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ORIGINAL ARTICLE

Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors

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ABSTRACT

Aim We developed a model enabling us to evaluate the contribution of both natural and human-related factors to butterfly species richness in Catalonia, a Mediterranean area that harbours one of the most diverse butterfly faunas in Europe.

Location The study was carried out in Catalonia (north-east Iberian Peninsula), a region of 31,930 km^2 lying between the Pyrenees, the Ebro depression and the Mediterranean sea.

Methods Data from the Catalan Butterfly Monitoring Scheme were used to assess butterfly species richness from 55 transects spread all over the region. Three groups of environmental variables likely to affect the presence of butterfly species were calculated, above all from geographic information system data: (1) climatology and topography, (2) vegetation structure and (3) human disturbance. Because climatic and topographic variables are expected to be strongly correlated, we first performed a principal component analysis (PCA) to create a summarizing factor that would account for most of the variance within this set of variables. Subsequently, a backward stepwise multiple regression was performed in order to assess the effects of environmental factors on butterfly species richness.

Results A total of 131 species were detected in the monitoring transects, representing 75.7% of the butterfly fauna known from Catalonia. Mean species richness per transect and per year was 41.4, although values varied greatly among sites (range: 14–76.8). The final regression model explained more than 80% of the total variance, which indicated a strong association between butterfly species richness and the studied environmental factors. The model revealed the very important contribution of climatic and topographic variables, which were combined into a single factor in the PCA. In contrast to what has been found in other, more northerly countries, species richness was negatively correlated with temperature and positively correlated with rainfall, except for extreme cold and wet conditions. This may be a consequence of the predictably adverse effects of the Mediterranean summer drought on herbivorous insects, and the fact that the limits of distribution of many butterflies correlate well with climatic variables. Human disturbance (defined as the proportion of urban and agricultural landscape cover in buffer areas of 5 km around the transect sites) was the second most important predictor for species richness. We found that a significant decrease in species numbers was associated with an increase in human pressure, a finding that indicates that not only building development, but also modern-day agricultural practices are detrimental to the conservation of Mediterranean butterflies. Surprisingly, vegetation variables had an almost negligible effect on butterfly species richness.

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Main conclusions Our findings strongly indicate that the current motors of global change will have a negative effect on Mediterranean butterfly assemblages. First, changes in land-use are transforming and fragmenting the landscape into an inhospitable and less permeable matrix for butterflies. Secondly, the negative correlation between species richness and temperature will lead to a predictable loss of diversity over the coming years, as predicted in the most plausible scenarios of climate change. Considering the high butterfly richness characterizing the Mediterranean Basin, this future trend will pose a serious threat to biodiversity.

Keywords

Species richness, climate, range margins, farmland, urban development, habitat fragmentation, butterflies, Catalonia, north-east Spain, Mediterranean Basin.

INTRODUCTION

The Mediterranean Basin has long been recognized as one of the biologically richest regions in the world (Blondel & Aronson, 1999) and its insect fauna, in particular, is especially diverse. For instance, Balletto & Casale (1991) estimated that about 75% of European insect species (i.e. *c.* 150,000 species) are found in the Basin. This high figure is consistent with the well-known trend of increasing species richness with decreasing latitude (e.g. Gaston & Blackburn, 2000 and references therein) and applies to most insect groups, including butterflies (Dennis & Williams, 1995). For example, of the 576 butterfly species known to occur in Europe, almost 220 have been recorded from Spain, a number only comparable with that of other southern European countries such as Italy, Greece and Turkey (van Swaay & Warren, 1999).

This geographical pattern, together with the recent general decline experienced by butterflies across Europe (van Swaay & Warren, 1999), highlights the importance of the Mediterranean region for butterfly conservation and the need to identify those factors generating the characteristic high species richness of this area. In this respect, we believe that this goal can only be achieved by means of an integrative approach that takes into account the interaction between natural processes (both biotic and abiotic) and human activities when attempting to explain local patterns of species richness (see e.g. Wettstein & Schmid, 1999). This is especially true in the light of studies that have clearly shown that patterns of butterfly species richness do generally respond to a number of basic environmental variables, upon which modifications caused by human activities should be superimposed. To date, however, no such an approach has been used in the investigation of the species richness of Mediterranean butterfly communities. Thus, for example, in the case of the Iberian Peninsula, most of the studies focusing on the subject essentially describe how species richness and habitat type are associated (e.g. Viejo *et al.*, 1988; Molina & Palma, 1996), or analyse the effects of a few factors on a given habitat (Baz & García-Boyero, 1995). At the other extreme, a study by Martín & Gurrea (1990) revealed an interesting macro-ecological pattern for butterfly diversity on a national scale, but did not take into account the many factors that could potentially be operating on a local scale.

