduced CTI for forested areas has also been

10 documented for birds (Clavero *et al.*, 2011; Barnagaud *et al.*, 2013), and could be explained as: (1) a direct consequence of microclimatic variation (e.g. Suggitt *et al.*, 2011), and/or (2) a local signal of the biogeographical history of species (e.g. Barnagaud *et al.*, 2012). However, the hypothesis regarding an effect of shading by trees on local microclimate does not explain lower CTI in sites with greater cover of meadow/pasture. Furthermore, we found an effect of

15 habitat type on CTI, over and above the effect of local temperature, which itself will have been affected by topography and land cover. Therefore, it appears that habitat type could exert a buffering effect on community responses to climate change because of additional features of the habitat (e.g. habitat-specific biotic interactions), beyond direct effects of land cover on microclimate.

20 **(B) Time lag in community response to climate change**

Changes to the CTI-elevation gradient over time were equivalent to a *c.* 160 m upward shift in species composition. Over the same 40-year period, the 1.78 ℃ annual mean temperature increase was equivalent to a 307 m upward shift in isotherms. The difference between rates of change in CTI and temperature (also supported by the CTI-temperature models including

'Period' as an explanatory variable; Table 1) suggests that composition of butterfly communities is following climate change, but that the biogeographic thermal associations of constituent species are not maintained. This difference (which assumes that species' responses are associated with temperature, but there could be exceptions, see Thomas, 2010), previously

5   reported for birds and butterflies over latitudinal gradients, has been interpreted as a 'time lag' or 'climate debt' in community responses to climate change (Devictor *et al.*, 2008, 2012; Lindström *et al.* 2013). Interestingly, we found no evidence for this lag in previous studies of the same system (Wilson *et al.*, 2005, 2007). These discrepancies could arise because the CTI approach integrates changes throughout species' regional distributions instead of focusing

10   solely on range limits, as well as explicitly accounting for species-specific effects of temperature changes, which are ignored by standard community indices (Kampichler *et al.*, 2012).

Reasons for a time lag in the elevational shift in community composition cannot be precisely established, but could reflect either the absence of a disproportionately high rate of

15   colonisation of sites by species possessing warm geographic ranges, perhaps because of dispersal and/or resource limitation; or greater levels of persistence by species with cool geographic ranges than expected under warming, due to microclimatic buffering. Low colonisation rates at high elevations appear more likely because: (1) there is stronger evidence for species loss at low-elevation range limits than for high-elevation expansions (Wilson *et*

20   *al.*, 2005); and (2) species richness decreased throughout the elevation gradient between 1967-1973 and 2004-2005 (Wilson *et al.*, 2007).

Nevertheless, it is unlikely that movement distances required to track temperature increases over 40 years have been prohibitive for many species in our study, as in mountains the velocities required are slower than over latitudinal climate gradients (Loarie *et al.*, 2009).

25   However, specific resources such as larval host plants might not respond to temperature

changes as fast as butterflies (Roth *et al.*, 2014), limiting rates of uphill range expansion. In this system, the butterfly *Aporia crataegi* disappeared between 1967-1973 and 2006 from low elevations where its larval host plants remain, but its capacity to expand its distribution above its upper-elevation limit has been constrained by the absence of host plants at higher

5 elevations (Merrill *et al.*, 2008). The generality of this pattern remains to be tested, but potential host plant limitation for several butterfly species at upper-elevation limits has been reported elsewhere (Hanspach *et al.*, 2014).

Microclimatic buffering can arise if temperature increases are attenuated by canopies becoming progressively denser in habitats like forests, limiting population increases in warm-

10 associated species, or decreases in cool-associated species (e.g. De Frenne *et al.*, 2013). Our data do not permit evaluation of habitat changes over time, because historical and modern sites do not match. However, independent research in an area including several of our study sites over 1975-2009 suggests that land cover changes have been relatively limited (20% of area), and mostly due to agricultural abandonment, forest encroachment and urban

15 development (López-Estébanez *et al.*, 2012). It is possible that increased forest cover has contributed to a time lag in butterfly community response to increasing temperatures. However, the degree to which habitat change buffered communities against warming was much less than in northeastern Spain, where land-use change reversed expected positive CTI trends in butterfly communities by favouring generalist, woodland species with lower STI

20 values than Mediterranean specialists (Stefanescu *et al.*, 2011).

