Butterfly diversity in the Montseny Mountains: Patterns and processes

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Work Contribution:

The execution of the work by the student began in March 2014. Butterfly data had been collected prior to the masters program by Constantí Stefanescu, Jordi Dantart, Roger Vila, Jordi Jubany and Vlad Dinca. All other data sets were provided from sources as stated in the manuscript. The student was responsible for the extraction, filtering and formatting of data from several source formats, and using several R packages (MASS, stats, pscl and AER), exploring and statistically analyzing the data. With the guidance of both tutors, the student performed exploratory data analysis and built statistical models. The student created all of the tables and figures of the manuscript and supplementary materials and wrote the final manuscript with revisions, contributions and corrections by tutors. The article is formatted for the journal Global Ecology and Biogeography.

Butterfly diversity in the Montseny Mountains:
Patterns and processes

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ABSTRACT

Aim To describe spatial patterns of Mediterranean butterfly species richness by functional groups, analyze their main landscape and climatic drivers, test the existence of extinction debt effects, and predict past species richness distributions using past climatic and landscape data.

Location A transect of 186 x 1 km^2 quadrats in the Montseny region and surrounding plains in the area of Catalonia (NE Spain), located between the Mediterranean Sea and the Pyrenees mountains.

Methods From 2003 to 2010 we systematically recorded the presence of butterfly species in each quadrat for a total 123 different butterfly species. Times series data were analyzed for average monthly temperature and average monthly precipitation to determine significant trends in climate. Proportions of landscape types per quadrat were calculated for years 1956, 1993 and 2005. Using these geographic, climatic and landscape data for each quadrat, a generalized linear model was built to determine the significant factors affecting butterfly species richness patterns.

Results Butterfly species richness followed a hump-shaped pattern along the altitudinal gradient. The highest species richness occurred at an average elevation range between 600 and 800 m. Of the landscape and climatic data, species richness was best explained by the interaction of temperature and precipitation (quadratic effect) as well as the amount of artificial unproductive land (negative effect), natural unproductive land (positive effect), and meadows and pastures present (positive effect). No extinction debt was found using past climatic and landscape data from the 1950s and 1990s.

Main conclusions Significant increases in temperature and large increases in artificial unproductive land may be attributable for the change in the predicted distribution of species from 1956 to 2005. These effects could also be filtering out certain functional groups, selecting for species most suited to higher temperatures and urbanized areas (i.e. species with high temperature preference, high dispersal ability and most generalist in habitat specialization), particularly at lower elevations.

INTRODUCTION

With an elevation of 1712 m, Montseny represents the highest mountain in the pre-coastal range in Catalonia. This circumstance, together with its isolation from other high pre-Pyrenean mountains, and the fact that it is also surrounded by lowland agricultural plains, makes the whole massif a very interesting area from a bio-geographical point of view. For many taxa, the co-occurrence of species of different bio-geographical origin (i.e. typical Mediterranean, European and boreo-alpine elements) has led to a notable diversity, which underlined the declaration of the whole area as a UNESCO Man and the Biosphere (MAB) reserve in 1978 and as a Natural Park in 1987 (Guinart *et al.*, 2014). Thus, botanists have long noted the presence of relict populations of subalpine and central European plants (Bolòs, 1983), and the same applies to various animal taxa, ranging from insects (Barrientos, 1995) to vertebrates (Carranza & Amat, 2005). The importance of the Montseny massif as a biodiversity hotspot was, for example, recently noted for butterflies, when it was declared a Prime Butterfly Area in Europe (out of two existing in Catalonia, and fourteen in Spain) (Munguira *et al.,* 2003).

However, there are some claims that an important part of this high biodiversity may be at risk because of different factors related to global change (Guinart *et al.,* 2014). Climate change has been noted as a main factor affecting the distribution of plant species and biomes on this mountain (Peñuelas & Boada, 2003), a phenomenon that will have predictable negative effects on species restricted to the highest areas. In addition, loss of traditional agriculture practices has led to a strong increase of forest cover, with negative effects on species linked to open habitats (Guinart *et al.*, 2014). Moreover, in the lowland plains surrounding the mountain, increased urbanization and agricultural intensification has similarly led to the loss of natural habitats and increasing fragmentation, two factors that have traditionally been considered as the main threat for biodiversity in highly humanized landscapes (Sanderson *et al.,* 2002). The butterfly fauna, in particular, is expected to have been strongly affected by these climatic and land use changes, given the well-established indicator properties of butterflies to global change (Thomas, 2005; Devictor *et al.*, 2012) and what has been observed in a comparable Mediterranean mountain area (Wilson *et al.*, 2005, 2007).

In this article, we explore these issues by using an extensive dataset of the butterfly fauna from the Montseny mountains and surrounding plains. From 2003 to 2010, butterfly assemblages were systematically mapped in a large fraction of the region, allowing for the first time to model species richness according to several geographical and landscape variables. Likewise, the availability of detailed historical landscape and climatic data allowed us to explore the possible existence of an extinction debt and the impact of a warming climate in the butterfly fauna (Kuussaari *et al.,* 2009).

More specifically, our aims in this study were: (1) To describe the changes in land uses and climate variables in the study area during 1950 to 2012; (2) to describe the geographical patterns of butterfly species richness variation; (3) to model butterfly species richness and test which key landscape and climate variables explain current trends; (4) to describe species richness patterns by functional groups; (5) to test for extinction debt effects, using current and past landscape and climate variables; and (6) to use the derived species richness models to predict past trends of species richness in this region (1950s, 1990s).

METHODS

Study area

An area of 600 km^2 in northeastern central Catalonia (Northeastern Spain) was chosen to include the Montseny Natural Park and immediate surrounding plains. Natural boundaries such as rivers and strategic road networks were used in determining the delineation of the total sampling region (Fig. 1). The sampling area was divided into 600 x 1 km^2 UTM quadrats (European Datum 1950). A subsample of 200 x 1 km^2 quadrats were selected to form a south to north transect, from the lowest southern agricultural plain around the town of Granollers (150 m a.s.l.) to the highest rock elevations around the peak of Matagalls (1696 m a.s.l.). The 200 quadrats were chosen to capture as much of geographic and climatic variation found within the Montseny massif and surrounding plains, and to be representative of the total area of interest.

Sampling method

Geographic, climatic and landscape data

A digital elevation model with a resolution of 15 m^2 provided by the Institut Cartogràfic de Catalunya was used to calculate the average, maximum and minimum elevation of each quadrat (http://www.icc.cat/cat/Home-ICC/Geoinformacio-digital). For modeling, each quadrat was characterized by its average elevation (mean for all quadrats=671 m, min=169 m, max=1549 m, SD=342 m).

Average monthly precipitation and temperature values of more than 500 weather stations distributed across Catalonia were provided by the Catalan Meteorological Service, covering the 1950 to 2012 time period (see http://www20.gencat.cat/portal/site/meteocat). Interpolated climatic maps were derived applying a mixed spatial interpolation method that combines sequentially two interpolation techniques (Ninyerola *et al.,* 2006, 2007; Pons & Ninyerola, 2008; Carnicer *et al.,* 2011). The method applies a global statistical interpolation (multiple regression) using geographical variables, and subsequently calculates a local interpolation (inverse distance weighted) that uses the residuals of the regression fitting to generate a local anomalies corrector (see Ninyerola *et al.,* 2006, 2007; Pons & Ninyerola, 2008; Carnicer *et al.,* 2011 for further details). For both precipitation and temperature, monthly values were averaged over the 1 km^2 sampling quadrat and then averaged for a period of several years. Average values of temperature and precipitation were calculated for the years in which butterfly and land coverage data were available (1956, 1993, 2005), including all butterfly-sampling years (2003-2010). For values representing 1956, data was averaged from January to December for years 1950 to 1960; for 1993, data was averaged from January to December for years 1990 to 1997; for the study period, data was averaged from January to December for years 2003 to 2010.

Land coverage proportions for each quadrat were mined from land coverage raster image files available for the study region during 1956, 1993 and 2005 (Basnou *et al*., 2013). Each raster contained ten land use types at a pixel resolution of 25 m^2. Of the ten land coverage types, only seven types were considered in the model analysis due to negligible proportion amounts in three of the types (wetlands, inland waters, and recently burned). The land coverage types considered were artificial unproductive land, natural unproductive land, crops, meadows and pastures, dense forest, clear forest, and thickets.

Butterfly data

To gather complete information about the butterfly assemblages, each sampling quadrat was first comprehensively inspected to select a recording route representative of its landscape heterogeneity. Thereafter, each quadrat was visited three more times at different periods: (1) spring (from 10 April to 15 May); (2) early summer (from 10 June to 15 July); and (3) late summer (from 1 to 30 August). In spring, quadrats were sampled for 1.5 h between 10:00 and 16:00, while in summer they were sampled for 2.25 h between 09:00 and 18:00. During each visit, all the butterflies seen along the recording route (the same in all three visits) were identified to species level; butterflies were only collected when identification in the field was not possible and a closer inspection in the laboratory (e.g. to look at their genitalia structure) was required. For each species, abundance was categorized into four classes (1: one individual; 2: 2-10 individuals; 3: 11-100 individuals; 4: more than 100 individuals); however, in this analysis, only presence/absence data were taken into account. The fieldwork was carried out between 2003 and 2010 by five butterfly experts: Constantí Stefanescu (70 quadrats), Jordi Dantart (66 quadrats), Roger Vila (27 quadrats), Jordi Jubany (23 quadrats) and Vlad Dinca (20 quadrats). Four quadrats out of the 200 could not be sampled due to inaccessibility. For the final analysis, ten more quadrats were discarded for being under sampled, which made the final dataset consist of 186 quadrats (Fig. 1).

Butterfly functional groups

We considered the following functional groups (model naming convention in parenthesis):

(1) Temperature preference of a given species, defined according to the Species Temperature Index (STI), which estimates the average temperature (°C) found throughout the species' range – species with low temperature preference (STI1), mid-low temperature preference (STI2), mid-high temperature preference (STI3), and high temperature preference (STI4). STI values were obtained from the Climatic Risk Atlas of European Butterflies (Settele *et al*., 2008). See Appendix S1 in Supporting Information for species list according to grouping.

(2) Habitat specialization, measured by means of the Species Specialization Index (SSI) as defined in Julliard *et al*. (2006). Low index values (i.e. SSI1) indicate the species is homogeneously distributed across all habitats and exhibits more generalist habits, and high index values (i.e. SSI4) indicate the species distribution is restricted to certain habitat types, exhibiting more specialist habits. See Appendix S2 in Supporting Information for species list according to grouping.

(3) Mobility or adult dispersal ability. Each butterfly species was assigned an index of increasing mobility ranging from 1 to 4, according to the following criteria – 1 - species living in meta-populations with little dispersal between populations (MOBIL1); 2 - species living in meta-populations with high dispersal between populations (MOBIL2); 3 - species living in patchy populations with non-seasonal migration (MOBIL3); 4 - species living in patchy populations with seasonal migration (MOBIL4) (Stefanescu *et al.,* 2011). See Appendix S3 in Supporting Information for species list according to grouping.

(4) Overwintering stage, as an egg (OVERWINT1), larva (OVERWINT2), pupa (OVERWINT3) or adult (OVERWINT4), according to García-Barros *et al.* (2013). See Appendix S4 in Supporting Information for species list according to grouping.

(5) Trophic specialization of larvae, distinguishing between monophagous (LARV1) - butterflies feeding on plants of a single genus; oligophagous (LARV2) - butterflies feeding on plants of various genera belonging to the same family; and polyphagous (LARV3) - butterflies feeding on a diversity of plants belonging to various families. Data were based on García-Barros *et al*. (2013) and unpublished observations by C. Stefanescu. See Appendix S5 in Supporting Information for species list according to grouping.