In this paper, we explore the patterns of butterfly species richness in Catalonia (in the north-east of the Iberian Peninsula), basing our analysis on the data set provided by the Catalan Butterfly Monitoring Scheme (CBMS) (Stefanescu, 2000). The sites in the scheme encompass a broad range of biotopes, from farmland, urban areas, coastal sites and wetlands, to protected mountainous areas and beyond. Our general goal is to develop a model that accounts for variations in butterfly richness across the whole region, thus enabling us to evaluate the contribution of both natural and human-induced factors on the variable under study. More particularly, in light of the framework provided by the literature, we use an integrative approach to explain the patterns of species richness considering major natural factors as climate (Turner *et al.*, 1987; Pollard, 1988; Dennis, 1993; Parmesan *et al.*, 1999; Dingle *et al.*, 2000; Roy *et al.*, 2001; Hill *et al.*, 2003), plant diversity (Murdoch *et al.*, 1972; Gaston, 1992; Hawkins & Porter, 2003) and soil acidity (van Swaay, 2002), as well as man-induced factors as farmland and urban development (Erhardt, 1985; Feber & Smith, 1995; Dover, 1996; Cowley *et al.*, 1999; van Swaay & Warren, 1999).

MATERIALS AND METHODS

Study area

Field work was carried out in Catalonia, north-east Spain, a region of 31,930 km^2 lying between the Pyrenees, the Ebro depression and the Mediterranean sea (Fig. 1). As a result of its complex topography, with many highly variable mountain chains, the region has a highly diverse climate (Clavero *et al.*, 1996).

Overall, three biogeographical domains can be defined, namely the Mediterranean, the Eurosiberian and the Alpine regions (Folch i Guillèn, 1981; Fig. 1). The climax vegetation of the Mediterranean region consists of evergreen oak forests (mainly *Quercus ilex* L.) in the more humid areas, and dense shrublands (mainly Oleo-Ceratonion) in the drier ones. The