In conclusion, our results provide evidence for the effects of climatic conditions on butterfly community composition over both space and time. In this respect, CTI was found to be a useful indicator of community responses to spatial and temporal climate variation, adding a geographic-scale perspective to research showing regional changes to species distributions

25 and diversity. The results also add support to the supposition that local variation in

topography or habitat can delay the effects of climate change on ecological communities, emphasising the potential importance of local habitat protection and management in adapting biodiversity conservation to climate change (Heller & Zavaleta, 2007; Morecroft *et al.*, 2012).

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(A) References

Barnagaud, J.-Y., Barbaro, L., Hampe, A., Jiguet, F. & Archaud, F. (2013) Species' thermal preferences affect forest bird communities along landscape and local scale habitat gradients. *Ecography*, **36**, 1218-1226.

5   Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I. & Archaux, F. (2012) Relating habitat and climatic niches in birds. *PLoS ONE*, **7**, e32819.

Bartoń, K. (2012) MuMIn: multi-model inference. R package version 1.9.13. *http://CRAN.R-project.org/package=MuMIn*. Accessed: 5 Feb 2014.

Bennie, J., Hodgson, J.A., Lawson, C.R., Holloway, C.T.R., Roy, D.B., Brereton, T., Thomas,

10   C.D. & Wilson, R.J. (2013) Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, **16**, 921-929.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference. A practical information-theoretic approach*. Second Edition. Springer-Verlag, New York, NY.

15   Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.

Clavero, C., Villero, D. & Brotons, L. (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS ONE*, **6**, e18581.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeteb, G., Vellend,

20   M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kely, D.L., Kirby, K.J., Mithchell, F.J.G., Naaf, T., Mewman, M., Peterken, G., Petrík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J. & Verheyen, K. (2013)

Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences USA*, **46**, 18561-18565.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743-2748.

Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Scheweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., Wallis De Vries, M., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121-124.

Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479-488.

Dormann, C.F., Elith. J., Bacher, S., Buchmann, C., Carls, G., Carré, G., García Marquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkermüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Launtenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27-46.

ESRI (2001) *Arcgis 8.1*. Environmental System Research Institute Inc., Redlands, CA.

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D. & Alsdorf, D. (2007) The Shuttle Radar Topography Mission. *Reviews in Geophysics*, **45**, RG2004.

Filz, K.J., Wiemers, M., Herrig, A., Weitzel, M. & Schmitt, T. (2013) A question of adaptability: climate and habitat change lower trait diversity in butterfly communities in south-western Germany. *European Journal of Entomology*, **110**, 633-642.

García-Barros, E., Munguira, M.L., Martín Cano, J., Romo Benito, H., Garcia-Pereira, P. & Maravalhas, E.S. (2004) *Atlas de las mariposas diurnas de la península Ibérica e islas Baleares (Lepidoptera: Papilionoidea & Hesperioidea)*. Sociedad Entomológica Aragonesa, Zaragoza.

5   García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives Moreno, A. (2013) *Lepidoptera Papilionoidea. Fauna Ibérica vol. 37*. Museo Nacional de Ciencias Naturales, CSIC, Madrid.

Gillingham, P.K., Palmer, S.C.F., Huntley, B., Kunin, W.E., Chipperfield, J.D. & Thomas, C.D. (2012) The relative importance of climate and habitat in determining the

10   distributions of species at different spatial scales: a case study with ground beetles in Great Britain. *Ecography*, **35**, 831–838.

Godet, L., Jaffré, M. & Devictor, V. (2011) Waders in winter: long-term changes of migratory bird assemblages facing climate change. *Biology Letters*, **7**, 714-717.

