Research

Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change

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Although it is well established that butterfly richness is affected by climate and human factors (e.g. habitat disturbance and degradation) at different spatial scales, the drivers behind these changes vary greatly according to the geographical region and the ecology of the species concerned. It is essential that this variation be understood if trends in diversity are to be predicted with any degree of confidence under a scenario of global change. Here we examine patterns of butterfly species richness among groups differing in degree of habitat specialization, diet breadth and mobility in the north-west Mediterranean Basin, a European hotspot for this taxon. We analyze a large number of butterfly communities and take into consideration the main potential drivers, that include climatic, geographic and resource variables, landscape structure and human environmental impact at different spatial scales. Our study shows that both climatic and anthropogenic factors play an important role in determining butterfly species richness in the north-west Mediterranean Basin, but that their relative impact differs between specialist and generalist groups. At lower altitudes, water availability, a product of the interplay between temperature and rainfall, and negative effects of temperature appear as the most determinant factors. Maximum diversity was observed at mid-altitudes, which reveals the importance from a conservation point of view of Mediterranean mountain ranges. The results suggest serious population declines in specialist species restricted to mountain areas as a result of climate warming in combination with habitat loss caused by the abandonment of grazing and mowing. They also suggest negative trends for generalist species due to an increase in aridity in combination with an increase in intensification of human land use in lowland areas. Such synergies are expected to lead to rapid declines in Mediterranean butterfly populations in the coming years, thereby posing a severe threat for the conservation of European biodiversity.

Previous studies have explored patterns in butterfly species richness in various regions and at different spatial scales. Climatic factors, whether acting directly on insects or indirectly on their trophic resources, have been found to play a key role in most cases, especially where analyses have been conducted at regional or continental scales (Turner et al. 1987, Kerr et al. 1998, Hawkins and Porter 2003a, b, Menéndez et al. 2007). Although normally somewhat less evident, habitat diversity (Kerr et al. 2001) and human influences (e.g. habitat disturbance and degradation; Konvicka et al. 2006, White and Kerr 2006) have also been recognised as driving forces in butterfly diversity at these large scales. Finally, at smaller and local scales, it has been seen that landscape structure, habitat management and resource availability (both nectar for adults and hostplants for larvae) become increasingly important (Weibull et al. 2000, Krauss et al. 2003, Kuussaari et al. 2007).

However, other sources of variation complicate richness patterns considerably. For instance, it has been shown that drivers of butterfly species richness vary according to geographical area and the ecology of the species under consideration. Thus, in the Palaearctic there is a clear latitudinal gradient in the importance of climatic factors: temperature and sunshine hours act as the main limiting factors for butterfly richness in more northerly regions (Turner et al. 1987), while water availability is the main limiting factor in hotter areas (Hawkins and Porter 2003b, Stefanescu et al. 2004). Moreover, a recent analysis of British butterflies showed that climate variables had greater effects on habitat generalists than on habitat specialists, which, in turn, were more affected by hostplant species richness and habitat diversity (Menéndez et al. 2007). These particular relationships have important implications for conservation biology, as they can be used to predict with

greater confidence trends in butterfly diversity under a scenario of global change (Warren et al. 2001).

Butterflies have been identified as a useful indicator group for many other terrestrial insects for which there is only a very limited amount of distributional data (Thomas 2005). In addition, they respond quickly to climate change (Parmesan et al. 1999, Stefanescu et al. 2003, Wilson et al. 2005, González-Megías et al. 2008) and seem to be more sensitive to habitat transformation than other better-known indicator groups such as birds (Thomas et al. 2004). Therefore, a better understanding of patterns in butterfly diversity and the drivers operating upon them may well help predict trends in overall diversity in a range of ecosystems and regions affected by climate warming and habitat degradation. Although the strongest changes in the patterns of species richness and range distributions are predicted at the species' borders (see Pöyry et al. 2009, for an empirical example), few studies have focused on the processes occurring at the southern margins (but see Wilson et al. 2005, 2007, for an exception). This is much unfortunate in the case of European butterflies, taking into account that some areas of maximum diversity do generally occur at these southern margins.

In this paper we examine patterns of butterfly species richness in north-east Spain, an area in the Mediterranean Basin with one of the greatest diversities of butterflies in Europe (Van Swaay and Warren 2003). To model butterfly diversity, we use very precise data regarding the composition of a large number of butterfly communities and take into consideration information on the main potential drivers (including climatic, geographic and resource variables), landscape structure and human environmental impacts at different spatial scales. In contrast to previous work using the same kind of data (Stefanescu et al. 2004), here we distinguish between patterns for different ecological groups with increasing specialization and mobility in order to assess how these ecological traits interact with the drivers of butterfly diversity. Finally, we use our results to infer the changes in the butterfly communities of this highly diverse region that are most likely to occur in response to global change.