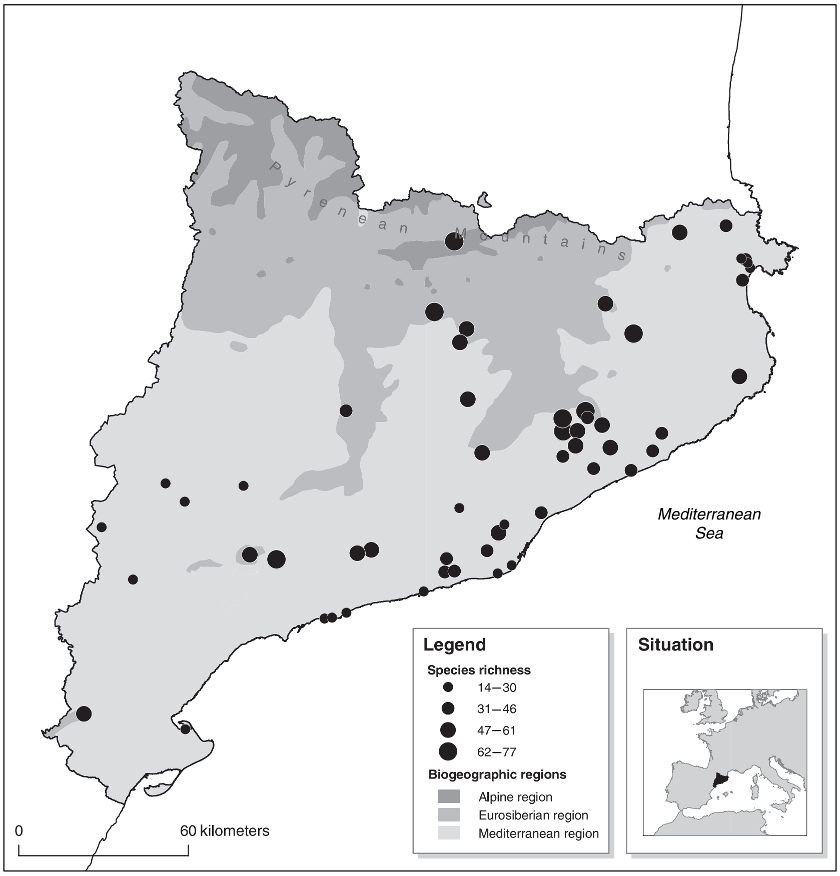

Figure 1 Map of the study region, showing butterfly species richness at the 55 census sites. The approximate extension of the three biogeographical domains present in Catalonia has also been mapped in accordance with Folch i Guillèn (1981).

Eurosiberian region is dominated by deciduous and coniferous forests (e.g. beech *Fagus sylvatica* L., oaks *Quercus* spp. and Scots pine *Pinus sylvestris* L.) at mid-altitude between 800 and 1600 m a.s.l. Finally, the Alpine region is situated above this latter level and its vegetation consists mainly of alpine grasslands and forests of mountain pine *Pinus mugo* ssp. *uncinata* Ramond.

Catalonia harbours the most diverse butterfly fauna in the Iberian Peninsula (Martín & Gurrea, 1990) and one of the richest in the whole of Europe (Dennis & Williams, 1995). A comprehensive list of the 193 species recorded in this region as of 1990 was published by Viader (1993). Six more species have been added to this list over the last 13 years.

Butterfly data

Data from the CBMS (Stefanescu, 2000) have been used to assess the species richness of 55 transects from all over the region (Fig. 1). Sampling sites were located at 0–1651 m a.s.l. (mean altitude = 389.1 m; SD = 963.2 m), thus providing a wide range of habitat types. Weekly butterfly counts were made along a fixed route (mean length = 1906.6 m; SD = 963.2; range: 728–4909 m) within 2.5 m on each side and 5 m in front of the recorder (see Pollard & Yates, 1993, for details on the methodology). These counts, which provide reliable presence/absence data for species at each transect site, began on 1 March and ended on 26 September, a period of 30 recording weeks per year. Available recording years varied greatly from site to site (from 1 to 8 years, except for a single site where records exist for a 13-year period); recording effort was accordingly standardized and so the annual mean species richness instead of the total species richness was calculated for each transect site.

Because of identification problems during counts, skippers (family Hesperiidae) have not been considered in this paper and have thus been excluded from our analyses.

Environmental variables

Three groups of environmental variables potentially affecting the presence of butterfly species were measured: (1) climatology and topography, (2) vegetation structure and (3) human disturbance.

Climatology and topography

The following five climatological variables were chosen to represent the dominant climatic regime at each site: (1) mean annual temperature (°C), (2) mean minimum January temperature (°C), (3) mean maximum July temperature (°C), (4) mean annual rainfall (mm) and (5) water deficit (mm). Water deficit is a categorical variable that includes seven classes, from negative values (i.e. a water excess over a whole year period) to > 500 mm. All these variables were derived from the Digital

Climatic Atlas of Catalonia (Ninyerola *et al.*, 2000), which has a spatial resolution of 180 m, and were calculated as the average over the whole transect.

Given its close relationship with climate (see below), we also calculated the mean altitude of each transect. This measurement was extracted from a digital elevation model (DEM) with a spatial resolution of 30 m, which was generated by the Cartographic Institute of Catalonia (ICC) from topographical 1 : 5000 scale maps. The range in elevation within each site was not taken into account, as it was always very small (usually <50 m) and we felt it to be irrelevant in the context of this study.

As all these climatic and topographic variables are expected to be mutually and very strongly correlated, we performed a principal component analysis (PCA) with a varimax normalized rotation (Legendre & Legendre, 1998) to create a summarizing factor that would account for most of the variance within this set of variables. The Bonferroni correction was applied to calculate significant levels of correlation between the original variables and factors. The PCA produced only one factor with an eigenvalue greater than 1, which accounted for 78% of data matrix variance (Table 1). This factor, referred to henceforth as CLIMATE, was negatively associated with altitude, precipitation and water deficit and positively associated with temperature variables, thus indicating a clear gradient from cold and humid climates (negative values) to warm and dry climates (positive values).