(6) Voltinism, defined according to the typical number of generations a species has in one year – univoltine (VOLT1), bivoltine (VOLT2), and multivoltine (VOLT3). Data came from the Catalan Butterfly Monitoring Scheme database (www.catalanbms.org) and from the compilation by García-Barros *et al*. (2013). See Appendix S6 in Supporting Information for species list according to grouping.

Statistical analyses

To understand the environmental changes in the study area, we analyzed the changes in landscape and climate from 1950 to 2012. To evaluate climate trends, we applied time series analyses to explore the temporal trends in average monthly temperature and precipitation in the study area (Shumway & Stoffer, 2006; Carnicer *et al*., 2011). To explore changes in landscape, we plotted and compared the altitudinal changes in artificial unproductive land, natural unproductive land, crops, meadows and pastures, dense forest, clear forest, and thickets in 1956, 1993 and 2005.

When evaluating the butterfly data, we were first interested in simply describing the geographical pattern of butterfly species richness. To do that we started with a descriptive model using butterfly species richness in each quadrat as the dependent variable, and a set of geographic variables as independent variables: average elevation of each quadrat, the square term of elevation, directional orientation and geographical location.

Secondly, to further investigate the species richness pattern, we used a new set of independent variables. Instead of geographic variables, climatic and landscape variables were introduced to assess the relative importance of these factors in driving species richness trends.

And thirdly, we repeated the modeling process with climatic and landscape variables for subsets of functional groups. Here we were interested in the patterns and the underlying causes for groups of species sharing some functional trait (e.g. a certain range of preferred temperatures, overwintering stage, mobility level, and so on). Species richness and relative species richness values for each functional group were calculated for each 1 km^2 quadrat. The relative richness for each group was calculated as the number of species observed with such functional trait divided by the total richness of the quadrat. Continuous variables (i.e. temperature preference (STI) and habitat specialization (SSI)) were divided into four levels based on the interquartile ranges to capture equal numbers of species within groups.

All the previous models were built with the current values of variables, that is, values for the period 2003-2010. In a second step, we repeated the modeling process for total species richness considering historical values of climatic and landscape variables, that is, for 1950 to 1960 and for 1990 to 1997. Our main objective here was to see if models using historical data over present data better explained current species richness considering significant environmental changes. This method was suggested by Kuussaari *et al.* (2009) for exploring the existence of an extinction debt when past species richness data are not available but past landscape and/or climatic data are. Krauss *et al*. (2010) later applied this same method for plants and butterflies occurring in meadows that have been subjected to abandonment and encroachment in several Catalan mountain areas (but not Montseny).

Finally, we used past climatic and landscape data to predict past species richness patterns, assuming that the relationships that we found in models with present day data (which were selected as the best models) were the same in the past.

A generalized linear model (GLM) using a log link function and a poisson error distribution was used to evaluate species richness as a function of geographic, climatic and landscape variables. First, models were built using single variables to determine the relative explanatory ability and significance. From there, the stepAIC function was utilized from the R package "MASS". This package adds and subtracts variables depending on their reduction in AIC, building a model using forward logic (adding variables) and backward logic (subtracting variables) based on their relative contribution to the AIC. Further model refinement was performed by removing variables with non-significant p-values and contributing very little to the AIC value for a more parsimonious model. Cragg and Ulher's pseudo-r^2 was calculated using the function pR2 of the R package "pscl" to assess the goodness of fit. Overdispersion was evaluated using the dispersiontest function from the R package "AER". When significant overdispersion was detected in the models, we applied a quasipoisson link function. To predict richness, the predict.glm function was utilized in the package "stats". A smooth spline or lowess line (also found in R package "stats") was fitted to the total species richness and relative richness of functional group data to reveal the richness patterns with the elevation gradient.

RESULTS

Current landscape and climatic patterns

We first examined the spatial variation in current landscape and climate variables along the altitudinal transect. Markedly, the altitudinal transect was divided into northern and southern halves by the highest elevation range situated around the Matagalls peak (boundary denoted in Fig. 1). Different altitudinal bands showed contrasting patterns in current climate and landscape variables. For example, in the very southern region of the transect, most quadrats are relatively planar and characterized by a low average elevation, between 150 to 400 m. In this altitudinal band, and due to the low elevation, we observed warmer temperatures and lower precipitation (Appendix S8 in Supporting Information). Moreover, due to its planar nature, it also contains high proportions of artificial unproductive land (urbanized areas), and high proportions of cropland but also dense forest (Figs 2a, b and c). The area also contains a substantially lower proportion of thickets, meadows and pastures (Figs 2d and e). In the study area, artificial unproductive land and cropland are positively correlated and both very strongly negatively correlated with dense forest. Proceeding north, elevation increases quite rapidly from 400 to 500 m; quadrats here consist mostly of dense forest. In the 550 to 800 m altitudinal band, we observed two contrasting areas located on either side of the highest elevation divide. The quadrats in the northwestern side contain large proportions of artificial unproductive land and cropland, and correspond to the planar rural area around the villages of Seva, Tona and Centelles. On the contrary, quadrats in the southern half mainly consist of dense forest. Continuing higher in elevation and approaching the divide, at approximately 1100 m, a large increase in thickets, meadows and pastures, and natural unproductive land (all strongly positively correlated) occur as the proportion of dense forest decreases (negatively correlated).

Historic climatic and landscape patterns

Time series analyses indicate that average monthly temperature has significantly increased from 1950 to 2012 (estimate= 0.045±0.003; t-value=14.94; p<2e-16). More precisely, from the 1950s to 1970s, the temperature trend largely fluctuated (Appendix S10 in Supporting Information). However, from the 1970s to the 1990s, fluctuations became less with a significant, steady upward trend until the beginning of the 1990s where the trend began to plateau into the 2010s. On the other hand, time series analyses did not detect a significant trend in rainfall trends (estimate = -0.077±0.089; t-value= -0.867; p=0.386). A slight, non-significant decrease was observed from the 1970s to the 2010s (Appendix S10 in Supporting Information).

Changes in landscape in our sampled quadrats are shown in Fig. 2. The most relevant patterns can be summarized as follows. Artificial unproductive land increased substantially from 1956 to 1993, and increased still from 1993 to 2005 but to a lesser degree, in both the planar areas situated between 150 to 400 m (southern lowlands) and 550 to 800 m (northwestern rural area) (Fig. 2a). This increase mainly relates to an urbanization process, which, in the last period, also coincided with the reduction of cropland in the southern lowlands (Fig. 2b).

Dense forest has steadily but minimally increased throughout the years, especially at mid elevations (Fig. 2c). On the other hand, thickets increased with elevation up to 1993, but afterwards -with the exception of a few quadrats - underwent a depression between 600 m and 1100 m (Fig. 2d).

The last three land uses, meadows and pastures, natural unproductive and clear forest, are relatively poorly represented in the area. Meadows and pastures largely increased above 1150 m from 1956 to 1993, but drop back to 1956 proportions in 2005 (Fig. 2e). They have also experienced some increase at all elevations in the last decade, after a significant reduction in the preceding years.

While natural unproductive has experienced small changes over the study period, clear forest decreased strongly up to 1993, and only a few quadrats rebounded to the 1956 amounts in the last decade (Fig. 2f and g).

Current species richness patterns

A total of 123 species were recorded in the 186 km^2 area, with an average value of forty-two species per quadrat (min=8, max= 72, SD= 13). A list of all the observed species, together with the number of quadrats from which they were detected, is provided in Appendix S7 in Supporting Information. The highest values of species richness were mainly recorded in the northern half of the sampled area, especially in the western side, while the lowest were recorded in the southern plains (Fig. 1).

Species richness followed approximately a hump-shaped pattern with elevation (Fig. 3). Starting with the lowest values at the lowest elevations, richness increased, peaking between 600 to 800 m, also having a notable secondary peak at 1250 m, before decreasing to medium values at the highest elevations.

Species richness modeling

The best geographical model of species richness explained 70% of the data, and included elevation, UTM northing, the interaction term between elevation and northing, and planar orientation of the quadrat as significant independent variables (Table 1a). Negative effects of planar areas are possibly associated with the presence of urbanized areas (see below for complementary models testing these effects). As one travels north in the altitudinal transect, richness increases; nevertheless, this also depends on elevation and hence the significance of the interaction between elevation and northing.

In all single variable models (i.e. total richness as a function of dense forest), all climatic and landscape variables were significant but with varying degrees of explanatory power. Of all nine variables, temperature, artificial unproductive land and cropland performed as negative predictors of species richness.

Model fit of species richness increased from 70% to 85% when climatic and landscape variables were used as independent variables instead of geographical ones (Table 1b). Species richness was nonlinearly related with climatic variables, and was best explained by negative effects of temperature and precipitation and by positive effects of their interaction. This corresponds to a typical hump-shaped relationship, with maximum species richness values in mid-altitudinal zones of intermediate rainfall and temperature values. Three landscape variables were significant in the best model (Table 1b). Artificial unproductive had the strongest negative effect on species richness, meaning that an increase in urbanization and infrastructures lowered species richness in a given quadrat, hence the detectable sudden decrease of richness at low elevations (Figure 3). Conversely, more cover of natural unproductive areas, and meadows and pastures increased species richness, which contributes to the two peaks in the richness distribution (Figs 2e, 2f, and 3).

Elevation patterns and modeling of functional groups

Herewith, we focus on the results for the first three functional groups, namely species temperature preference, habitat specialization and dispersal ability. For the details on the other traits, we refer the reader to Figs 4(d), (e) and (f) and Appendices S11-S16 in Supporting Information.

STI

Figure 4(a) shows the diverging altitudinal patterns observed for the four STI groups. The relative richness of STI1 and STI2 shows a gradual linear increase with elevation. Higher STI2 relative richness is observed over the entire elevation range and is the group with the highest proportions. In the group STI3, relative richness shows a hump-shaped pattern that peaks between 600 to 800 m and decreased as elevations get higher. For STI4, there is a clear downward trend in relative richness from low to high elevations.

When modeling climatic and landscape variables for STI1, STI2 and STI3, the best and most significant variables in explaining richness were generally precipitation, temperature, artificial unproductive, natural unproductive, and meadows and pastures, as seen also in the total richness model (Appendix S11; Table 1b). STI4 was the only group to also be dependent on dense forest and thickets. All variables have varying degrees of influence and significance for each group (Appendix S11). Interestingly, contrasting effects of precipitation were observed in the four STI groups. Precipitation has a positive effect on group STI1, whereas in STI2 it was not significant, a non-linear effect in STI3 (interaction of precipitation and temperature) and a negative effect in the group STI4. All groups were largely negatively affected by artificial unproductive landscapes except for STI4, where it was not significant.

SSI

The relative richness of each SSI group decreased with increasing specialization (Fig. 4b). The shapes of the trends of each group, however, were very different. SSI1 relative richness decreased with elevation, having the highest values in the lowlands (i.e., quadrats at low elevation were increasingly dominated by generalist species). However, from 800 m upwards, the trend flattened out and values stabilized. SSI2 and SSI4 showed a similar trend of a very gradual increase with elevation. SSI3 followed nearly the opposite pattern of SSI1, a steep increase in relative richness with elevation before gradually flattening out in the upper elevation range.

Precipitation, temperature and the interaction thereof were significant in all SSI group models except SSI1 (Appendix S12 in Supporting Information). Of the climate variables, SSI1 was the only group positively influenced by temperature, whereas all other SSI groups were negatively affected by this variable. Artificial unproductive (with a negative effect) and natural unproductive land (with a positive effect) were significant in all SSI groups, with the exception of SSI2 where meadows and pastures took its place.

MOBILITY

MOBIL1 and MOBIL4 have lower relative richness than MOBIL2 and MOBIL3 (Fig. 4c). As with the SSI analysis, MOBIL 1 and MOBIL 3 followed reverse trends. MOBIL1 had the lowest relative richness in the lowlands, steeply increased with elevation to a peak at around 800 m, and then gradually leveled off in the upper elevations. MOBIL3, on the other hand, had the highest relative richness in the lowlands, steeply decreased with elevation into a slight depression at approximately 800 m, and then rebounded to slight higher values at upper elevations. MOBIL4 showed an upward facing scoop-shape pattern, with the highest relative richness in the lowlands.