Material and methods

Butterfly data and species richness

Data were collected between 1994 and 2007 at 82 sites in Catalonia, north-east Spain, and two sites in Andorra, the whole region comprising 32 398 km^2 and lying between the Pyrenees, the Ebro depression and the Mediterranean sea (Fig. 1). Sampling sites were located at 0–1930 m a.s.l. (mean altitude = 412; SD = 430.1 m). Butterflies are regularly monitored in this region as part of the Catalan Butterfly Monitoring Scheme or CBMS (<www.catalanbms.org/>) and the Andorran Butterfly Monitoring Scheme or BMSAnd (<www.bmsand.ad/>). At each site, counts along fixed routes (mean length = 1785 m; SD = 821 m; range:
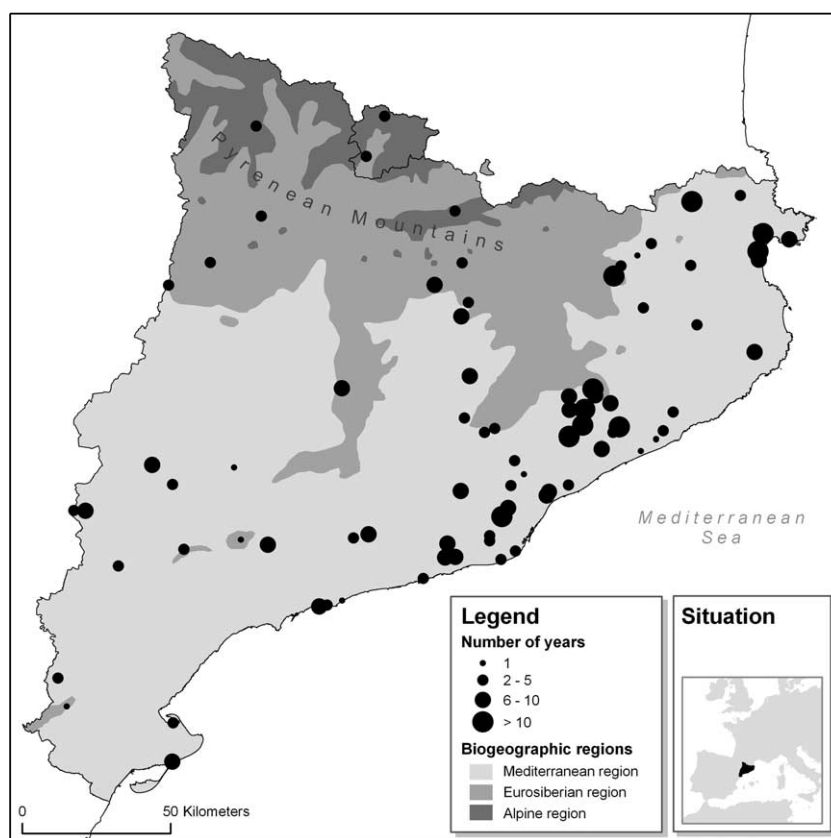

Figure 1. Map of the study region showing the location of the 84 butterfly transects. The size of the circles is proportional to the number of recording years of each sampling site. Also shown are the generally accepted boundaries of the biogeographical regions present in Catalonia.

565–4909 m) are made on a weekly basis starting on 1 March and ending on 26 September, a total of 30 recording weeks per year. All butterflies within 2.5 m on each side and 5 m in front of the recorder are counted, as per the standard procedure described by Pollard and Yates (1993). A total of 169 butterfly species were recorded between 1994 and 2007 and all are considered in this study (see the complete list in Supplementary material Table S1).

For each site we calculated the yearly mean number of species recorded as a measure of species richness. This simple measure has been criticised because the sample sizes are different at each site (Gotelli and Colwell 2001). However, the use of rarefaction for a standardized sample size of 1000 butterflies in a subset of 68 sites indicated that the expected number of species in the rarefied samples was very highly correlated with the yearly mean number of species ($r = 0.95$, $p < 0.001$). Given that the effect of different sampling efforts was so minimal, we decided to use the yearly mean number of species as a more straightforward estimation of butterfly diversity.

Ecological groups: the degree of resource specialization and mobility

Each butterfly species was classified as belonging to a different group on the basis of its resource specialization and dispersal ability (see Supplementary material Table S1, for details for each species).

The degree of resource specialization was defined at two levels: 1) the trophic specialization of larvae, distinguishing between monophagous (butterflies feeding on plants of a single genus), oligophagous (butterflies feeding on plants of various genera but belonging to the same family), and polyphagous species (butterflies feeding on a diversity of plants belonging to various families); and 2) habitat specialization, measured by means of the "species specialization index" (SSI) as per Julliard et al. (2006). Data from the CBMS were first used to calculate butterfly species densities across 17 different habitat types (see details in Stefanescu and Traveset 2009). An index of the degree of habitat specialization (SSI) was then measured for each species as the coefficient of variation of the average densities within these 17 habitat classes. SSI is closely related to the

number of occupied habitat classes, with low values for species homogeneously distributed across all habitats, and the opposite for species restricted to certain habitat types. Quartiles for the whole set of SSI values were subsequently used to classify butterfly species into four classes of habitat specialization (SS1 to SS4, from maximal to minimal habitat specialization).

We also distinguished between classes of dispersal ability, as this life history trait has been shown to highly influence butterfly distribution in changing landscapes (Thomas et al. 1998, Warren et al. 2001). Each butterfly species was assigned an index of increasing mobility ranging from 1 to 4, according to the following criteria: 1 – species living in metapopulations with very little dispersal between populations; 2 – species living in metapopulations with a lot of dispersal between populations; 3 – species living in patchy populations with non-seasonal migration; 4 – species living in patchy populations with seasonal migration. Data on dispersal ability and population structure were extracted from Pollard and Eversham (1995), Dennis and Shreeve (1996), adapted from personal observations in the study region.