Gutiérrez Illán, J., Gutiérrez, D. & Wilson, R.J. (2010a) The contributions of topoclimate and

15   land cover to species distributions and abundance: fine-resolution tests for a mountain butterfly fauna. *Global Ecology and Biogeography*, **19**, 159-173.

Gutiérrez Illán, J., Gutiérrez, D. & Wilson, R.J. (2010b) Fine-scale determinants of butterfly species richness and composition in a mountain region. *Journal of Biogeography*, **37**, 1706-1720.

20   Gutiérrez, D. & Wilson, R.J. (2014) Climate conditions and resource availability drive return elevational migrations in a single-brooded insect. *Oecologia*, **175**, 861-873.

Hanspach, J., Schweiger, O., Kühn, I., Plattner, M., Pearman, P.B., Zimmermann, N.E. & Settele, J. (2014) Host plant availability potentially limits butterfly distributions under cold environmental conditions. *Ecography*, **37**, 301-308.

Heller, N.E. & Zavaleta, E.S. (2007) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, **142**, 14-32.

Iriondo, J.M., Torres, E. & Escudero, A. (2008) Métodos para analizar variables continuas y categóricas: Correlogramas y estadísticos "join count". *Introducción al Análisis Espacial de Datos en Ecología y Ciencias Ambientales: Métodos y Aplicaciones* (ed. by F.T. Maestre, A. Escudero & A. Bonet). Servicio de Publicaciones Universidad Rey Juan Carlos, Madrid.

Kampichler, C., Van Turnhout, C.A.M., Devictor, V. & Van Der Jeugd, H.P. (2012) Large-scale changes in community composition: determining land use and climate change signals. *PLoS ONE*, **7**, e35272.

Kingsolver, J.G. (1989) Weather and the Population Dynamics of Insects: Integrating Physiological and Population Ecology. *Physiological Zoology*, **62**, 314-334.

Lindström, A., Green, M., Paulson, G., Smith, H.G. & Devictor, V. (2013) Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography*, **36**, 313-322.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052-1055.

López-Estébanez, N., Allende, F., Fernández-Sañudo, P., Roldán Martín, M.J. & De Las Heras, P. (2012) Cartography of Landscape Dynamics in Central Spain. *Cartography – A Tool for Spatial Analysis*. (ed. by C. Bateira). InTech.

MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press, Princeton, New Jersey.

Mace, G., Masundire, H. & Baillie, J. (2005) Biodiversity. *Ecosystems and Human Well-being: Current State and Trends, Volume 1*. (ed. by R. Hassan & R. Scholes). Millenium Ecosystem Assessment, Washington DC.

Merrill, R.M., Gutiérrez, D., Lewis, O.T., Gutiérrez, J., Díez, S.B. & Wilson, R.J. (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, **77**, 145-155.

Ministerio de Medio Ambiente (2000) *''Mapa forestal de España'' Provincia de Madrid*. Escala 1:50000. Ministerio de Medio Ambiente. Organismo Autónomo de Parques Nacionales, Madrid.

Ministerio de Medio Ambiente (2002a) *"Mapa forestal de España" Provincia de Guadalajara.* Escala 1:50000. Ministerio de Medio Ambiente, Organismo Autónomo de Parques Nacionales, Madrid.

Ministerio de Medio Ambiente (2002b) *"Mapa forestal de España" Provincia de Ávila.* Escala 1:50000. Ministerio de Medio Ambiente, Organismo Autónomo de Parques Nacionales, Madrid.

Ministerio de Medio Ambiente (2003) *"Mapa forestal de España"* Provincia de Segovia. Escala 1:50000. Ministerio de Medio Ambiente, Organismo Autónomo de Parques Nacionales, Madrid.

Monserrat, V.J. (1976) *La distribución ecológica de las mariposas diurnas del Guadarrama*. Thesis, Universidad Complutense de Madrid, Madrid.