Models for MOBIL groups progressively get worse in their ability to explain richness patterns (Appendix S13). MOBIL1 had an outstanding pseudo-r^2 value of 0.94, whereas MOBIL4 had a very poor value of 0.10, with MOBIL2 (r^2=0.59) and MOBIL3 (r^2=0.26) in the middle. MOBIL1 and MOBIL2 were highly negatively influenced by precipitation, temperature and artificial unproductive land, and positively influenced by the interaction of precipitation and temperature as well as natural unproductive land. In MOBIL3, of those variables, only temperature remains (with a positive effect) and a whole new set of landscape variables becomes relevant. These new landscape variables, dense forest, thicket, meadows and pastures, and crops, all positively affected richness of MOBIL3. For MOBIL4, the only variable with explanatory value was temperature, which positively affected richness.

Extinction debt analysis

When replacing current variables with historical data from1956 and 1993 to see how well past data can explain current total species richness, AIC increased for 1990s data (Table 2a) and further increased for 1950s data (Table 2b) indicating no extinction debt. However, all variables were still significant for both time periods.

Forecast of past species richness trends (1950s, 1990s)

For comparison with actual and past-predicted trends, current climatic and landscape variables were used to predict species richness for the 2000s (Fig. 5a). The predicted trend followed the trend of the actual modeled data (Fig. 3) very well, with low richness at low elevations, increasing with elevation with two notable peaks between 600 to 800 m and 1200 to 1300 m before decreasing at higher elevations. The predicted richness, though, had less scatter and the peak from 600 to 800 m became less prominent and secondary to the peak between 1200 to 1300 m. With these minor differences, the total species model had strong predictive power.

Applying the total richness model to predict past species richness distributions, we observe a transition from an overall trend of higher richness at lower elevations and lower richness at higher elevations in the 1950s to the opposite in the 2000s (Figs 3, 5a and c). A transitional state is observed in the 1990s, with richness increasing at higher elevations and trending downward at lower elevations (Fig. 5b). Also notable is the resultant spread of richness values per quadrat from the 1950s to the 2000s, except for the mid-elevation ranges between 600 and 800 m.

DISCUSSION

Species richness pattern

Albeit there was considerable scattering in actual values, our data showed a distinctive hump-shaped pattern of butterfly species richness along the elevation gradient. In the Montseny range, total species richness is low at low elevations and steeply increases with altitude, reaching two distinct peaks at 600 to 800 m and, again, at 1200 to 1300 m, before tapering down at the highest elevations (Fig. 3). This same pattern was found in two other studies of Catalan butterflies, albeit at a much larger regional scale and using completely independent datasets to the one used here (Stefanescu *et al*., 2004, 2011). Likewise, in a recent review, Gutiérrez (2009) reanalyzed various butterfly datasets from several Spanish mountain areas and found this same characteristic pattern of species richness peaking at mid elevations. Indeed, the hump-shaped pattern with elevation has been found by many authors working with unrelated taxonomic groups around the globe, and has been summarized by Rahbek (1995) and others.

For Mediterranean butterflies, at least, climatic reasons are the most likely of explanation for such a pattern. It has been suggested that the combination of decreasing temperatures and increasing rainfall along the altitudinal gradient attains optimal levels at intermediate heights, both in terms of the thermal requirements of most butterfly species, and host plant growth and condition (Stefanescu *et al*., 2004; Gutiérrez, 2009; see also Hawkins & Porter (2003) for a similar explanation dealing with the latitudinal pattern of western Palearctic butterflies). The fact that climate variables alone described 66% of the richness pattern in our data seems to support this hypothesis (results not presented in text). However, we do not have any explanation for the existence of two distinct richness peaks at different heights, which almost exactly coincided with the findings by Stefanescu *et al.* (2011).

It must be noted that the current pattern of species richness is also influenced by landscape factors, such as the predominance of some landscapes at certain elevations with positive or negative effects on butterfly diversity. It would seem that landscape variables play an additional role in defining peaks and valleys in the diversity curve, not predicted by climate variables alone. For instance, it was very obvious that habitat destruction (i.e. artificial unproductive land) occurring at the ranges of 150 to 400 m and, to a lesser extent at 600 to 800 m, lowered species richness below what could be expected according to our climatic model. In this respect, our study system confirms the importance of human impacts on the altitudinal species richness pattern pointed out by Nogués-Bravo *et al*. (2008). The large variance in richness at 600 to 800 m can be attributed to the mix in landscape as quadrats contain large proportions of artificial unproductive land and cropland, but also contain the largest proportions of natural unproductive land, and meadows and pastures, of which positively influence richness.

Functional group analysis

When the species richness pattern was broken down into different functional groups, some interesting findings arose. For instance, in the lower range, an obvious filtering of functional groups is occurring. The lower quadrats were clearly dominated not only by the species preferring the highest temperatures (the STI4 group, an expected result given that this is the warmer area), but also by generalist species (those belonging to the SSI1 group) and highly mobile species (those belonging to the MOBIL3 and MOBIL4 groups). As already noted by Carnicer *et al.* (2013), these traits tend to co-vary along a so-called adaptive trait continuum, which summarizes the life-history strategies that are selected under certain environmental conditions. In lowland areas subjected to strong human impact, the only butterflies able to survive are generalist and highly mobile species; on the other hand, specialists (SSI4 group) living in metapopulations (MOBIL1 group) show declining trends, eventually leading to their complete disappearance. This same process has been documented in many butterfly studies (e.g. Hanski & Thomas, 1994; Steffan-Dewenter & Tscharntke, 2000; Warren *et al*., 2001) and lies at the heart of considering these insects as an excellent bioindicator group for terrestrial ecosystems (Thomas *et al*., 2004). Another interesting result was the fact that the STI4 group was largely unaffected by artificial unproductive land and negatively affected by precipitation. This means that it is this group of species that will become selected under a scenario of global change in our area, with expected increasing summer droughts (Della-Marta et al., 2007) and habitat uniformity.

Extinction debt effects and past species richness patterns

Our analysis did not show evidence of extinction debt, as richness models with current climatic and landscape variables better fit current richness trends than those with past variables. This is in line with previous findings (Krauss et al. 2010), and can be interpreted as the rapid response of the short-lived butterflies to environmental change. On the other hand, both the functional group analyses (Fig 4a-f; Appendices S11-S16 in Supporting Information) and the modeling of past species richness trends (Fig. 5) suggested strong changes in the functional composition of butterfly communities during the last 60 years in some areas. These changes would have mainly affected the higher and lower altitudinal bands. In the lowland planar areas, the impacts of urbanization and fragmentation are associated with a strong decline of habitat specialists and less mobile species and a sharp decline in diversity (Fig. 5). In contrast, qualitatively different processes possibly caused remarkable changes in butterfly composition at higher altitudes. Firstly, the documented dynamic expansions and retractions in thicket cover, meadows and pastures, possibly associated with changes in domestic grazing pressure, may have acted as an important driver during the last decades in these areas. On top of this, the significant increase of temperature detected in time series analyses (Appendix S10 in Supporting Information) may have progressively induced an upward altitudinal shift and/or positive demographic responses in some butterfly populations. Further statistical tests and species-specific analyses are warranted to assert this possibility and disentangle the relative importance of land use changes and temperature effects on butterfly populations at high altitudes. In contrast, species richness patterns in the 600 to 800 m peak might have remained largely stable, compared with other parts of the gradient (Fig. 5).

Conservation implications

Our study highlights the importance of conservation practices applied in mid altitude areas. The mid-altitudinal region (600-800 m) harbors important reservoirs of butterfly diversity and shows a different functional composition when compared to lowland planar areas, strongly affected by the urbanization and fragmentation of habitat. With the evident decline of butterfly diversity in the lowland region (southern transect), the hotspot region (northwestern transect) would possibly require active measures to avoid the spread of urbanized and intensive agricultural areas for the protection of this prime butterfly habitat and to encourage the cultivation of supportive landscape types for butterfly diversity. Suggestible action would be to further expand park boundaries to protect diversely rich areas currently outside park limits and to educate and enlist local government and citizens to adopt conservation strategies in city development and agricultural practices.

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Table 1. Butterfly species richness models – (a) generalized linear model uses only geographical parameters elevation, location (UTM coordinate) and directional orientation. Planar orientation was the only direction found to be significant; (b) generalized linear model uses only landscape and climatic variables from the 2000s.

(a)	**β**	**SE**	**z**	**p**	**AIC**	**Pseudo-R^2**
Intercept		19.37	-7.90	***	1657.5	0.7
Average Elevation	0.19	0.03	5.47	***		
Northing	3.39E-05	4.19E-06	8.09	***		
Orientation Planar	-0.23	0.05	-4.69	***		
Ave. Elev.: Northing	-4.08E-08	7.47E-09	-5.47	***		
(b)						
Intercept		0.72	10.04	***	1519	0.85
Average Temperature	-0.29	0.05	-5.51	***		
Average Precipitation	-0.06	0.01	-5.95	***		
Artificial Unproductive	-1.05	0.10	-10.30	***		
Natural Unproductive	1.87	0.41	4.52	***		
Meadows and Pastures	1.58	0.35	4.47	***		
Ave. Temp: Ave. Precip	0.01	8.88E-04	5.81	***		

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

Table 2. Extinction debt analysis – past climatic and landscape data were used in place of current data in the total species richness model to evaluate if past environmental conditions better explained current richness patterns; (a) generalized linear model of species richness with climatic and landscape data from the 1990s; (b) generalized linear model of species richness with climatic and landscape data from the 1950s.

(a)	**β**	**SE**	**z**	**p**	**AIC**	**Pseudo-R^2**
Intercept		0.89	12.20	***		
Average Temperature	-0.55	0.08	-7.31	***		
Average Precipitation	-0.09	0.01	-7.45	***		
Artificial Unproductive	-1.26	0.12	-10.12	***	1533.60	0.84
Natural Unproductive	1.33	0.28	4.73	***		
Meadows and Pastures	0.98	0.24	4.04	***		
Ave. Temp: Ave. Precip	0.01	1.14E-03	6.51	***		
(b)						
Intercept		0.59	14.47	***		
Average Temperature	-0.44	0.05	-9.33	***		
Average Precipitation	-0.07	0.01	-8.28	***		
Artificial Unproductive	-2.10	0.38	-5.57	***	1611.10	0.76
Natural Unproductive	1.54	0.34	4.48	***		
Meadows and Pastures	1.44	0.34	4.27	***		
Ave. Temp: Ave. Precip	0.01	7.32E-04	8.67	***		

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

Figure 1. Map of study region showing the 1 km^2 sampled quadrats and the associated butterfly species richness. Increasing circle size is proportional to increasing species richness. The main roads and rivers that were used to delimit the study area are also shown. Solid line denotes the highest elevations, peak of Matagalls, in the transect which separates the lowlands in the south and the highlands in the northwest.

Figure 2. Landscape proportions per quadrat by elevation for years 1956, 1993 and 2005 – (a) artificial unproductive land, (b) cropland, (c) dense forest, (d) thickets, (e) meadows and pastures, (f) unproductive land and (g) clear forests.

Figure 3. Current species richness per quadrat along altitudinal gradient. A smooth spline was fit to the data to uncover the distribution pattern.

Figure 4. Relative richness per quadrat of all functional groups along altitudinal gradient - (a) species temperature preference (STI1=low: STI4=high)(fitted lowess line); (b) habitat specialization (SSI1=generalist: SSI4=specialist)(fitted smooth spline); (c) dispersion ability (MOBIL1=low: MOBIL4=high)(fitted smooth spline); (d) overwintering stage in Catalonia (OVERWINT1=egg, OVERWINT2=larva, OVERWINT3=pupa and OVERWINT4=adult)(fitted smooth spline); (e) trophic specialization of larvae (LARV1=monophagous, LARV2=oligophagous and LARV3=polyphagous)(fitted smooth spline); and (f) number of generations per year (VOLT1=univoltine, VOLT2=bivoltine and VOLT3=multivoltine)(fitted smooth spline).