Correspondence analyses were used to compare the association between groups in all three ecological classifications (i.e. the three categories of trophic specialization vs the four categories of habitat specialization vs the four classes of dispersal ability; Fig. 2). The analyses showed a strong correspondence between dispersal class 1, monophagous species and the two classes of maximum habitat specialization, SSI 1 and SSI 2. On the other hand, classes of decreasing resource specialization and increasing dispersal ability were grouped together. Following these results, we distinguished between "specialists" (monophagous species, and species belonging to habitat specialization classes SSI 1 and SSI 2, and dispersal class 1) and "generalists" (oligophagous and polyphagous species, and species belonging to habitat specialization classes SSI 3 and SSI 4, and dispersal classes 2, 3 and 4). This classification is comparable to the one used by Warren et al. (2001) and Menéndez et al. (2007), and highlights the strong correlation existing between a number of ecological traits in butterflies (Shreeve et al. 2001).
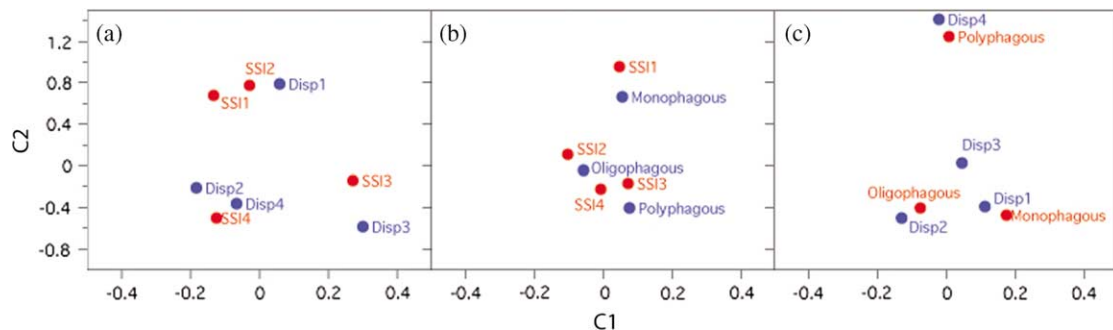

Figure 2. Correspondence analyses comparing the association between ecological groups differing in their degree of resource and habitat specialization and dispersal ability. Three paired correspondence analyses are shown, derived from contingency tables of the functional group variables. Groups of increasing larval trophic specialization: polyphagous, oligophagous, monophagous; groups of decreasing habitat specialization: SSI 1, SSI 2, SSI 3 and SSI 4; groups of increasing dispersal ability: Disp 1, Disp 2, Disp 3 and Disp 4. (a) Associations between dispersal ability and habitat specialization categories; (b) associations between habitat and trophic specialization categories; and (c) associations between dispersal ability and trophic specialization categories.

Predictor variables

Butterfly species richness was examined in relation to ten independent environmental variables, which can be classified into the following four groups.

a) Climatic variables

For each sampling station, we calculated mean annual temperature, mean annual rainfall and an aridity index based on data derived from the Digital Climatic Atlas of Catalonia (Ninyerola et al. 2000). Initially, we also considered mean maximum July temperatures and mean minimum January temperatures, but these variables were highly correlated with mean annual temperatures ($r^2 > 0.6$ and 0.7, respectively) and were eventually removed from the analyses to avoid colinearity problems during model selection. Aridity was calculated by means of a modified Gaussen index of aridity (precipitation/2 × temperature), as in Peñuelas et al. (2007a), and accounted for the interaction between the temperature and precipitation variables.

b) Geographic variables

For each transect we calculated: 1) mean latitude (UTM Y coordinate), and 2) mean longitude (UTM X coordinate). The digital cartography for the CBMS network was generated by digitalising transects onto topographical 1:5000 scale maps and was then used to calculate the mean X and Y UTM coordinates. Latitude and longitude were introduced as coordinate variables in the spatial models (following Dormann et al. 2007).

c) Resource variables

We distinguished two resource types that have an obvious influence on the presence of butterfly species at a given site: larval trophic resources and habitat resources.

Trophic resources. It has been argued – and in some cases demonstrated (Siemann et al. 1998) – that herbivore diversity should mirror plant diversity. However, the exact number of plant species present for each butterfly transect was not available and so the number of plant communities (as defined in the CORINE Biotope's Manual) was used as a surrogate for plant species richness.

Plant composition has a strong influence on both butterfly species richness and communities. While some plant species are used as larval resources by a large number of butterfly species, many others are not used at all. In particular, previous work carried out in the study area (Stefanescu et al. 2004) has suggested that butterfly diversity is higher on calcareous than on acidic soils, mainly as a result of the occurrence of a few key, strongly calcicolous hostplants (e.g. the Leguminoseae *Anthyllis vulneraria*, *Hippocrepis comosa* and *Onobrychis* spp.). This factor is further explored here on the basis of data published in the geological 1:50 000 scale map of Catalonia (<www.icc.cat>). Soil types were first classified into four classes of soil acidity (1 – highly acid; 2 – acid; 3 – neutral; 4 – basic), and subsequently an average value was calculated for the whole transect area.