Vegetation

Two variables measuring different aspects of the vegetation occurring over each transect were used: (1) the number of plant communities and (2) an index of soil acidity. Given that data on plant species richness were not available for the transects, we used another variable which is regarded as being highly relevant, namely the number of community types. This was also one of the variables used by Hawkins & Porter (2003) to characterize plant richness in their analysis of the relationship between plant and butterfly diversity in California. In our study, plant communities within the 2.5-m belt on each side of the progression line of the transect were defined by a botanist in accordance with the CORINE Biotopes Manual (Moss *et al.*, 1990).

Table 1 Factor loadings of each individual climatic and topographic variable in the only factor obtained from the principal component analysis with an eigenvalue of greater than 1. All variables were highly significantly related to this factor ($P < 0.0001$), which was referred to as CLIMATE

	CLIMATE
Mean altitude of the transect	−0.931
Mean yearly rainfall	−0.853
Water deficit	−0.893
Mean yearly temperature	0.958
Mean of the January minima temperatures	0.794
Mean of the July maxima temperatures	0.862
Eigenvalue	4.682
Percentage of total variance	78.041

Soil acidity was inferred from the plant species present and provides an indication of the relative importance of plant communities dominated by calcicolous or by acidophilous species in each transect. As no indicator values such as those given to Central European plant species in Ellenberg's system (Ellenberg *et al.*, 1991) were available, a similar scale was produced for the local vegetation. Plant communities were thus assigned to one of five categories, from 1 (associated with highly basic soils) to 5 (associated with highly acid soils), and an index of acidity was calculated by multiplying the relative cover of each plant community by its category.

We did not include any variable related to vegetation structure (i.e. the relative importance of grasslands, shrublands and woodlands) because, in the CBMS, routes are selected to include a good sample of the variety of habitat types in a given landscape and so this variable becomes highly homogeneous within the set of transects.

Human disturbance

We constructed two different variables in order to assess the potential effects of farmland and urban development on butterfly species richness. Both variables were derived from a land-use raster with a spatial resolution of 30 m and were calculated for a buffer area of 5 km around the transects. The land-use raster was generated by the ICC using multispectral Thematic Mapper images obtained in 1997 by the satellite Landsat 5 and included the 21 thematic categories shown in Table 2. The variable FARMLAND was calculated as the sum of the percentages of the five categories associated with some kind of agricultural practice (herbaceous crops on non-irrigated land, herbaceous crops on irrigated land, fruit trees on non-irrigated land, fruit trees on irrigated land and vineyards) within the buffer area. Likewise, the variable URBAN provided an estimate of the percentage of the buffer area occupied by types of land cover associated with urbanization (road network, housing developments, urban communities and industrial and commercial estates).

We set the buffer areas at 5 km as an approximation to the maximum distance of dispersal reported for most sedentary butterflies (e.g. Hanski & Kuussaari, 1995). Furthermore, work based on BMS data has shown a high synchrony in the fluctuations of butterfly populations within a radius of up to 2–4 km and a sharp decrease beyond this range (Sutcliffe *et al.*, 1996), suggesting that processes acting within the 5 km buffer area are likely to influence the populations being monitored during the transects.

Analyses

In order to assess the effects of environmental factors on butterfly species richness, we performed a backward stepwise multiple regression (Legendre & Legendre, 1998). Apart from

Table 2 Landsat landscape units (1997) and their corresponding surface area (km^2) in the 5 km buffer areas around the 55 transects considered in this study

Landsat landscape covers	Area (km^2)
Outside Catalonia	10.10
Continental water	18.87
Sea water	449.98
Road network*	71.92
Housing developments*	204.38
Urban communities*	75.99
Industrial and commercial estates*	56.68
Herbaceous crops on unirrigated land†	585.72
Herbaceous crops on irrigated land†	398.50
Fruit trees on unirrigated land†	240.33
Fruit trees on irrigated land†	69.25
Vineyard†	83.98
Supraforest meadows	8.86
Scrub and meadows	1161.98
Sclerophyll forest	626.22
Deciduous forest	257.11
Aciculifolia forest	817.27
Wetland vegetation	34.51
Soil with scarce or no vegetation	108.74
Burnt areas	20.83
Sands and beaches	14.66
Total area	5315.89