Figure 5. Predicted species richness pattern along altitudinal gradient in 1956, 1993 and 2005 (fitted smooth spline).

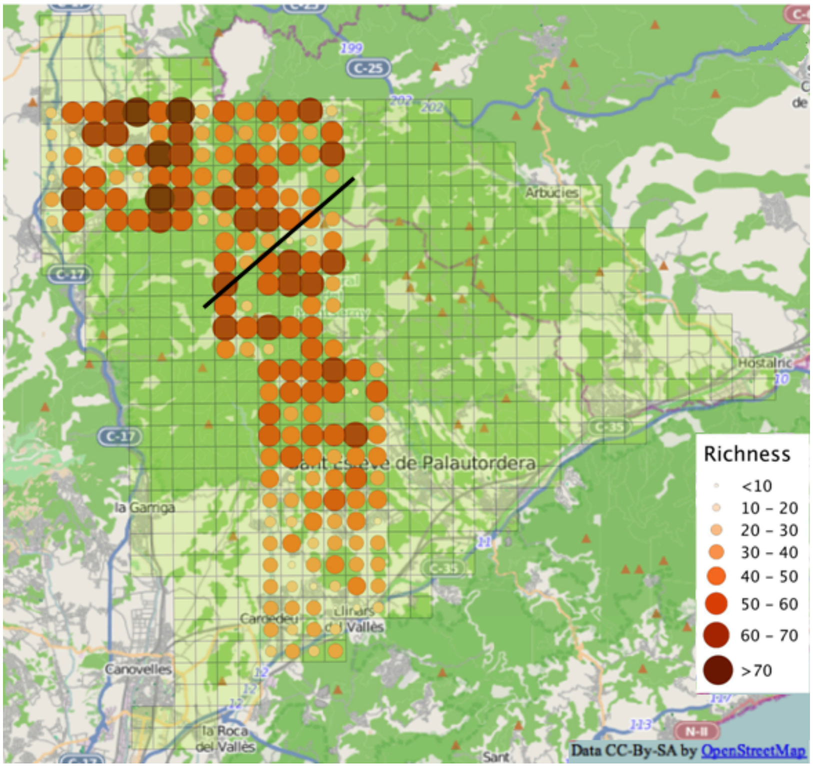
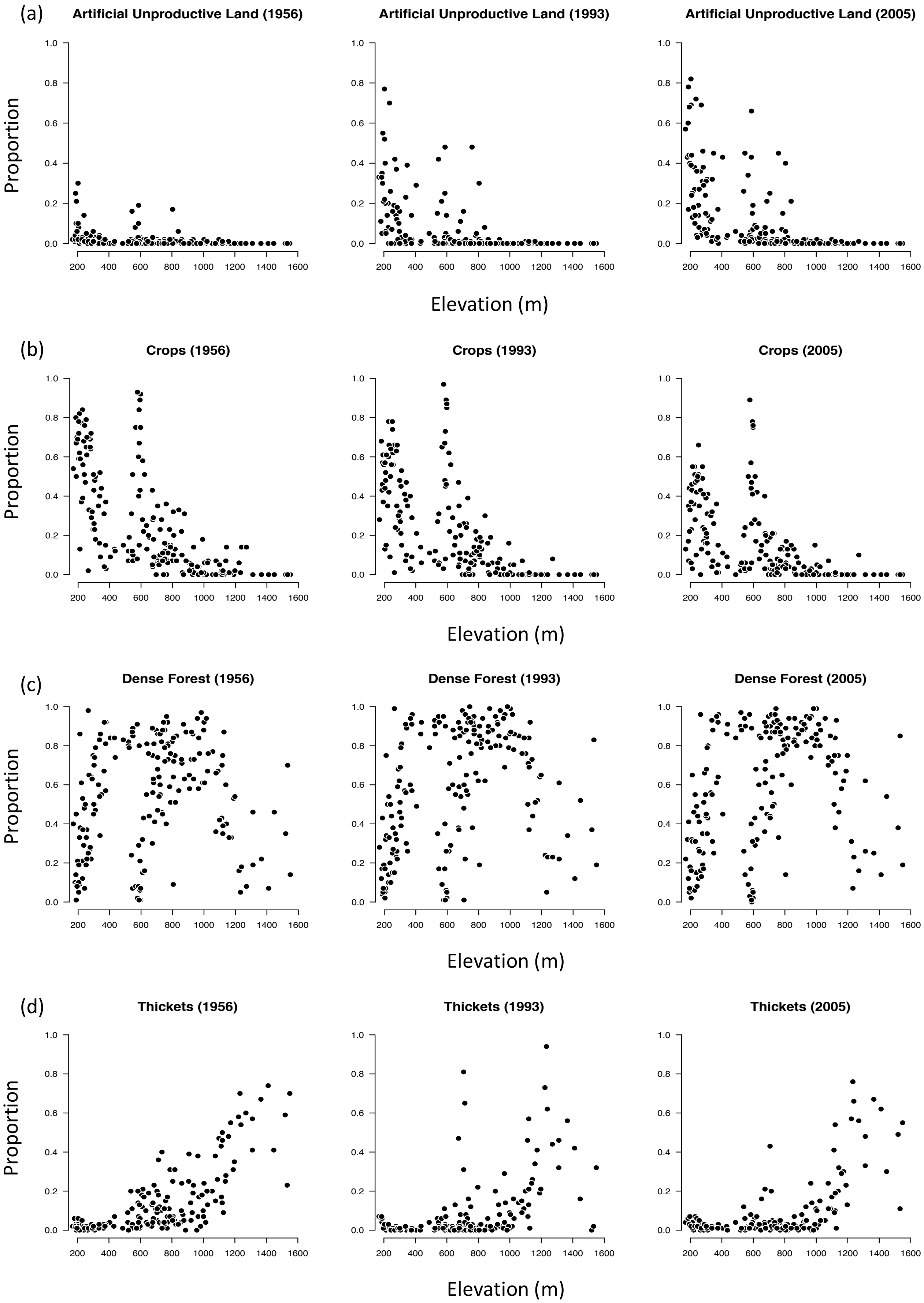

Richness
<10
10 – 20
20 – 30
30 – 40
40 – 50
50 – 60
60 – 70
>70
C-25
199
202
Arbúcies
C-17
Hostalric
C-35
Sant Esteve de Palautordera
la Garriga
Cardedeu
Llinars del Vallès
Canovelles
la Roca del Vallès
N-II
Sant
Data CC-By-SA by OpenStreetMap

Figure 1.


(a)
Artificial Unproductive Land (1956)
Artificial Unproductive Land (1993)
Artificial Unproductive Land (2005)
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
200
400
600
800
1000
1200
1400
1600
Elevation (m)
(b)
Crops (1956)
Crops (1993)
Crops (2005)
Proportion
Elevation (m)
(c)
Dense Forest (1956)
Dense Forest (1993)
Dense Forest (2005)
Proportion
Elevation (m)
(d)
Thickets (1956)
Thickets (1993)
Thickets (2005)
Proportion
Elevation (m)

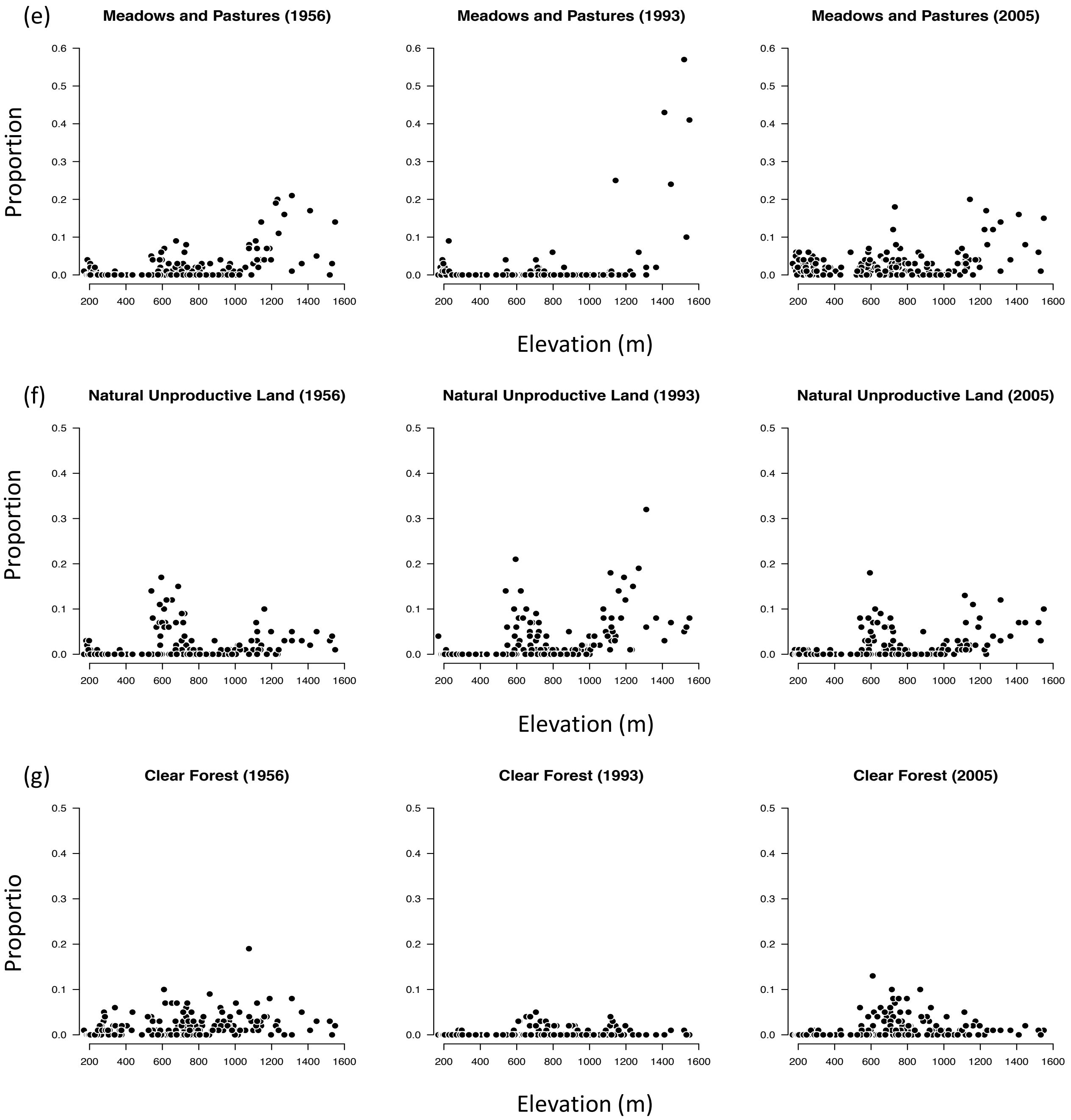
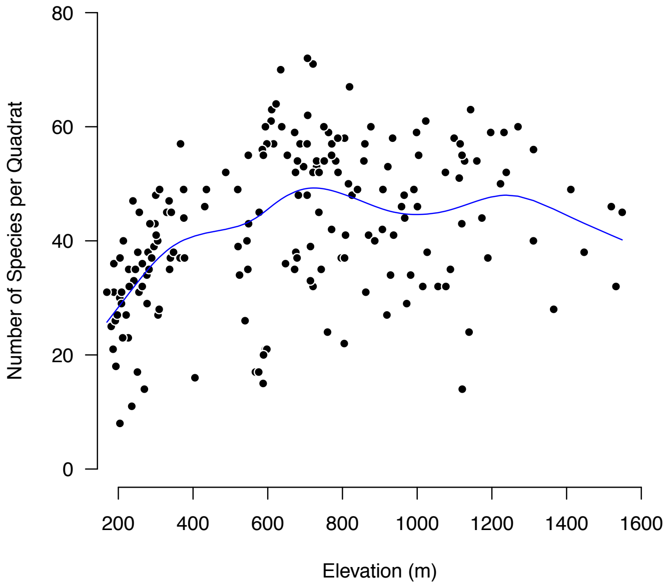

(e)
Meadows and Pastures (1956)
Meadows and Pastures (1993)
Meadows and Pastures (2005)
Proportion
0.0
0.1
0.2
0.3
0.4
0.5
0.6
200
400
600
800
1000
1200
1400
1600
Elevation (m)
(f)
Natural Unproductive Land (1956)
Natural Unproductive Land (1993)
Natural Unproductive Land (2005)
Proportion
0.0
0.1
0.2
0.3
0.4
0.5
Elevation (m)
(g)
Clear Forest (1956)
Clear Forest (1993)
Clear Forest (2005)
Proportio
0.0
0.1
0.2
0.3
0.4
0.5
Elevation (m)

Figure 2.