Morecroft, M.D., Crick, H.Q.P, Duffield, S.J. & Macgregor, N.A. (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547-551.

Munguira, M.L., García-Barros, E. & Martín Cano, J. (2003) Spain. *Prime Butterfly Areas in Europe: Priority Sites for Conservation* (ed. by C.A.M. Van Swaay & M.S. Warren). National Reference Centre for Agriculture, Nature and Fisheries, Ministry of Agriculture, Nature Management and Fisheries, Wageningen, The Netherlands.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637-669.

Pearson, R.G. Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNees, J. & Akçakaya, H.R. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, **4**, 217–221.

Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation.* Chapman & Hall, London.

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: */http://www.R-project.org/*. Accessed: 1 Feb 2012.

Reif, J., Prylová, K., Šizling, A.L., Vermouzek, Z., Štastný, K. & Bejček, V. (2013) Changes in bird community composition in the Czech Republic from 1982 to 2004: increasing biotic homogenization, impacts of warming climate, but no trend in species richness. *Journal of Ornithology*, **154**, 359-370.

Richards, S.A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, **86**, 2805-2814.

Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, **45**, 218-227.

Rivas-Martínez, S., Fernández González, F. & Sánchez-Mata, D. (1987) *La vegetación de España. El Sistema Central*. Servicio de publicaciones de la Universidad de Alcalá de Henares, Madrid.

Rosenzweig, C., Casassa, G., Karoly, D.J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T.L., Seguin, B. & Tryjanowski, P. (2007) Assessment of observed changes and responses in natural and managed systems. *Climate Change 2007: Impacts, Adaptation*

and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (ed. by M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. Linden & C.E. Hanson). Cambridge University Press, Cambridge.

Roth, T., Plattner, M. & Amrhein, V. (2014) Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. *PLoS ONE*, **9**, e82490.

Roy, D.B., Rothery, P., Moss, D., Polard, E. & Thomas, J.A. (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201-217.

Sawada, M. (1999) Rookcase: an Excel 97/2000 visual basic (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**, 231-234.

Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406-416.

Scholes, R. & Settele, J. (2014) Terrestrial and Inland Water Systems. *Climate Change 2014: Impacts, Adaptation, and Vulnerability.* (IPCC Working Group II). Accesible in: *http://ipcc-wg2.gov/AR5/report/final-drafts/*

Schweiger, O., Harpke, A., Wiemers, M. & Settele, J. (2014) CLIMBER: Climatic niche characteristics of the butterflies in Europe. *ZooKeys*, **367**, 65-84.

Stefanescu, C., Torre, I., Jubany, J. & Páramo, F. (2011) Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation*, **15**, 83-93.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1-8.

Suggitt, A.J., Stefanescu, C., Páramo, F., Oliver, T., Anderson, B.J., Hill, J.K., Roy, D.B, Brereton, T. & Thomas, C.D. (2012). Habitat associations of species show consistent but weak responses to climate. *Biology Letters*, **8,** 590-593.

Thomas, C.D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions*, **16**, 488–495.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R. (1999) Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology*, **13**, 55-64.

Thuiller, W., Lavorel, A., Sykes, M.T. & Araújo, M.B. (2006) Using niche-based modeling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, **12**, 49-60.

Tingley, M.W. & Beissinger, S.R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution*, **24**, 625–633.

Tolman, T. & Lewington, R. (2011) *Mariposas de España y Europa, 2nd edition*. Lynx Ediciones, Madrid.

Van Asch, M., Van Tienderen, P.H., Holleman, L.J.M. & Visser, M.E. (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology*, **13**, 1596-1604.

Van Swaay, C.A.M., Van Strien, A.J., Julliard, R., Schweiger, O., Brereton, T., Heliölä, J., Kuussaari, M., Roy, D., Stefanescu, C., Warren, M.S. & Settele, J. (2008) *Development*

of the methodology for a European Butterfly Climate Change Indicator. Report

VS2008.040, De Vlinderstichiting, Wageningen.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J.M.,

Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change.