*Landscape covers used in the calculation of the URBAN variable.
†Landscape covers used in the calculation of the FARMLAND variable.

the standard linear terms, we included quadratic terms for each variable to account for potential quadratic relationships with species richness (see Kurki *et al.*, 1998, for a similar procedure). In addition, because sampling efforts differed among the transects (i.e. there was a great variation in transect length), we forced the inclusion of transect length as an adjustment variable in the model building process (e.g. Luoto *et al.*, 2001).

Predictor variables were not transformed as they conformed to a normal distribution in all cases (after Kolmogorov–Smirnov tests for goodness-of-fit; data not shown).

As a previous step to the model building, a correlation matrix was performed to test for possible associations between predictor environmental variables (Table 3a). The analysis showed significant positive correlations between CLIMATE and the two human-related variables, FARMLAND and URBAN, indicating a likelihood that human activities will occur in lowlands with warm climates. To account for this multicolinearity problem, we performed simple regressions between CLIMATE (independent variable) and the two human-related variables, and extracted the residuals representing the part of the variance of FARMLAND and URBAN not explained by CLIMATE. In both cases the regression models were highly significant (CLIMATE-FARMLAND, $F_{1,53} = 27.54$, $P < 0.0001$; CLIMATE-URBAN, $F_{1,53} = 15.14$, $P < 0.001$) and the residual variables, referred to as RESIDFARMLAND and RESIDURBAN, maintained a strong and positive correlation with the original variables, FARMLAND and URBAN ($r = 0.81$, $P < 0.0001$; $r = 0.88$, $P < 0.0001$, respectively). Following this approach, we obtained a set of independent predictor variables for analysing those factors influencing butterfly species richness (Table 3b).

All statistical analyses were run with Statistica Statsoft (StatSoft, Inc., 1999).

RESULTS

Butterfly communities

A total of 131 species were detected in the 55 monitoring transects (Appendix S1 in Supplementary Material), representing 75.7% of the butterfly fauna known from Catalonia (excluding the 24 species belonging to the Hesperiidae). Mean

Table 3 Correlation matrix for (a) the original predictor environmental variables and (b) the independent predictor environmental variables entered in the model building

	CLIMATE	Plant communities	Soil acidity	FARMLAND	URBAN
(a)					
CLIMATE	1.00				
No plant communities	0.09	1.00			
Soil acidity	−0.15	0.13	1.00		
FARMLAND	0.58*	−0.10	−0.23	1.00	
URBAN	0.47*	0.06	0.14	0.02	1.00
				RESIDFARM	RESIDURBAN
(b)					
CLIMATE	1.00				
No plant communities	0.09	1.00			
Soil acidity	−0.15	0.13	1.00		
RESIDFARMLAND	0.00	−0.19	−0.17	1.00	
RESIDURBAN	0.00	0.01	0.24	−0.35	1.00

*$P < 0.01$.

Table 4 Multiple regression model conducted by means of a backward stepwise procedure (P-to-enter = 0.05, P-to-remove = 0.05, n = 55 transects), using both main and quadratic effects in the design for predictor variables. Transect length was forced into the model as an adjustment variable correcting for the sampling effort effect

Butterfly species richness	β	SE	*F*	*P*	r^2
Intercept		4.25	160.15	***	
Transect length	0.07	0.00	1.13	0.294	0.40
Soil acidity	−0.18	1.20	8.34	**	2.97
RESIDFARMLAND	−0.24	0.05	12.29	***	4.37
RESIDURBAN	−0.18	0.10	6.58	*	2.34
CLIMATE	−1.09	1.32	179.66	****	63.99
$CLIMATE^2$	−0.45	0.89	27.27	****	9.71
Model					83.80

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$.

species richness per transect and year was 41.4 (SD = 16.3), but values varied greatly among sites (range: 14–76.8; Fig. 1).

Associations between butterflies and environmental factors

The final regression model explained more than 80% of the total variance, which indicated a strong association between butterfly species richness and the studied environmental factors (Table 4).