Habitat availability. Conservation work on European butterflies has shown that grasslands constitute the main habitat for most species. Thus, of the 436 butterfly species for which information on habitat type is available, 382 (88%) occur on grasslands in at least one country in Europe, and for 280 species (57%) grasslands is their main habitat (Van Swaay et al. 2006). The proportion of grasslands in the butterfly sites was thus used as a general measure of habitat availability for the whole butterfly community. This variable was defined at local scale (i.e. the proportion of any kind of grassland within the 5-m wide census area along the transects) and at landscape scale (i.e. the proportion of any kind of grassland in a buffer area of 5 km around the transect site).

d) Landscape structure and human environmental impact

Landscape structure at butterfly sites was characterized by means of a land cover 1:25 000 scale map of Catalonia, based on colour aerial photographs taken in 1993 (<www.creaf.uab.es/mcsc/>). The percentage of surface area occupied by dense and open forest, shrubland, farmland, bare ground and built-up areas was calculated at local scale (within the 5-m wide census area) and at landscape scale (in a buffer area of 5 km around the transects). Two composite measures of landscape structure were obtained by performing PCA analyses using, respectively, the local 5-m and the landscape 5-km measurements. We finally only included the landscape measure in the analyses as it performed as a better predictor of variation in species richness than the analogous measure obtained at the local scale. The first axis (PCA1) accumulated 31% of the variability and was interpreted as a gradient of landscape intensification, from landscapes subjected to high human pressure in which intensive farming and infrastructures predominate (negative values) to more natural habitats mainly occupied by forests and shrubs (positive values) (Supplementary material Table S2). The PCA1 axis was significantly correlated with climatic (aridity; $R^2 = 0.24$) and geographic factors (altitude; $R^2 = 0.31$). Mean altitude of the transects was extracted from a Digital Elevation Model (DEM) with a spatial resolution of 30 m. The DEM was generated by the Inst. Cartogràfic de Catalunya from topographical 1:5000 scale maps. To avoid colinearity problems during the model selection we extracted the residuals of PCA1 with altitude and aridity and obtained a PCA1r residual variable that was independent from them. This variable was subsequently used as a measurement of the degree of land use conversion or human environmental impact.

Statistical analyses

Model selection

Modelling process was carried out in two steps. Firstly, we extensively explored the bivariate relationships between species richness and predictor variables and computed single-predictor models (using linear and quadratic functions). Secondly, we applied multiple regression models. We used three different approaches for model

building: ordinary least squares (OLS), spatial generalized least squares (spatial GLS) and spatial simultaneous autoregressive models (SAR). Models were selected according to the Akaike information criterion (lower AIC value) (Diniz-Filho et al. 2008). Corrected AIC values (AICc) were used because of small sampling size in relation to the number of potential predictors. We also provide adjusted R^2 values for OLS models, as they are useful for comparing two or more regression models that predict the same dependent variable with different number of independent variables. Step functions on R and JMP packages (R Development Core Team 2008, SAS Inst. 1989–2002) were used to introduce and select the predictor variables, using forward, backward and all-subset functions. A maximum of four predictor variables were introduced in a single model.

Cross-validation of the models was precluded by the low number of sample sites available (n = 84), but model performance was evaluated by following a Jack-knife approach. The Jack-knife procedure systematically recomputed the model estimates leaving out one observation at a time from the sample set. From this set of independent subsamples we estimated the amount of variance explained by the models (Jack-knife R^2, hereafter). Finally, to assess OLS model performance, we contrasted the Jack-knife R^2 estimate and the variance explained by the OLS models (OLS adjusted R^2).

Spatial autocorrelation

Spatial autocorrelation should be taken into account when analyzing geographic patterns of species richness (Dormann et al. 2007). Species richness patterns often display spatial autocorrelation that might remain in the residuals of the statistical models, thereby violating the assumption of the identical and independent distribution of residuals. The degree of spatial autocorrelation in the residuals of the models was assessed using Moran's I correlograms and plotting spatial maps of the distribution of residuals, following Dormann et al. (2007). To assess the level of significance at each distance class in the Moran's I correlograms, we computed 1000 permutations using resamp argument in the correlog function (ncf package, R package). When significant autocorrelation in the residuals was detected in ordinary least squares models (OLS), we applied spatial statistical modelling methods (spatial simultaneous autoregressive models (SAR) and spatial generalized least squares models (GLS)) to remove – or at least reduce – the spatial autocorrelation in the residuals of the models (Wall 2004, Beguería and Pueyo 2009).

Results

Species richness trends

Species richness showed strong relationships with some of the predictor variables (Fig. 3), increasing linearly with annual rainfall ($R^2 = 0.41$) and following a quadratic relationship with temperature ($R^2 = 0.59$). Species richness was negatively affected by temperature when the mean annual temperature was above ca 10°C, but it was positively affected below this threshold. A linear and very strong
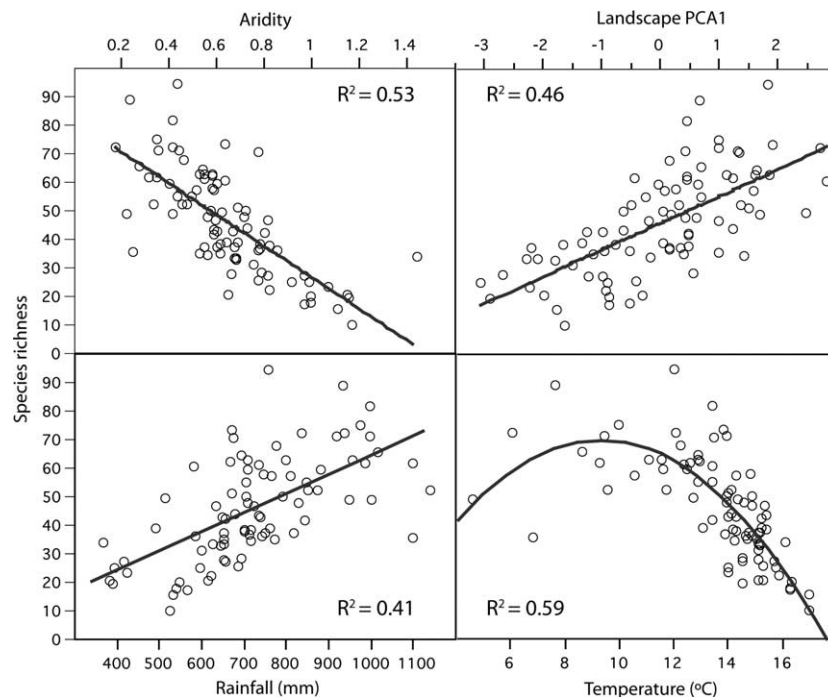