Nature, **416**, 389-395.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J. (2007) An elevational shift in

butterfly species richness and composition accompanying recent climate change. *Global

Change Biology*, **13**, 1873-1887.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005)

Changes to the elevational limits and extent of species ranges associated with climate

change. *Ecology Letters*, **8**, 1138-1146.

Zografou, K., Kati, V., Grill, A., Wilson, R.J., Tzirkally, E.L., Pamperis, L.N. & Halley, J.M.

(2014) Signals of climate change in butterfly communities in a Mediterranean protected

area. *PLoS ONE*, **9**, e87245.

(A) Biosketch

Susana Nieto-Sánchez is a PhD student at the Universidad Rey Juan Carlos, Spain. She is interested in effects of climate change on fauna.

David Gutiérrez is senior lecturer in Ecology at the Universidad Rey Juan Carlos, Spain. He is a specialist in metapopulation dynamics of butterflies in fragmented landscapes, and in the biogeography of insect communities in mountain systems in the context of climate change.

Robert J. Wilson is senior lecturer in Conservation Biology at the University of Exeter, UK. He studies the distributions and dynamics of butterfly species near their geographic range margins, as exemplar systems for the responses of biodiversity to environmental change.

Author contributions: D.G. and R.J.W. conceived the ideas; all authors collected the data; S.N. and D.G. analysed the data; all authors wrote the manuscript.

Table 1 Confidence set models for comparisons between periods (1967-1973 vs. 2006-2012) for the relationships: (a) mean temperature (°C) vs. elevation (m) (n = 10 meteorological stations in 1967-1973 and n = 7 stations in 2006-2012), (b) presence-absence CTI (°C) vs. elevation (n = 17 sites in 1967-1973 and n = 24 sites in 2006-2012) and (c) presence-absence

5   CTI vs. mean temperature (same sample sizes as in (b)). The table indicates the variables included in the model and the direction of their coefficients (+/-), intercept, number of parameters in the model (K, including one extra parameter for variance in regression models), R^2, Akaike Information Criterion (AIC_c); differences in AIC_c between current and best model (ΔAIC_c) and Akaike Information Criterion weight ($AIC_c w$). Period is a categorical variable

10   with 1967-1973 as reference level (i.e. a positive sign indicates that the value for 2006-2012 was larger than that for 1967-1973). Relative importance (Imp), model-averaged coefficients (Coef) and unconditional standard errors (SE) for each variable are also shown.

(a)

Rank	Elevation	Period	Intercept	K	R^2	AIC_c	ΔAIC_c	$AIC_c w$
1	-	+	+	4	0.96	36.9	0	1
Imp	1	1						
Coef	-0.0058	1.78	14.82					
SE	0.00037	0.32	0.60					

(b)

Rank	Elevation	Period	Intercept	K	R^2	AIC_c	ΔAIC_c	$AIC_c w$
1	-	+	+	4	0.76	-6.6	0	0.83
2	-		+	3	0.72	-3.4	3.14	0.17
Imp	1	0.83						
Coef	-8.78e-4	0.14	11.22					
SE	8.89e-5	0.073	0.14					

(c)

Rank	Temperature	Period	Intercept	K	R^2	AIC_c	ΔAIC_c	AIC_cw
1	+	-	+	4	0.77	-7.4	0.00	0.68
2	+		+	3	0.74	-6.0	1.47	0.32
Imp	1	0.68						
Coef	0.16	-0.043	8.80					
SE	0.015	0.034	0.18					

Table 2 Results for spatial autocorrelation of abundance and presence-absence CTI. The table indicates: the assessed correlograms, lag interval analyzed (m), number of distance classes included (k), direction of Moran's I (+/-) and the distance classes (m) showing spatial autocorrelation (class '> 50000' was based on aggregated lag intervals to avoid small numbers of paired sites).