Butterfly species richness was highly and negatively related to CLIMATE following a quadratic equation, which accounted for a total of 74% of the data matrix variance, that is, 88% of the variance explained by the set of predictors. This result indicates the exceptional importance of climate for butterfly species richness in our study area. Species richness was positively affected by altitude, rainfall and low temperatures; nevertheless, for extreme values of these components, linearity was lost and the association became negative, as shown by the quadratic CLIMATE effect (Fig. 2a).

Interestingly, the two human-related variables, RESIDFARMLAND and RESIDURBAN, both entered the model with a negative effect (Fig. 2b,c), thus showing that butterfly species richness was negatively influenced by agriculture and urban development around the census stations. Soil acidity was also included in the final model and showed the slight positive effect of basic soils (low values in the constructed variable) on butterfly species richness (Fig. 2d). All three variables, however, had a comparatively low importance when compared with that of climate.

The number of plant communities was not related to butterfly species richness and was thus removed from the model. Neither was transect length a significant variable (Table 4), suggesting that the transects were generally long enough to detect the vast majority of the species that occur at a site.

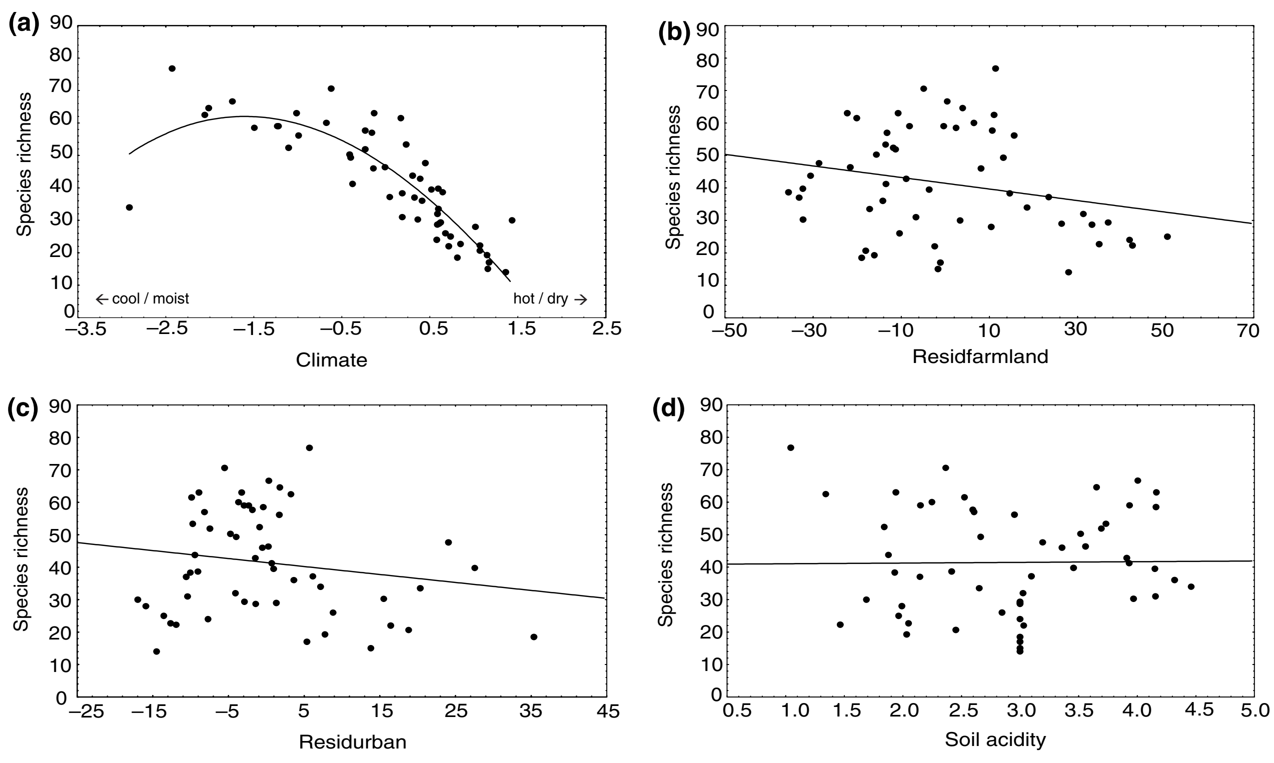

Figure 2 Relationships between butterfly species richness and the environmental variables found to be significant in the multiple regression model: (a) CLIMATE, (b) RESIDFARMLAND, (c) RESIDURBAN and (d) soil acidity.