Figure 3. Observed relationships between butterfly species richness and main single predictor variables. Aridity is calculated by the modified Gaussen aridity index (Peñuelas et al. 2007a). Landscape PCA1 is a measure of degree of land use conversion or human environmental impact, ranging from intensive open farmland landscapes (negative scores) to areas with progressively increasing undisturbed forest and shrublands (positive scores).

relationship was also found between species richness and the aridity index ($R^2 = 0.53$), with butterfly species being rapidly lost from sites showing increasing aridity.

Apart from climatic variables, species richness showed a strong positive linear relationship with landscape PCA1 ($R^2 = 0.46$), which indicates that the number of species decreased regularly as the degree of intensification of human land use increased.

Multiple-regression models for ecological groups

The selected models according to the AIC criterion are shown in Table 1. The best fits were obtained for SAR models (9 cases) and OLS models (2 cases); on the other hand, GLS models performed worst in all cases (results not shown). Except for the most mobile species (dispersal class 4), a great proportion of the variance in the data (R^2 0.56–0.71) was accounted for by the models. Jack-knife models explained a considerable proportion of variance when compared to OLS models, thus providing a validation test for the models presented with independent subsamples (Table 1).

Pooling all the species together, the main predictors selected were aridity, landscape PCA1r and temperature. The quadratic effect of temperature means that this climatic variable is negatively correlated with butterfly species richness, except for extreme low values (i.e. those found in the high mountains). This relationship is paralleled by a clear altitudinal gradient in species richness, with low numbers at low and high altitudes (Fig. 4a). The number of species peaked at mid-altitudes, where both aridity and intensification of human land use are low and temperature is not a limiting factor. Moreover, the temporal coefficient of variation in species richness increased at the extremes of the altitudinal gradient, an effect that was mostly driven by reductions in the total number of individuals that localities support (results not shown).

Interestingly, there were some important differences between the models for specialists and generalists, although the quadratic effect of temperature was present in most cases for both groups of species (Table 1). The only exceptions were for the stronger habitat specialists (SSI 1) and most mobile species (Disp 4). These two groups were unique in presenting linear relationships with temperature, albeit of opposite sign, whereas all the other groups presented hump-shaped relationships (Fig. 5). The same contrasting pattern was consistent with the species richness altitudinal trends. In the case of habitat specialists (SSI 1), species were mainly concentrated at higher altitudes and were almost entirely absent from lowland areas (Fig. 4b). In the case of the most mobile species (Disp 4), a gradual decline was observed along the altitudinal gradient, with significantly higher species richness values at low altitudes (Fig. 4d).

The remaining predictors greatly differed between generalists and specialists. Again with the exception of the most mobile species, for generalists the second most important predictor was aridity, which always had a negative effect and decreased in importance with increasing butterfly specialization (Table 1). As well, landscape intensification or its interaction with aridity were also

important in determining species richness. The positive effect of PCA1r indicates that the number of generalists decreased under strong land use conversion. The positive interaction term between PCA1r and aridity means that landscape structure becomes more important in more arid areas, that is, species disappear more quickly in hot and dry areas that have been subjected to landscape intensification.

Specialists were more influenced by temperature (Table 1). Temperature had a strong negative effect for all groups of specialists, highlighting their clear preference for cold areas at mid- or high altitudes (Fig. 4). Apart from climatic variables, specialists were associated with habitat availability (percentage of grasslands) (Table 1, Supplementary material Fig. S1).

Soil type (pH) was a poor predictor of trends in species richness in most of groups and was not selected in the model selection approach in any group. Likewise, the number of plant communities was positively associated with butterfly species richness in most groups, but was a relatively poor predictor variable when compared with the rest of variables and was thus not selected.

Spatial autocorrelation

Generally, observed Moran's I values were low in all the groups and suggested minor spatial effects in the models (Supplementary material Fig. S2, S3). Spatial simultaneous autoregressive models (SAR) performed best in most cases, as they lessened the probability of type I errors by reducing the presence of spatial autocorrelation in the residuals. The significant spatial autocorrelation that still remained in the residuals was mainly due to the highly heterogeneous distribution of autocorrelative variation at large distance classes, that was not effectively captured by the spatial models (Supplementary material Fig. S2, S3).