Correlogram	Lag interval	k	Moran's I	Autocorrelated class
CTI presence-absence (1967-1973, n = 17, vs. 2006-2012, n = 24)	10000	5	+ -	0 – 10000 > 50000
CTI abundance for spatial variation (2006-2008, n = 40)	10000	5	+ -	0 – 10000 > 50000
CTI presence-absence for spatial variation (2006-2008, n = 40)	10000	5	+ + -	0 – 10000 10000 – 20000 > 50000

Table 3 Confidence set models for mean (a) abundance CTI and (b) presence-absence CTI in 2006-2008. The table indicates the variables included in the model: Temperature (mean temperature for 2006-2008 period in units of ºC), Forest (proportional cover of forest), Meadows/Pasture (proportional cover of meadows/pasture); and the direction of their coefficients (+/-) (n = 40 monitored sites in both cases). For explanation of terms, see Table 1.

(a)

Rank	Temperature	Intercept	K	R^2	AIC_c	ΔAIC_c	AIC_cw
1	+	+	3	0.77	27.6	0.00	1
Imp	1						
Coef	0.22	8.29					
SE	0.020	0.19					

(b)

Rank	Temperature	Forest	Meadows/Pasture	Intercept	K	R^2	AIC_c	ΔAIC_c	AIC_cw
1	+	-	-	+	5	0.85	3.5	0.00	0.91
2	+	-		+	4	0.82	8.1	4.65	0.09
Imp	1	1	0.91						
Coef	0.23	-0.57	-0.42	8.42					
SE	0.018	0.14	0.17	0.14					

Fig. 1

Fig. 2

Fig. 3

(a)

(b)