Number of Species per Quadrat
0
20
40
60
80
Elevation (m)
200
400
600
800
1000
1200
1400
1600

Figure 3.

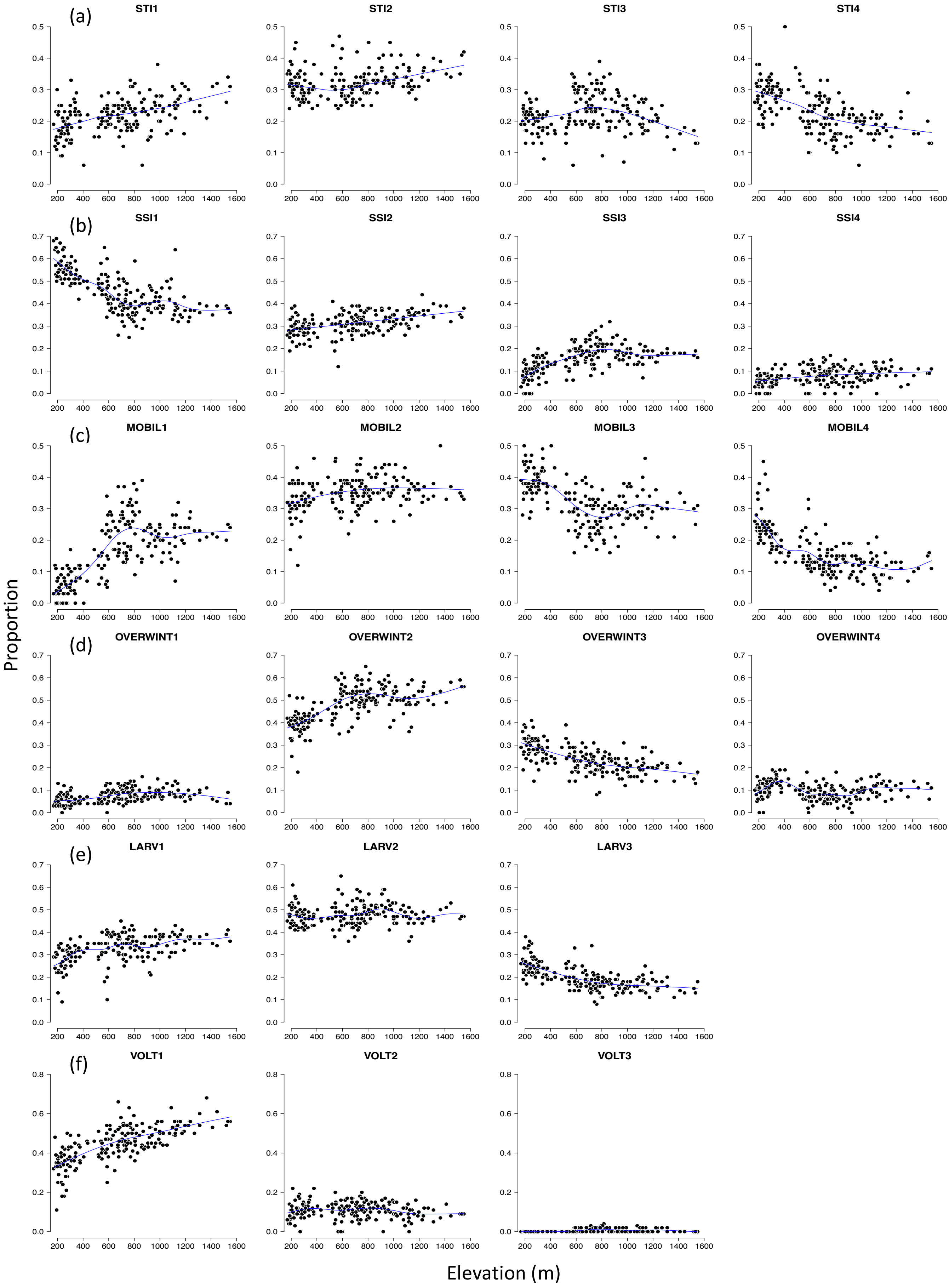

(a)
STI1
STI2
STI3
STI4
(b)
SSI1
SSI2
SSI3
SSI4
(c)
MOBIL1
MOBIL2
MOBIL3
MOBIL4
(d)
OVERWINT1
OVERWINT2
OVERWINT3
OVERWINT4
(e)
LARV1
LARV2
LARV3
(f)
VOLT1
VOLT2
VOLT3
Proportion
Elevation (m)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
200
400
600
800
1000
1200
1400
1600

Figure 4.

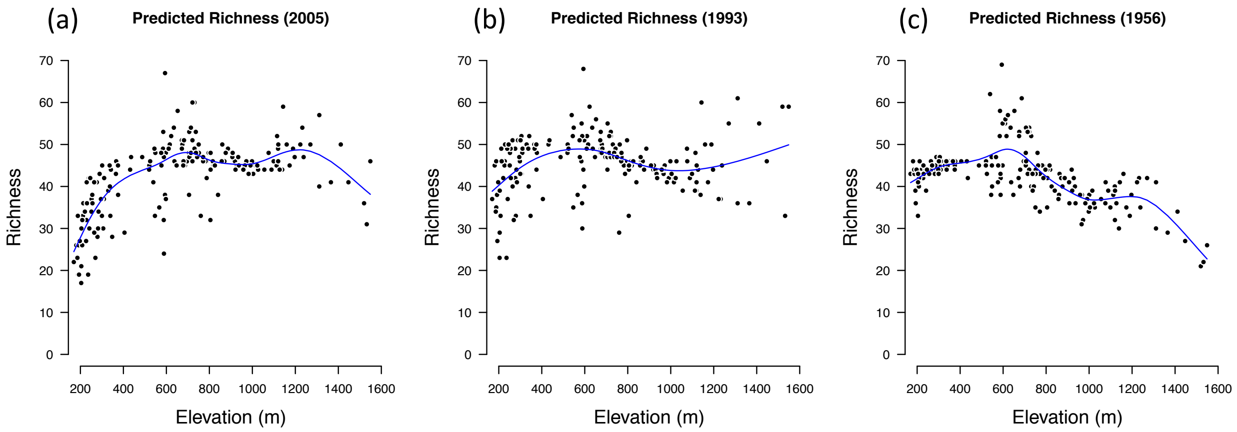

(a)
Predicted Richness (2005)
(b)
Predicted Richness (1993)
(c)
Predicted Richness (1956)
Richness
0
10
20
30
40
50
60
70
Elevation (m)
200
400
600
800
1000
1200
1400
1600

Figure 5.

SUPPORTING INFORMATION

Appendix S1 Species list of STI groups

Appendix S2 Species list of SSI groups

Appendix S3 Species list of MOBIL groups

Appendix S4 Species list of OVERWINT groups

Appendix S5 Species list of LARV groups

Appendix S6 Species list of VOLT groups

Appendix S7 Butterfly species recorded in this study

Appendix S8 Bivariate plots of elevation and average temperature and precipitation per quadrat for time periods 1950s, 1990s, and 2000s

Appendix S9 Descriptive statistics for climatic data for time periods 1950s, 1990s, and 2000s

Appendix S10 Trend analysis of average monthly temperature and precipitation from 1950 to 2012

Appendix S11 Richness models summary table for STI

Appendix S12 Richness models summary table for SSI

Appendix S13 Richness models summary table for MOBIL

Appendix S14 Richness models summary table for OVERWINT

Appendix S15 Richness models summary table for LARV

Appendix S16 Richness models summary table for VOLT

Appendix S1 Species list by STI (species temperature preference) functional group - species with low temperature preference (STI1), mid-low temperature preference (STI2), mid-high temperature preference (STI3), and high temperature preference (STI4).

STI1	STI2	STI3	STI4
Aglais urticae	Aporia crataegi	Arethusana arethusa	Anthocharis euphenoides
Anthocharis cardamines	Aricia agestis	Brenthis daphne	Argynnis pandora
Apatura ilia	Boloria dia	Brintesia circe	Aricia cramera
Aphantopus hyperantus	Carcharodus floccifera	Carcharodus alceae	Cacyreus marshalli
Araschnia levana	Carcharodus lavatherae	Chazara briseis	Callophrys avis
Argynnis adippe	Celastrina argiolus	Colias crocea	Carcharodus baeticus
Argynnis aglaja	Coenonympha arcania	Cupido alcetas	Charaxes jasius
Argynnis paphia	Colias alfacariensis	Cupido osiris	Coenonympha dorus
Callophrys rubi	Erynnis tages	Hipparchia alcyone	Euchloe crameri
Coenonympha pamphilus	Euphydryas aurinia	Hipparchia fagi	Gegenes nostrodamus
Cupido minimus	Glaucopsyche alexis	Iolana iolas	Glaucopsyche melanops
Cynthia cardui	Hamearis lucina	Iphiclides podalirius	Gonepteryx cleopatra
Erebia meolans	Hipparchia semele	Lasiommata megera	Hipparchia fidia
Gonepteryx rhamni	Issoria lathonia	Limenitis reducta	Hipparchia statilinus
Hesperia comma	Leptidea sinapis	Melitaea didyma	Laeosopis roboris
Inachis io	Lycaena alciphron	Melitaea parthenoides	Lampides boeticus
Lasiommata maera	Lycaena phlaeas	Melitaea phoebe	Leptotes pirithous
Limenitis camilla	Maniola jurtina	Melitaea trivia	Libythea celtis
Melitaea athalia	Melitaea cinxia	Polyommatus bellargus	Melanargia lachesis
Nymphalis antiopa	Neozephyrus quercus	Polyommatus escheri	Melitaea deione
Ochlodes venata	Nymphalis polychloros	Polyommatus ripartii	Pieris mannii
Pieris napi	Papilio machaon	Polyommatus thersites	Polyommatus fulgens
Plebeius argus	Pararge aegeria	Pontia daplidice	Pseudophilotes panoptes
Polygonia c-album	Pieris brassicae	Pyrgus armoricanus	Pyrgus malvoides
Polyommatus amandus	Pieris rapae	Pyrgus cirsii	Pyronia bathseba
Polyommatus semiargus	Polyommatus coridon	Pyronia tithonus	Pyronia cecilia
Pyrgus alveus	Polyommatus icarus	Satyrium acaciae	Satyrium esculi
Satyrium w-album	Pyrgus carthami	Satyrium ilicis	Satyrus actaea
Scolitantides orion	Thymelicus sylvestris	Satyrium spini	Thymelicus acteon
Thecla betulae	Vanessa atalanta	Spialia sertorius	Tomares ballus
Thymelicus lineola			Zerynthia rumina

Appendix S2 Species list of SSI (habitat specialization) functional group - Low index values (i.e. SSI1) indicate the species is homogeneously distributed across all habitats and exhibits more generalist habits, and high index values (i.e. SSI4) indicate the species distribution is restricted to certain habitat types, exhibiting more specialist habits.