Discussion

The results in the present work highlight the impact of a small number of climatic and landscape factors (e.g. human land conversion) on butterfly species richness at a regional scale. Quite predictably in this Mediterranean region the key factor is water availability. While the input of solar energy has been suggested as the most powerful descriptor of species richness for butterflies and many other groups of organisms in more northern areas (Turner et al. 1987, Currie 1991, Hawkins et al. 2003, Menéndez et al. 2007), water availability is the main limiting factor in more arid areas (Hawkins and Porter 2003b, Stefanescu et al. 2004). This finding coincides with the more general framework of ecosystem functioning whereby higher latitude ecosystems are typically limited by temperature (Chapin et al. 1995, O'Brien 1998) and lower latitude Mediterranean and continental ecosystems by drought (Peñuelas et al. 2001). Both direct physiological effects on insects and indirect effects on host-plants may account for the importance of water availability in Mediterranean areas (Hawkins and Porter 2003b).

Another very strong and general relationship was the peak in species richness at mid-altitudes, also revealed by

Table 1. Multiple regression models of butterfly species richness for different groups of generalists and specialists (in brackets, number of species in each group). The model selected by AICc criterion for each group (either OLS or SAR model) is shown in bold type. The sign $(+/-)$ of the coefficient estimate (β) for each predictor variable introduced in the model is shown, and significance values are indicated as: * $p < 0.05$, ** $p < 0.001$, *** $p < 0.001$, **** $p < 0.0001$.

|	Landscape structure and human impact		Climate and topography			Habitat availability		Model selection				
	PCA1$_r$	Aridity $\times$ PCA1$_r$	Aridity	Temp	Temp^2	Grasslands (km)	Grasslands (m)	DF	AICc		R^{2}adj OLS	R^2 Jack knife
									OLS	SAR		
All species	+****		−***	+****	−****	+*	+*	6,77	613	**607.8**	0.76	0.73
Generalists												
SSI 4 (37)	+***	+**	−***	+***	−****			5,78	472.5	**471.2**	0.71	0.68
SSI 3 (38)	+**		−***	+**	−***			4,79	**503.5**	504.4	0.66	0.64
Polyph. (14)		+**	−**	+***	−***			5,78	300.4	**299.6**	0.56	0.51
Oligoph. (75)	+****		−*	+****	−****			4,79	554.7	**553.4**	0.66	0.63
Disp 4 (12)		+*		+**				4,79	**225.7**	227.6	0.19	0.11
Disp 3 (20)			−***	+**	−**			3,80	399.3	**396.7**	0.66	0.63
Disp 2 (60)	+**		−**	+****	−****			4,79	520.0	**518.7**	0.70	0.67
Specialists												
SSI 2 (37)				+**	−***		+***	4,79	502.1	**496.1**	0.57	0.54
SSI 1 (38)				−****		+***	+**	3,80	367.2	**363.0**	0.70	0.59
Monoph. (80)				+***	−****			2,81	559.5	**556.3**	0.62	0.60
Disp 1 (77)	+***			+*	−**		+**	4,79	559.9	**561.2**	0.67	0.64
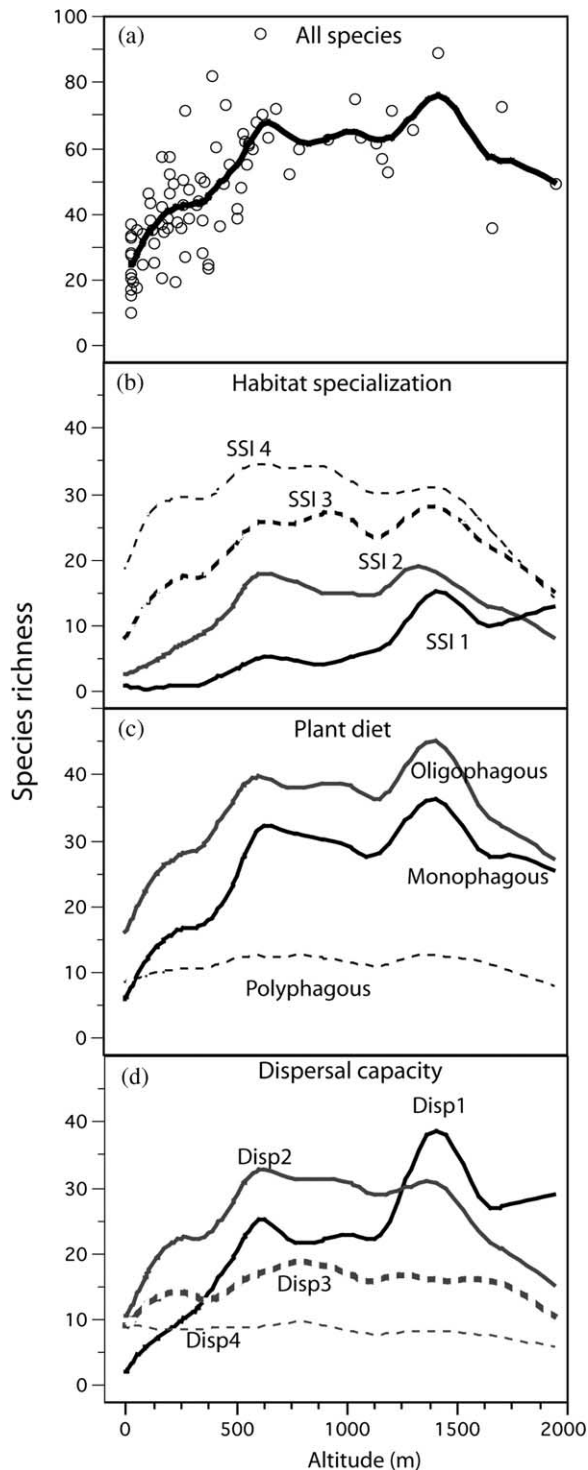
Figure 4. Species richness curves along the studied altitudinal gradient showing (a) the overall pattern for all species combined, and patterns for species groups of (b) decreasing habitat specialization (from SSI 1 to SSI 4), (c) increasing larval trophic specialization (polyphagous, oligophagous, monophagous), and (d) increasing dispersal ability (from Disp 1 to Disp 4). Smoothed trends were fitted using the cubic spline method.