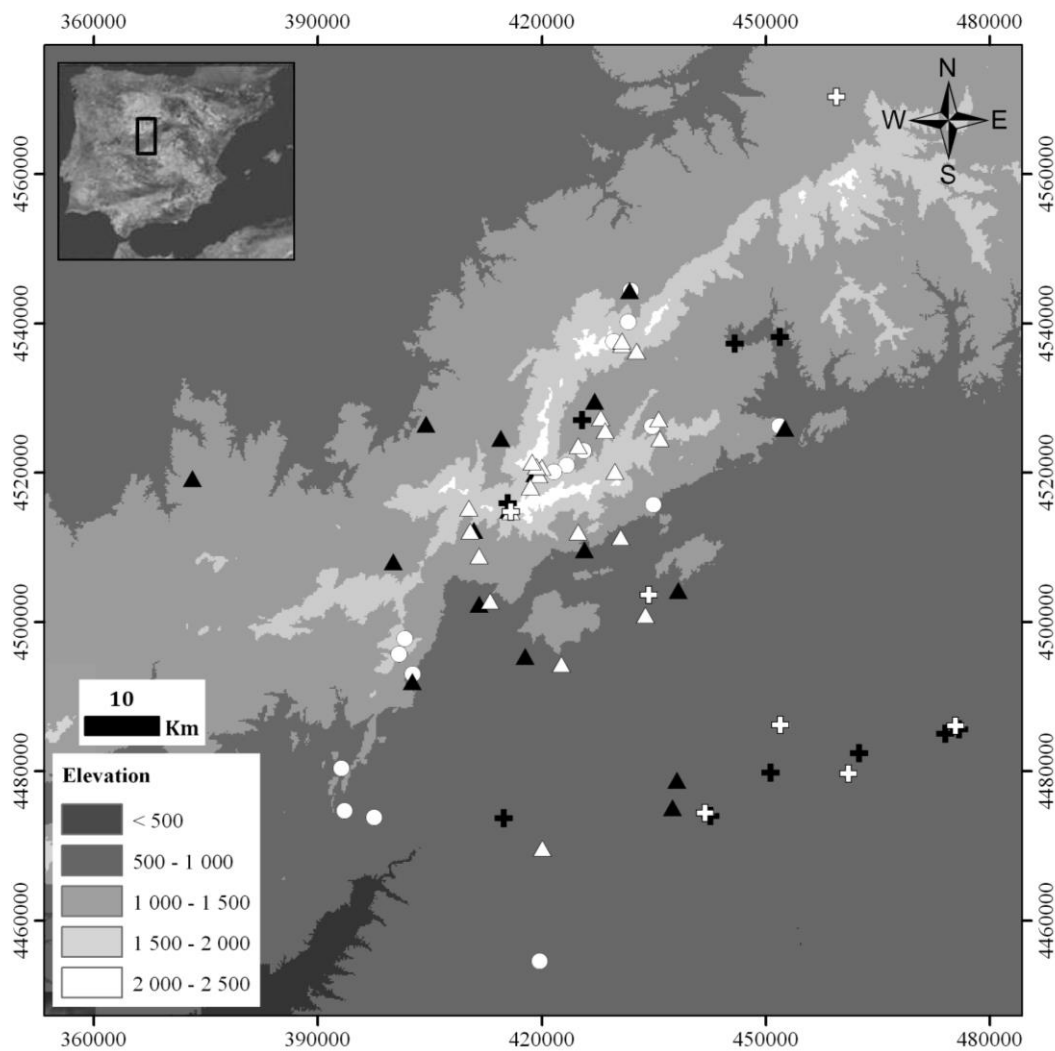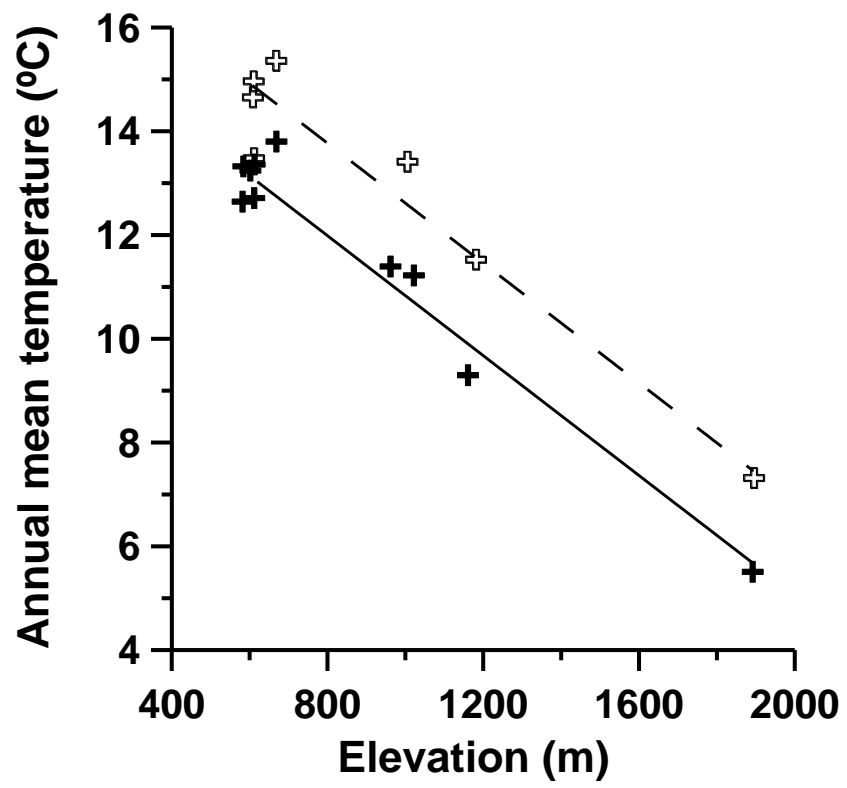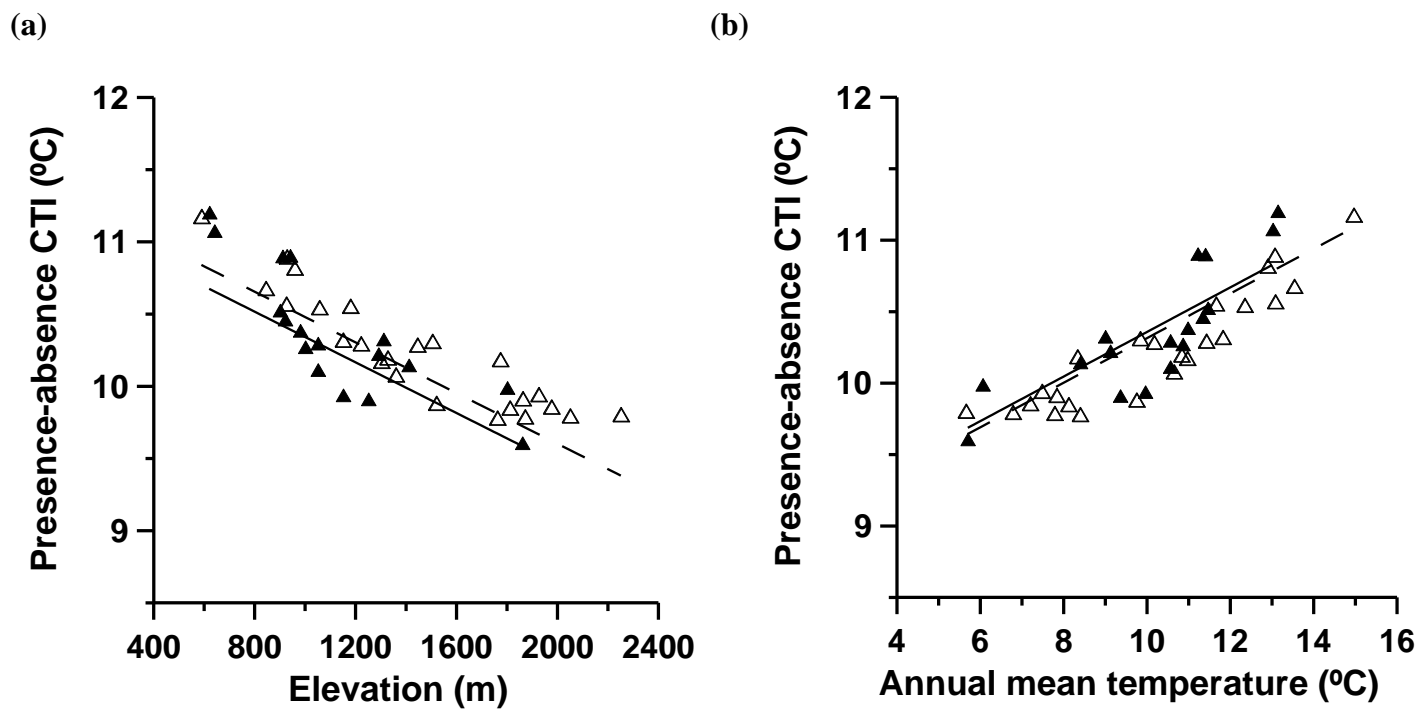**Figure legends**

Fig. 1 Map showing the location of sites sampled for butterflies in the Sierra de Guadarrama for both study periods and AEMET (Spanish Agencia Estatal de Meteorología) meteorological stations. Triangles show sampling sites for the long-term study (black for the

5   seventeen sites sampled in 1967-1973 and white for the twenty-four sites visited in 2006-2012); circles represent the sixteen additional sites used for the spatial analysis sampled in 2006-2008; crosses show location of AEMET meteorological stations (black for ten stations with data for 1967-1973 and white for seven stations for 2006-2012 period). The inset map shows geographical context in Spain. Georeferencing units are in UTM (30T; ED50).

10

Fig. 2 Annual mean temperature plotted against site elevation for 1967-1973 (black crosses, solid line) and 2006-2012 (white crosses, dashed line). Symbols represent data from AEMET meteorological stations. Regression lines according to the model in Table 1.

15   **Fig. 3** Relationship between presence-absence CTI and (a) elevation or (b) annual mean temperature for 1967-1973 (black triangles, solid lines) and 2006-2012 (white triangles, dashed lines). Regression lines according to the models in Table 1.