DISCUSSION

Factors affecting species richness

Climate

The most important set of environmental variables determining butterfly species richness is that which pertains to climatic and topographic variables (i.e. temperature, rainfall and altitude), which in our study area were highly correlated and were combined into a single factor in a PCA. Data were best explained by a model that included a quadratic effect of these variables; hence, species richness was negatively correlated with temperature and positively correlated with rainfall and altitude, except for extreme values (i.e. those found above some altitudinal range in the Pyrenean mountains; Fig. 2a). The highest transect in our dataset was at 1651 m, and showed a dramatic decrease in mean species richness (34 vs. 64.7 species) with respect to six other transects at altitudes greater than 1000 m (range: 1027–1405 m). Circumstantial data from other sites belonging to the alpine domain (i.e. above 1600 m) also indicate that butterfly species richness is sharply reduced, most probably as a result of the increasingly harsh climatic conditions prevailing there (C. Stefanescu, unpubl. data). Moreover, several other studies in the Mediterranean and elsewhere have also shown the same altitudinal trend in butterfly richness, with the number of species peaking at intermediate levels and quickly decreasing at higher altitudes (e.g. Thomas & Mallorie, 1985; Gutiérrez & Menéndez, 1995; Sánchez-Rodríguez & Baz, 1995; Fleishman *et al.*, 1998). We hope that, in the future, additional transect data from a more complete altitudinal range in the Pyrenees will allow a better understanding of the relationship of species richness with altitude.

Our findings are consistent with earlier works showing that both temperature and rainfall have a strong influence on the distribution and abundance of butterflies (e.g. Turner *et al.*, 1987; Pollard, 1988; Roy *et al.*, 2001; Hill *et al.*, 2003). However, in contrast to what has been found in other, more northerly countries (e.g. Britain, see Turner *et al.*, 1987), species richness was not negatively affected by cold and wet climates, but, instead, positively influenced for much of the studied range (Fig. 2a). This result can be explained by taking into account the peculiarities of the Mediterranean climate in combination with the niche theory of species distributions (Hengeveld & Haeck, 1982; Brown, 1984; see Thomas *et al.*, 1998, for a discussion applied to butterflies).

The Mediterranean climate is characterized by a rigorous (hot and dry) summer, with a severe drought that limits most plant growth to two short periods in spring and autumn (Dunn *et al.*, 1977). Summer drought has a predictably adverse effect on herbivorous insects and, more particularly, on butterflies, if the desiccation of both host plants and nectar sources occurs (e.g. Ehrlich *et al.*, 1980; Murphy *et al.*, 1983). Thus, it is not surprising that Lepidopteran assemblages in Mediterranean habitats show low diversity during this period (e.g. Shapiro, 1975; Yela & Herrera, 1993). Unfavourable conditions become more extreme towards the south of the Mediterranean Basin, where summer drought can last for 5–6 months instead of the 2 months usually recorded in the north (Blondel & Aronson, 1999). Albeit on a lesser scale, the same trend is also recorded within Spain (Font, 1983) and Catalonia (Clavero *et al.*, 1996). These patterns of increasing dryness towards the south may well be paralleled by a decrease in butterfly species richness, as was indeed the case in the present study (Fig. 1) and as reported in a paper by Martín & Gurrea (1990).