the quadratic relationship of this variable with temperature. That species richness does not change monotonically with altitude, but follows instead a hump-shaped relationship,

has been shown by many studies covering a wide range of taxa, biogeographical regions and altitudinal gradients (Rahbek 1995). However, the reasons for such mid-altitude diversity peaks are still controversial and the patterns themselves are context-dependent due to confounding factors (e.g. moisture gradients showing different directions along the altitudinal gradient at specific sites: Körner 2007; habitat destruction in lowland habitats: Nogués-Bravo et al. 2008) and vary according to the geographical region and the ecology of the taxa under study (see Beck and Kitching 2009, for a recent discussion on a Lepidopteran taxon). This is exactly the situation that we have found here, with several peaks of species richness at different intermediate altitudes depending on the ecological group in question (Fig. 4). Our results support that species richness gradients are frequently the sum of several geographically divergent, group-specific trends and thus are best viewed as the combined response of different groups to diverse ecological and evolutionary factors (Carnicer and Díaz-Delgado 2008). For instance, here we have clearly documented a variety of divergent group-specific responses to temperature (Fig. 5).

Perhaps the most interesting finding was the presence of two different peaks in specialist species, one at around 500–700 m and another at 1200–1500 m. These two peaks are composed of endemic Mediterranean specialists and other more widely distributed species that are typically restricted to mountain ranges. In the case of the second peak, many species are strong habitat specialists of hay meadows and alpine grasslands, and have low dispersal abilities (cf. Supplementary material Table S1). From former broad distributions in the periglacial areas at least during the last glacial period, most of these habitat specialists have typically remained isolated in high mountain systems used as postglacial refugia. Populations isolated in this way have been selected for ecological specialization and have often differentiated into endemic genetic lineages (Schmitt 2009). The combination of species of different biogeographical origin has resulted in mountains harbouring rich butterfly communities characterised by the presence of rare taxa and high endemicity levels, a situation that can be extended to the rest of the Iberian Peninsula. This pattern is also found in other animal and plant taxa and emphasizes the high conservation value of these Mediterranean mountains (cf. García-Barros et al. 2002).

With respect to habitat specialists, multiple regression models indicate the strong negative effect of temperature and the positive effect of grassland availability on species richness (Table 1). This is a worrying result in light of the current global change that is associated with ever higher temperatures and increasingly more grasslands being lost due to the abandonment of traditional land uses (see Peñuelas et al. 2007b, for an example concerning our study area). As mentioned above, a high proportion of habitat specialists are restricted to mountains, where they exhibit narrow adaptations to their particular environments in terms of both climatic and habitat requirements. Climatic adaptation includes genetic differentiation as a result of thermal selection, which allows for greater cold tolerance and other features typical of alpine populations (Karl et al. 2009). It is not surprising, therefore, that temperature acts as the main factor establishing the low margins in the
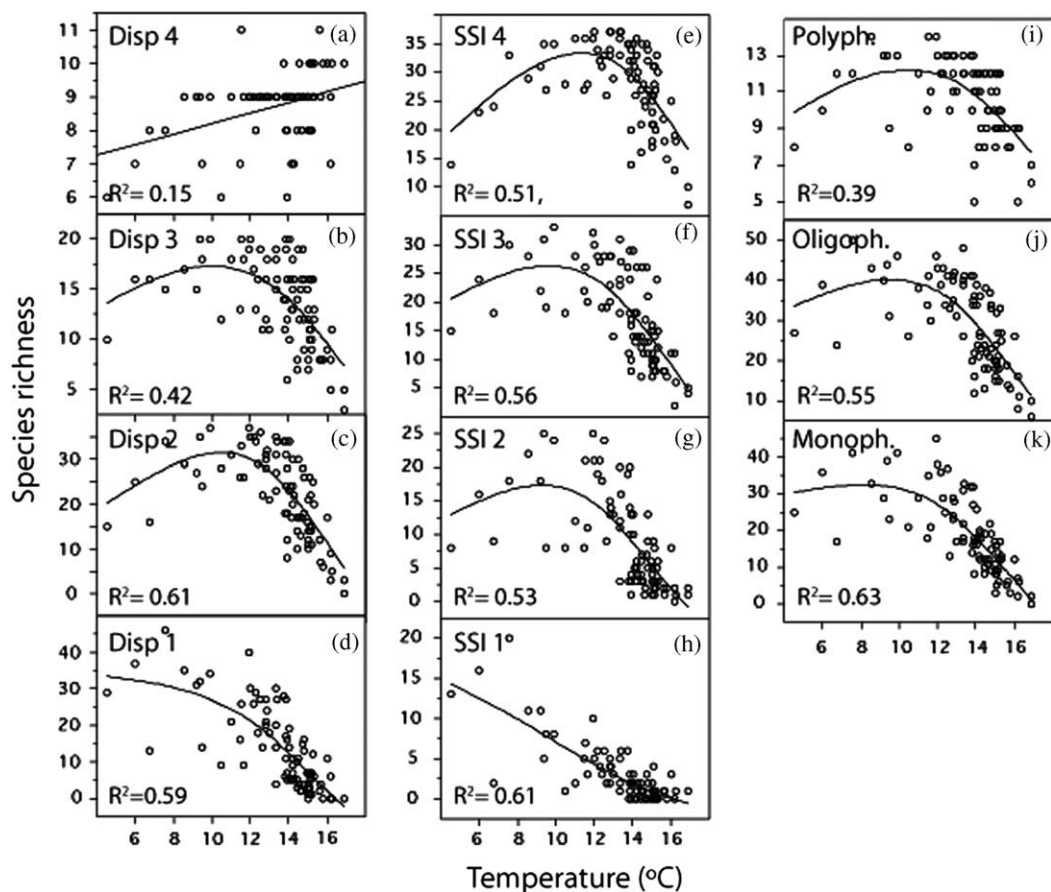
Figure 5. Observed relationships between species richness and temperature for all the groups. Linear (a) and smoothed fits (b–k, cubic spline method) are represented. The percentage of variation (R^2) explained by OLS models is indicated.