SSI1	**SSI2**	**SSI3**	**SSI4**
Anthocharis cardamines	Aporia crataegi	Apatura ilia	Aglais urticae
Anthocharis euphenoides	Argynnis aglaja	Argynnis pandora	Aphantopus hyperantus
Aricia cramera	Argynnis paphia	Cacyreus marshalli	Araschnia levana
Brintesia circe	Aricia agestis	Charaxes jasius	Arethusana arethusa
Celastrina argiolus	Boloria dia	Chazara briseis	Argynnis adippe
Colias crocea	Callophrys rubi	Coenonympha dorus	Brenthis daphne
Cynthia cardui	Carcharodus alceae	Coenonympha pamphilus	Callophrys avis
Euchloe crameri	Coenonympha arcania	Cupido alcetas	Carcharodus baeticus
Gonepteryx cleopatra	Colias alfacariensis	Cupido minimus	Carcharodus floccifera
Gonepteryx rhamni	Erebia meolans	Glaucopsyche alexis	Carcharodus lavatherae
Hipparchia fagi	Erynnis tages	Glaucopsyche melanops	Cupido osiris
Hipparchia fidia	Euphydryas aurinia	Hipparchia alcyone	Gegenes nostrodamus
Hipparchia statilinus	Hesperia comma	Laeosopis roboris	Hamearis lucina
Inachis io	Hipparchia semele	Lycaena alciphron	Iolana iolas
Iphiclides podalirius	Issoria lathonia	Melitaea athalia	Leptidea reali
Lasiommata maera	Lampides boeticus	Melitaea deione	Libythea celtis
Lasiommata megera	Melitaea cinxia	Melitaea parthenoides	Limenitis camilla
Leptidea sinapis	Melitaea didyma	Melitaea trivia	Ochlodes venata
Leptotes pirithous	Melitaea phoebe	Polygonia c-album	Pieris mannii
Limenitis reducta	Neozephyrus quercus	Polyommatus coridon	Plebeius argus
Lycaena phlaeas	Nymphalis antiopa	Polyommatus ripartii	Polyommatus amandus
Maniola jurtina	Nymphalis polychloros	Polyommatus semiargus	Polyommatus fulgens
Melanargia lachesis	Pararge aegeria	Polyommatus thersites	Pyrgus alveus
Papilio machaon	Polyommatus bellargus	Pseudophilotes panoptes	Pyrgus armoricanus
Pieris brassicae	Polyommatus escheri	Pyronia tithonus	Pyrgus carthami
Pieris napi	Polyommatus icarus	Satyrium acaciae	Pyrgus cirsii
Pieris rapae	Pyrgus malvoides	Satyrium ilicis	Satyrium w-album
Pontia daplidice	Pyronia cecilia	Satyrium spini	Scolitantides orion
Pyronia bathseba	Satyrium esculi	Satyrus actaea	Tomares ballus
Thymelicus acteon	Thymelicus sylvestris	Spialia sertorius	Zerynthia rumina
Vanessa atalanta		Thecla betulae	
		Thymelicus lineola	

Appendix S3 Species list of MOBIL (dispersal ability) functional group - 1 - species living in metapopulations with little dispersal between populations (MOBIL1); 2 - species living in metapopulations with high dispersal between populations (MOBIL2); 3 - species living in patchy populations with non-seasonal migration (MOBIL3); 4 - species living in patchy populations with seasonal migration (MOBIL4).

MOBIL1	**MOBIL2**	**MOBIL3**	**MOBIL4**
Lasiommata maera	Hipparchia fidia	Lasiommata megera	Pieris rapae
Hesperia comma	Aricia cramera	Gonepteryx cleopatra	Vanessa atalanta
Polyommatus bellargus	Maniola jurtina	Iphiclides podalirius	Colias crocea
Coenonympha arcania	Thymelicus acteon	Celastrina argiolus	Cynthia cardui
Melitaea cinxia	Leptidea sinapis	Gonepteryx rhamni	Papilio machaon
Callophrys rubi	Pyronia bathseba	Euchloe crameri	Pieris brassicae
Erynnis tages	Anthocharis euphenoides	Anthocharis cardamines	Pontia daplidice
Polyommatus escheri	Limenitis reducta	Lycaena phlaeas	Leptotes pirithous
Erebia meolans	Melanargia lachesis	Inachis io	Lampides boeticus
Satyrium acaciae	Hipparchia fagi	Pieris napi	Gegenes nostrodamus
Cupido minimus	Hipparchia statilinus	Pararge aegeria	
Polyommatus thersites	Brintesia circe	Nymphalis antiopa	
Pseudophilotes panoptes	Melitaea phoebe	Polyommatus icarus	
Polyommatus coridon	Pyronia cecilia	Nymphalis polychloros	
Glaucopsyche alexis	Colias alfacariensis	Issoria lathonia	
Spialia sertorius	Argynnis aglaja	Carcharodus alceae	
Melitaea trivia	Satyrium esculi	Hipparchia semele	
Glaucopsyche melanops	Argynnis paphia	Polygonia c-album	
Satyrium spini	Aricia agestis	Argynnis pandora	
Melitaea deione	Boloria dia	Charaxes jasius	
Melitaea athalia	Thymelicus sylvestris	Cacyreus marshalli	
Hipparchia alcyone	Neozephyrus quercus	Libythea celtis	
Lycaena alciphron	Melitaea didyma	Aglais urticae	
Polyommatus ripartii	Pyrgus malvoides		
Chazara briseis	Euphydryas aurinia		
Melitaea parthenoides	Aporia crataegi		
Satyrium ilicis	Coenonympha pamphilus		
Polyommatus semiargus	Pyronia tithonus		
Laeosopis roboris	Coenonympha dorus		
Thymelicus lineola	Cupido alcetas		
Carcharodus lavatherae	Satyrus actaea		
Cupido osiris	Apatura ilia		
Aphantopus hyperantus	Thecla betulae		
Plebeius argus	Argynnis adippe		
Polyommatus fulgens	Zerynthia rumina		
Pyrgus cirsii	Pieris mannii		
Pyrgus alveus	Limenitis camilla		
Tomares ballus	Pyrgus armoricanus		
Callophrys avis	Ochlodes venata		
Hamearis lucina	Leptidea reali		
Scolitantides orion	Araschnia levana		
Brenthis daphne	Iolana iolas		
Satyrium w-album	Arethusana arethusa		
Carcharodus baeticus			
Carcharodus floccifera			
Polyommatus amandus			
Pyrgus carthami			

Appendix S4 Species list of OVERWINT (overwintering stage) functional group - egg (OVERWINT1), larva (OVERWINT2), pupa (OVERWINT3) or adult (OVERWINT4).

OVERWINT1	**OVERWINT2**	**OVERWINT2 cont…**	**OVERWINT3**
Satyrium esculi	Lasiommata megera	Polyommatus thersites	Pieris rapae
Neozephyrus quercus	Hipparchia fidia	Pyronia tithonus	Papilio machaon
Satyrium acaciae	Aricia cramera	Spialia sertorius	Iphiclides podalirius
Polyommatus coridon	Maniola jurtina	Melitaea trivia	Celastrina argiolus
Satyrium spini	Thymelicus acteon	Charaxes jasius	Leptidea sinapis
Satyrium ilicis	Pyronia bathseba	Melitaea deione	Anthocharis euphenoides
Laeosopis roboris	Limenitis reducta	Coenonympha dorus	Euchloe crameri
Thecla betulae	Lycaena phlaeas	Melitaea athalia	Pieris brassicae
Plebeius argus	Melanargia lachesis	Hipparchia alcyone	Pontia daplidice
Brenthis daphne	Hipparchia fagi	Lycaena alciphron	Anthocharis cardamines
Satyrium w-album	Hipparchia statilinus	Polyommatus ripartii	Leptotes pirithous
	Brintesia circe	Chazara briseis	Pieris napi
	Melitaea phoebe	Melitaea parthenoides	Lasiommata maera
	Pyronia cecilia	Cupido alcetas	Lampides boeticus
	Colias alfacariensis	Polyommatus semiargus	Callophrys rubi
	Polyommatus icarus	Satyrus actaea	Pyrgus malvoides
	Argynnis aglaja	Apatura ilia	Pseudophilotes panoptes
	Argynnis paphia	Thymelicus lineola	Glaucopsyche alexis
	Aricia agestis	Argynnis adippe	Glaucopsyche melanops
	Hesperia comma	Carcharodus lavatherae	Zerynthia rumina
	Polyommatus bellargus	Gegenes nostrodamus	Pieris mannii
	Coenonympha arcania	Cupido osiris	Tomares ballus
	Boloria dia	Aphantopus hyperantus	Callophrys avis
	Melitaea cinxia	Limenitis camilla	Leptidea reali
	Thymelicus sylvestris	Pyrgus armoricanus	Hamearis lucina
	Carcharodus alceae	Polyommatus fulgens	Araschnia levana
	Melitaea didyma	Pyrgus cirsii	Iolana iolas
	Euphydryas aurinia	Pyrgus alveus	Scolitantides orion
	Hipparchia semele	Ochlodes venata	Gonepteryx cleopatra
	Aporia crataegi	Arethusana arethusa	Gonepteryx rhamni
	Erynnis tages	Carcharodus baeticus	Inachis io
	Polyommatus escheri	Carcharodus floccifera	Nymphalis antiopa
	Erebia meolans	Polyommatus amandus	Nymphalis polychloros
	Cupido minimus	Pyrgus carthami	Polygonia c-album
	Coenonympha pamphilus		Libythea celtis
	Argynnis pandora		Aglais urticae

Appendix S5 Species list of LARV (trophic specialization of larvae) functional group - monophagous (LARV1) - butterflies feeding on plants of a single genus; oligophagous (LARV2) - butterflies feeding on plants of various genera belonging to the same family; and polyphagous (LARV3) - butterflies feeding on a diversity of plants belonging to various families.

LARV1	**LARV1 cont…**	**LARV2**	**LARV2 cont…**	**LARV3**
Gonepteryx cleopatra	Pyrgus cirsii	Lasiommata megera	Thymelicus lineola	Pieris rapae
Anthocharis euphenoides	Aglais urticae	Vanessa atalanta	Carcharodus lavatherae	Aricia cramera
Gonepteryx rhamni	Hamearis lucina	Colias crocea	Gegenes nostrodamus	Cynthia cardui
Limenitis reducta	Araschnia levana	Hipparchia fidia	Aphantopus hyperantus	Papilio machaon
Lycaena phlaeas	Iolana iolas	Maniola jurtina	Pieris mannii	Celastrina argiolus
Inachis io	Scolitantides orion	Thymelicus acteon	Pyrgus armoricanus	Pieris brassicae
Pyronia cecilia	Brenthis daphne	Iphiclides podalirius	Pyrgus alveus	Pontia daplidice
Colias alfacariensis	Satyrium w-album	Leptidea sinapis	Ochlodes venata	Leptotes pirithous
Issoria lathonia	Carcharodus floccifera	Pyronia bathseba	Tomares ballus	Hipparchia statilinus
Argynnis aglaja	Pyrgus carthami	Euchloe crameri	Leptidea reali	Nymphalis polychloros
Satyrium esculi		Anthocharis cardamines	Arethusana arethusa	Lampides boeticus
Argynnis paphia		Pieris napi	Carcharodus baeticus	Callophrys rubi
Aricia agestis		Melanargia lachesis	Polyommatus amandus	Euphydryas aurinia
Hesperia comma		Lasiommata maera		Polygonia c-album
Boloria dia		Hipparchia fagi		Coenonympha dorus
Neozephyrus quercus		Brintesia circe		Polyommatus semiargus
Polyommatus escheri		Melitaea phoebe		Plebeius argus
Satyrium acaciae		Pararge aegeria		Callophrys avis
Cupido minimus		Nymphalis antiopa		
Argynnis pandora		Polyommatus icarus		
Polyommatus thersites		Polyommatus bellargus		
Pseudophilotes panoptes		Coenonympha arcania		
Polyommatus coridon		Melitaea cinxia		
Spialia sertorius		Thymelicus sylvestris		
Melitaea trivia		Carcharodus alceae		
Charaxes jasius		Melitaea didyma		
Satyrium spini		Pyrgus malvoides		
Lycaena alciphron		Hipparchia semele		
Polyommatus ripartii		Aporia crataegi		
Melitaea parthenoides		Erynnis tages		
Satyrium ilicis		Erebia meolans		
Cupido alcetas		Coenonympha pamphilus		
Laeosopis roboris		Pyronia tithonus		
Cacyreus marshalli		Glaucopsyche alexis		
Thecla betulae		Glaucopsyche melanops		
Argynnis adippe		Melitaea deione		
Cupido osiris		Melitaea athalia		
Zerynthia rumina		Hipparchia alcyone		
Limenitis camilla		Chazara briseis		
Libythea celtis		Satyrus actaea		
Polyommatus fulgens		Apatura ilia		

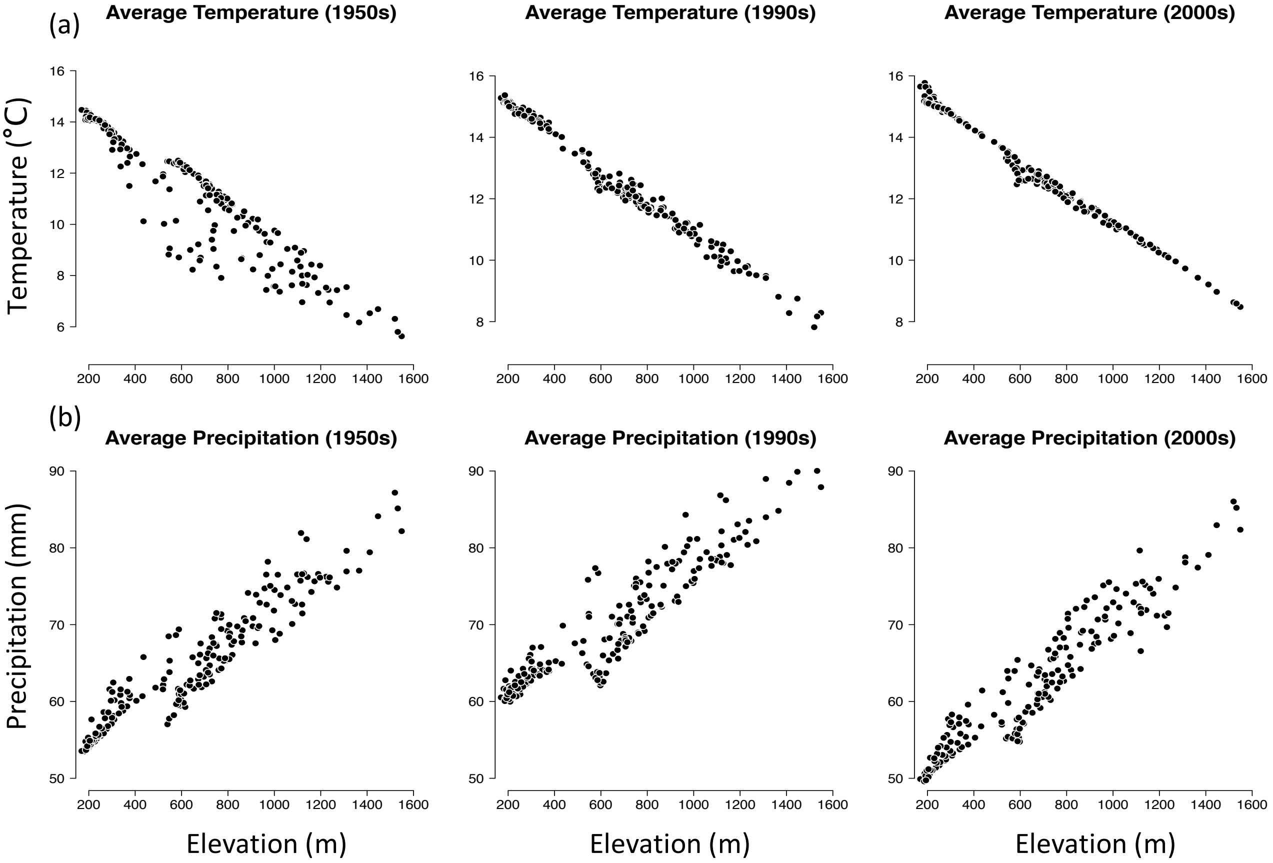
Appendix S6 Species list of VOLT (number of generations a species has in one year) functional group - univoltine (VOLT1), bivoltine (VOLT2), or multivoltine (VOLT3).

VOLT1	**VOLT1 cont…**	**VOLT2**	**VOLT3**
Hipparchia fidia	Satyrium spini	Gonepteryx cleopatra	Melitaea cinxia
Maniola jurtina	Coenonympha dorus	Euchloe crameri	Plebeius argus
Thymelicus acteon	Melitaea athalia	Lasiommata maera	Pieris rapae
Pyronia bathseba	Hipparchia alcyone	Melitaea phoebe	Lasiommata megera
Anthocharis euphenoides	Lycaena alciphron	Aricia agestis	Vanessa atalanta
Gonepteryx rhamni	Polyommatus ripartii	Melitaea didyma	Colias crocea
Anthocharis cardamines	Chazara briseis	Pyrgus malvoides	Aricia cramera
Melanargia lachesis	Melitaea parthenoides	Erynnis tages	Cynthia cardui
Hipparchia fagi	Satyrium ilicis	Spialia sertorius	Papilio machaon
Hipparchia statilinus	Polyommatus semiargus	Melitaea trivia	Iphiclides podalirius
Brintesia circe	Laeosopis roboris	Charaxes jasius	Celastrina argiolus
Nymphalis antiopa	Satyrus actaea	Apatura ilia	Leptidea sinapis
Pyronia cecilia	Thymelicus lineola	Gegenes nostrodamus	Limenitis reducta
Nymphalis polychloros	Thecla betulae	Limenitis camilla	Pieris brassicae
Argynnis aglaja	Argynnis adippe	Pyrgus armoricanus	Pontia daplidice
Satyrium esculi	Carcharodus lavatherae	Ochlodes venata	Lycaena phlaeas
Argynnis paphia	Cupido osiris	Leptidea reali	Inachis io
Hesperia comma	Aphantopus hyperantus		Leptotes pirithous
Coenonympha arcania	Zerynthia rumina		Pieris napi
Thymelicus sylvestris	Libythea celtis		Pararge aegeria
Callophrys rubi	Polyommatus fulgens		Colias alfacariensis
Neozephyrus quercus	Pyrgus cirsii		Polyommatus icarus
Euphydryas aurinia	Pyrgus alveus		Issoria lathonia
Hipparchia semele	Tomares ballus		Polyommatus bellargus
Aporia crataegi	Callophrys avis		Boloria dia
Polyommatus escheri	Hamearis lucina		Lampides boeticus
Erebia meolans	Iolana iolas		Carcharodus alceae
Satyrium acaciae	Scolitantides orion		Polygonia c-album
Cupido minimus	Brenthis daphne		Coenonympha pamphilus
Argynnis pandora	Arethusana arethusa		Melitaea deione
Polyommatus thersites	Satyrium w-album		Cupido alcetas
Pseudophilotes panoptes	Carcharodus floccifera		Cacyreus marshalli
Polyommatus coridon	Polyommatus amandus		Pieris mannii
Pyronia tithonus	Pyrgus carthami		Aglais urticae
Glaucopsyche alexis			Araschnia levana
Glaucopsyche melanops			Carcharodus baeticus

Appendix S7 List of the 123 observed species in study region. The value indicates the number of quadrats (n=186) the species were recorded in.

Aglais urticae	17
Anthocharis cardamines	132
Anthocharis euphenoides	25
Apatura ilia	38
Aphantopus hyperantus	10
Aporia crataegi	51
Araschnia levana	5
Arethusana arethusa	23
Argynnis adippe	52
Argynnis aglaja	32
Argynnis pandora	9
Argynnis paphia	155
Aricia agestis	1
Aricia cramera	4
Boloria dia	95
Brenthis daphne	43
Brintesia circe	130
Cacyreus marshalli	33
Callophrys avis	4
Callophrys rubi	130
Carcharodus alceae	118
Carcharodus baeticus	4
Carcharodus floccifera	21
Carcharodus lavatherae	4
Celastrina argiolus	138
Charaxes jasius	43
Chazara briseis	14
Coenonympha arcania	107
Coenonympha dorus	1
Coenonympha pamphilus	114
Colias alfacariensis	40
Colias crocea	169
Cupido alcetas	8
Cupido minimus	10
Cupido osiris	5
Cynthia cardui	171
Erebia meolans	14
Erynnis tages	13
Euchloe crameri	55
Euphydryas aurinia	22
Gegenes nostrodamus	5
Glaucopsyche alexis	41
Glaucopsyche melanops	41
Gonepteryx cleopatra	136
Gonepteryx rhamni	144
Hamearis lucina	12
Hesperia comma	46
Hipparchia alcyone	40
Hipparchia fagi	28
Hipparchia fidia	27
Hipparchia semele	96
Hipparchia statilinus	109
Inachis io	122
Iolana iolas	1
Iphiclides podalirius	145
Issoria lathonia	139
Laeosopis roboris	9
Lampides boeticus	116
Lasiommata maera	37
Lasiommata megera	179
Leptidea reali	2
Leptidea sinapis	16
Leptotes pirithous	78
Libythea celtis	97
Limenitis camilla	70
Limenitis reducta	103
Lycaena alciphron	36
Lycaena phlaeas	163
Maniola jurtina	177
Melanargia lachesis	178
Melitaea athalia	11
Melitaea cinxia	47
Melitaea deione	61
Melitaea didyma	73
Melitaea parthenoides	14
Melitaea phoebe	71
Melitaea trivia	30
Neozephyrus quercus	136
Nymphalis antiopa	56
Nymphalis polychloros	63
Ochlodes venata	114
Papilio machaon	115
Pararge aegeria	175
Pieris brassicae	141
Pieris mannii	25
Pieris napi	111
Pieris rapae	173
Plebeius argus	2
Polygonia c-album	129
Polyommatus amandus	1
Polyommatus bellargus	38
Polyommatus coridon	84
Polyommatus escheri	45
Polyommatus fulgens	9
Polyommatus icarus	173
Polyommatus ripartii	14
Polyommatus semiargus	14
Polyommatus thersites	29
Pontia daplidice	86
Pseudophilotes panoptes	101
Pyrgus alveus	8
Pyrgus armoricanus	33
Pyrgus carthami	10
Pyrgus cirsii	37
Pyrgus malvoides	105
Pyronia bathseba	121
Pyronia cecilia	67
Pyronia tithonus	134
Satyrium acaciae	49
Satyrium esculi	173
Satyrium ilicis	58
Satyrium spini	9
Satyrium w-album	20
Satyrus actaea	15
Scolitantides orion	13
Spialia sertorius	71
Thecla betulae	7
Thymelicus acteon	112
Thymelicus lineola	30
Thymelicus sylvestris	94
Tomares ballus	2
Vanessa atalanta	130
Zerynthia rumina	6

Appendix S8 Bivariate plots of elevation and average monthly temperature and precipitation per quadrat for time periods 1950s, 1990s, and 2000s.