altitudinal range of montane butterflies, as has recently been shown by Merrill et al. (2008) for *Aporia crataegi* in another Mediterranean mountain range, the Sierra de Guadarrama in central Spain. In this butterfly, a decrease in egg survival at higher temperatures combined with the warming trends recorded in the area has resulted in its disappearance from low elevations in the space of just three decades. Similar responses in other montane butterflies have already resulted in a decrease in species richness in this Mediterranean mountain range (Wilson et al. 2007), as is expected to occur in Catalonia, based on our species richness models.

A second threat for montane butterfly specialists is habitat loss as a result of changes in land use such as the abandonment of extensive grazing and mowing. Although this is a general problem affecting grassland butterflies throughout Europe (Van Swaay et al. 2006), it is particularly severe in Mediterranean uplands, where the abandonment of traditional agriculture has been dramatic in recent times (Debussche et al. 1999). Closely linked with this phenomenon is the fact that grassland butterfly specialists underwent very serious and significant declines in Catalonia between 1994 and 2008; nevertheless, during the same period woodland specialists slightly increased (Stefanescu 2010). Not surprisingly, some of the species showing the most negative trends include a number of grassland specialists occurring in montane areas (e.g.

Maculinea arion, Polyommatus semiargus, Coenonympha glycerion).

According to our models, the richness of generalist species is influenced above all by factors that are most relevant in lowland areas such as aridity and the degree of intensification of human land use. However, even for this group of more common species, global change will have a predictable negative impact. First, many climatic models predict more prevalent summer droughts in southern European regions in the coming years (IPCC 2007) and, second, urbanization and the intensification of agriculture have both dramatically increased in the north-west Mediterranean in recent decades (see Brotons et al. 2004 for a full discussion for Catalonia). Even though generalists are much more flexible than specialists, these landscape changes all lead to the destruction of habitats of even the most widespread butterfly species and the eventual extinction of many populations (Cowley et al. 1999, Van Dyck et al. 2009). Interestingly, we found the interaction between aridity and landscape intensification to be significant for the most generalist butterfly species (Table 1). This result seems to indicate that the complete homogenization of humanized landscapes has serious detrimental effects in the driest parts of our Mediterranean region. In such hostile areas, even the most mobile and ubiquitous species still need patches of the original vegetation if they are to survive.

Conclusions

Our study shows very clearly that climatic but also changes in land use play an important role in determining butterfly species richness at a regional scale in the north-west Mediterranean Basin. Although climatic factors have been repeatedly advocated as the principal ecological determinants of butterfly diversity, their effects radically differ between geographical areas. While in northern temperate regions temperature has a clear positive influence, in warmer Mediterranean areas it has a mainly negative effect (except for the lower part of the thermal range (mountain tops), where the pattern is reversed) and overall water availability – resulting from the interplay between temperature and rainfall – is the most determinant factor in Mediterranean ecosystems.

The fact that the most favourable thermal/water balance occurs in upland areas gives rise to a typical hump-shaped pattern of species richness with altitude, although the specific altitudinal range of the diversity peaks differs between ecological groups. In particular, specialist butterflies (i.e. those living in local populations closely linked to specific habitats) are mainly concentrated in mid-altitude areas, and the same is true for many other animal and plant taxa (Carnicer et al. 2007). This notable coincidence highlights the obvious conservation value of Mediterranean upland areas.

Our models for generalists and specialists indicate that both groups will be negatively affected by global change, albeit in a distinct manner. A warming climate trend is predicted to have a negative effect on specialists restricted to mountain areas, as indeed has already been shown in central Spain (Wilson et al. 2007). Unfortunately, population declines will probably accelerate due to the synergistic effect of another important driver – habitat loss following the abandonment of traditional grazing and mowing. As for generalists, we predict declining trends following an increase in aridity in combination with an increase of intensification of human land use in lowland areas.

The clear message from this work is that Mediterranean butterflies will face severe problems in light of global change. Contrary to the situation in northern temperate regions (Warren et al. 2001), a warmer climate will pose a severe problem immediately in this highly diverse area and due to synergy between habitat destruction and degradation the expected negative trends may occur at a much faster rate than previously thought (cf. Brook et al. 2008).

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