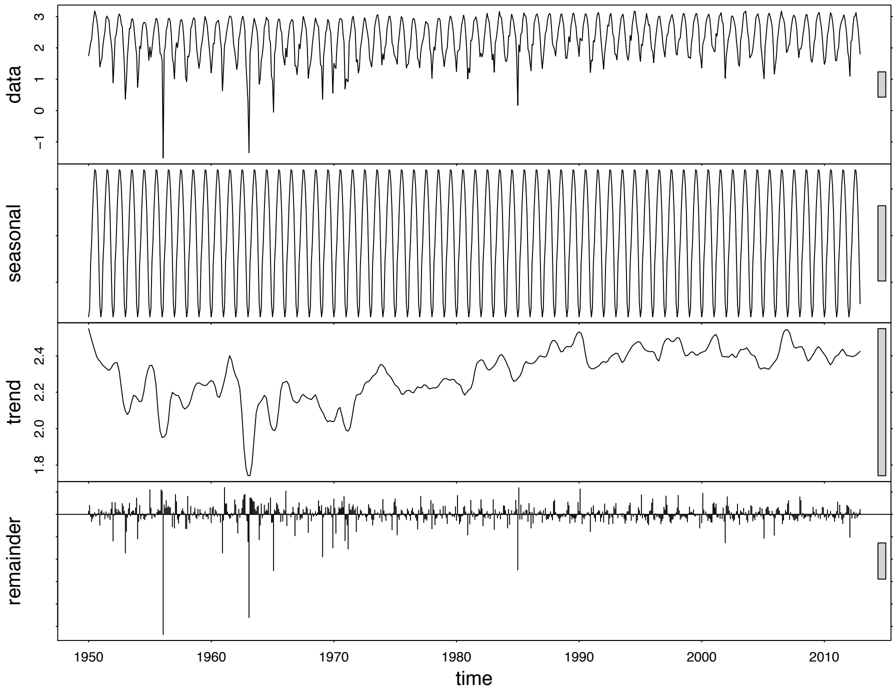


Appendix S9 Descriptive statistics for climatic data for time periods 1950s, 1990s and 2000s. Statistics are based on average monthly values of 186 km^2 transect.

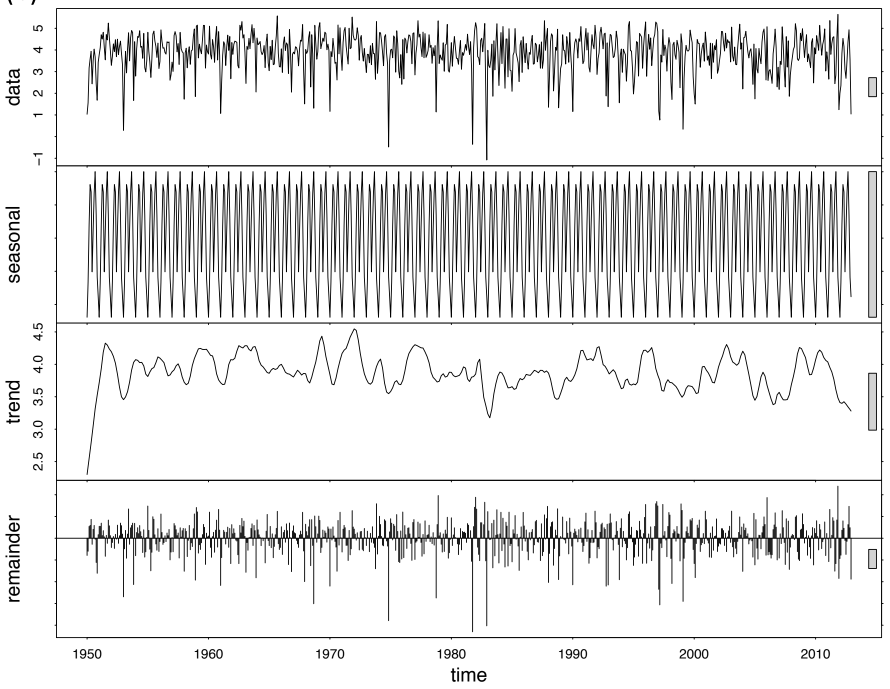
Parameter	Statistic	1950s	1990s	2000s
Temperature (°C)	Minimum	5.6	7.8	8.5
	Maximum	14.5	15.4	15.8
	Mean	11.0	12.5	12.8
	Std. Dev.	2.4	1.8	1.7
Precipitation (mm)	Minimum	53.5	60.0	49.6
	Maximum	87.2	93.7	86.0
	Mean	65.2	70.5	62.5
	Std. Dev.	7.7	7.8	8.6

Appendix S10 Times series analysis of climatic trends from 1950 to 2012 in the 186 km^2 transect - (a) average monthly temperature - times series analyses indicate that the residual trend (third panel) is significant (estimate= 0.045±0.003; t-value=14.94; p<2E-16); (b) average monthly precipitation – times series analyses indicate that the residual trend (third panel) is not significant (estimate = -0.077±0.089; t-value= -0.867; p=0.386)

(a)



(b)



Appendix S11 Richness models summary table for STI (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
			STI1		
Intercept		0.23	7.39	***	0.48
Average Precipitation	0.01	3.44E-03	2.90	**	
Artificial Unproductive	-1.16	0.20	-5.73	***	
Natural Unproductive	2.02	0.76	2.68	**	
			STI2		
Intercept		0.03	97.27	***	0.43
Artificial Unproductive	-1.21	0.14	-8.98	***	
Meadows and Pastures	1.47	0.52	2.84	**	
			STI3		
Intercept		1.57	8.86	***	0.56
Average Precipitation	-0.16	0.02	-6.93	***	
Average Temperature	-0.79	0.12	-6.60	***	
Artificial Unproductive	-1.01	0.22	-4.69	***	
Natural Unproductive	2.26	0.83	2.72	**	
Ave. Temp: Ave. Precip	0.01	1.95E-03	5.34	***	
			STI4		
Intercept		0.24	15.74	***	0.37
Average Precipitation	-0.04	4.74E-03	-7.59	***	
Natural Unproductive	3.09	0.89	3.48	***	
Dense Forest	1.06	0.12	8.85	***	
Thicket	1.26	0.25	5.01	***	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'

Appendix S12 Richness models summary table for SSI (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
SSI1					
Intercept		0.17	12.29	***	0.28
Average Temperature	0.07	0.01	5.60	***	
Artificial Unproductive	-0.92	0.13	-7.29	***	
Natural Unproductive	1.28	0.61	2.11	*	
SSI2					
Intercept		1.27	5.67	***	0.61
Average Precipitation	-0.06	0.02	-3.33	***	
Average Temperature	-0.32	0.09	-3.40	***	
Artificial Unproductive	-1.29	0.19	-6.82	***	
Meadows and Pastures	2.05	0.60	3.44	***	
Ave. Temp: Ave. Precip	4.03E-03	1.51E-03	2.68	**	
SSI3					
Intercept		1.89	7.55	***	0.68
Average Precipitation	-0.18	0.03	-6.66	***	
Average Temperature	-1.01	0.14	-6.99	***	
Artificial Unproductive	-1.18	0.29	-4.12	***	
Natural Unproductive	3.40	0.93	3.66	***	
Ave. Temp: Ave. Precip	0.01	2.30E-03	6.44	***	
SSI4					
Intercept		2.53	4.15	***	0.37
Average Precipitation	-0.12	0.04	-3.48	***	
Average Temperature	-0.71	0.19	-3.70	***	
Artificial Unproductive	-1.17	0.39	-2.99	**	
Natural Unproductive	3.42	1.30	2.63	**	
Ave. Temp: Ave. Precip	0.01	3.05E-03	3.10	**	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'

Appendix S13 Richness models summary table for MOBIL (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
MOBIL1					
Intercept		1.94	12.27	***	0.94
Average Precipitation	-0.28	0.03	-10.13	***	
Average Temperature	-1.61	0.15	-10.62	***	
Artificial Unproductive	-2.13	0.34	-6.30	***	
Natural Unproductive	4.00	0.82	4.89	***	
Ave. Temp: Ave. Precip	0.02	2.36E-03	8.65	***	
MOBIL2					
Intercept		1.22	6.46	***	0.59
Average Precipitation	-0.07	0.02	-4.37	***	
Average Temperature	-0.39	0.09	-4.28	***	
Artificial Unproductive	-1.14	0.18	-6.47	***	
Natural Unproductive	1.98	0.68	2.90	**	
Ave. Temp: Ave. Precip	0.01	1.46E-03	3.90	***	
MOBIL3					
Intercept		0.31	2.69	**	0.26
Average Temperature	0.07	0.02	3.90	***	
Dense Forest	0.96	0.15	6.56	***	
Thicket	1.12	0.25	4.50	***	
Meadows and Pastures	2.52	0.73	3.45	***	
Crops	0.70	0.21	3.41	***	
MOBIL4					
Intercept		0.22	4.05	***	0.10
Average Temperature	0.07	0.02	4.30	***	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

Appendix S14 Richness models summary table for OVERWINT (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
OVERWINT1					
Intercept		5.88	7.38	***	0.42
Average Precipitation	-0.55	0.08	-6.95	***	
Average Temperature	-3.13	0.40	-7.88	***	
Natural Unproductive	13.70	3.99	3.43	***	
Ave. Temp: Ave. Precip	0.04	0.01	6.66	***	
OVERWINT2					
Intercept		1.03	10.31	***	0.82
Average Precipitation	-0.10	0.01	-6.89	***	
Average Temperature	-0.56	0.08	-7.24	***	
Artificial Unproductive	-1.01	0.15	-6.63	***	
Natural Unproductive	2.10	0.57	3.70	***	
Ave. Temp: Ave. Precip	0.01	1.24E-03	5.90	***	
OVERWINT3					
Intercept		0.23	16.01	***	0.28
Average Precipitation	-0.02	3.48E-03	-5.57	***	
Artificial Unproductive	-1.31	0.18	-7.23	***	
OVERWINT4					
Intercept		1.77	-2.44	*	0.23
Average Precipitation	0.04	0.01	2.85	**	
Average Temperature	0.31	0.07	4.15	***	
Artificial Unproductive	-2.29	0.43	-5.32	***	
Dense Forest	-0.85	0.25	-3.39	***	
Crops	-1.04	0.37	-2.81	**	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

Appendix S15 Richness models summary table for LARV (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
LARV1					
Intercept		1.24	6.47	***	0.70
Average Precipitation	-0.07	0.02	-4.33	***	
Average Temperature	-0.40	0.09	-4.38	***	
Artificial Unproductive	-1.30	0.19	-6.93	***	
Natural Unproductive	2.85	0.67	4.23	***	
Ave. Temp: Ave. Precip	0.01	1.48E-03	3.86	***	
LARV2					
Intercept		1.05	6.90	***	0.56
Average Precipitation	-0.06	0.01	-4.31	***	
Average Temperature	-0.33	0.08	-4.32	***	
Artificial Unproductive	-0.90	0.15	-6.19	***	
Meadows and Pastures	1.45	0.51	2.85	**	
Ave. Temp: Ave. Precip	0.01	1.25E-03	4.10	***	
LARV3					
Intercept		0.23	5.13	***	0.16
Average Temperature	0.08	0.02	4.21	***	
Artificial Unproductive	-1.02	0.19	-5.26	***	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’

Appendix S16 Richness models summary table for VOLT (Generalized Linear Model)

Variable	β	SE	z	p	Pseudo-R^2
		VOLT1			
Intercept		1.057	7.973	***	0.87
Average Precipitation	-0.07	0.01	-5.11	***	
Average Temperature	-0.42	0.08	-5.36	***	
Artificial Unproductive	-1.45	0.17	-8.72	***	
Natural Unproductive	2.37	0.58	4.10	***	
Meadows and Pastures	1.57	0.50	3.15	**	
Ave. Temp: Ave. Precip	0.01	1.30E-03	4.56	***	
		VOLT2			
Intercept		0.40	7.23	***	0.29
Average Precipitation	-0.02	0.01	-2.90	**	
Artificial Unproductive	-1.74	0.29	-6.08	***	
Crops	-0.74	0.25	-2.99	**	
		VOLT3			
Intercept		29.64	3.75	***	0.35
Average Precipitation	-1.55	0.43	-3.63	***	
Average Temperature	-8.91	2.39	-3.72	***	
Ave. Temp: Ave. Precip	0.12	0.03	3.53	***	

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’