Furthermore, as discussed by Dennis & Shreeve (1991) and Quinn *et al.* (1998), the range limits of many European butterflies correlate with climatic variables rather than the distribution limits of their host plants. This has led to suggestions that climate rather than biotic factors is the main determinant of butterfly ranges, a point that is supported by several studies documenting changes in butterfly distributions associated with recent climate change (Parmesan, 1996; Parmesan *et al.*, 1999; Hill *et al.*, 2002; see also Crozier, 2002, for an experimental study confirming the effects of temperature on the changes in distribution of the Sachem Skipper, *Atalopedes campestris*). In the UK, where about 80% of resident butterflies reach their northern European limit, marginal populations are often associated with warm microclimates (Thomas, 1993; Thomas *et al.*, 1999), indicating that distributions may be constrained by low temperatures. The reverse is to be found in Catalonia, where typical European species at their southern limits (Tolman & Lewington, 1997) occur in cooler and moister microclimates (C. Stefanescu, unpubl. data). In other words, the potential habitats a species can occupy decrease when moving from the centre to the edge of its distribution, since climatic requirements are not fulfilled, being too cool and wet in the north and too warm and dry in the south (i.e. in Britain and Catalonia, respectively). In the case of Catalonia, this means that there is an impoverishment of the butterfly fauna towards the south, with the exception of sites located in mountain areas (Fig. 1), where the climate becomes cooler and wetter. Naturally, an opposite trend applies to species of African origin at the northern edge of their ranges somewhere in Catalonia. However, their contribution to overall species richness is minimal in comparison with that of species of European origin (cf. Tolman & Lewington, 1997).

Human disturbance

Once climatic factors have been taken into account, human disturbance (defined as the proportion of urban and agricultural landscape cover in buffer areas of 5 km around the transect sites) was the most important predictor for species richness. We found a significant decrease in species numbers associated with an increase in human pressure. Therefore, as reported in most European countries (van Swaay & Warren, 1999), both building (such as roads and housing) and modern agriculture (including several types of crops in irrigated and non-irrigated land) can be seen as detrimental to the conservation of Mediterranean butterflies and lead to a significant loss of breeding habitats and the fragmentation and isolation of remaining habitats. This is especially worrying in the case of agriculture, as it highlights the speed at which the intensification of farmland (i.e. conversion of unimproved grasslands to arable crops, fertilization of pastureland and increasing use of herbicides and pesticides) is taking place in an area that was formerly managed in a traditional way highly beneficial for wildlife in general (Di Castri, 1981; Pons & Quézel, 1985; Blondel & Aronson, 1999), and for butterflies in particular (Munguira, 1995).

Our findings are also interesting as they reveal the influence the landscape surrounding the sampling sites has on the processes taking place in the sites themselves. Thus, a loss in species richness is still detectable in highly humanized landscapes even if good butterfly habitats (e.g. different kinds of meadows and scrubland) predominate along the transects. Most probably, this reflects the higher risk of extinction in populations of sedentary species inhabiting sites isolated by inhospitable habitat. This explanation seems highly likely in the context of the many studies that have stressed the importance of metapopulation dynamics for sedentary butterflies and the need to maintain networks of suitable habitat for allowing dispersal and long-term population persistence (e.g. Thomas *et al.*, 1992; Warren, 1993; Hanski & Thomas, 1994). Further evidence in favour of this hypothesis is provided by the contrasting patterns of distribution of butterflies with 'open' vs. 'closed' populations at the CBMS sites (see Appendix S1). Thus, it can be seen that the few species present at virtually all sites (e.g. *Papilio machaon*, *Pieris brassicae*, *Pieris rapae*, *Pontia daplidice*, *Colias crocea*, *Gonepteryx cleopatra*, *Lycaena phlaeas*, *Lampides boeticus*, *Celastrina argiolus*, *Polyommatus icarus*, *Vanessa atalanta*, *Cynthia cardui*, *Pararge aegeria*, *Lasiommata megera*) all combine a high degree of mobility (e.g. Dennis & Shreeve, 1997; Cowley *et al.*, 2001) with the use of relatively widespread and disturbed habitats distributed throughout the landscape (Warren *et al.*, 2001). As pointed out by Thomas *et al.* (1998), these wide-ranging species tend to 'average the environment' over larger scales than more sedentary species, a feature that makes them almost unaffected by the barriers existing within the 5-km buffer areas in our study. Pollard & Eversham (1995) reached a similar conclusion in their analysis of the patterns of distribution of British butterflies based on data from the UK BMS.

Other factors

Albeit slight, we found a significant effect of soil acidity on butterfly species richness. As reported by van Swaay (2002), butterfly assemblages tended to be richer in sites with basic soils. This was more noticeable for some groups than others (e.g. species in the Polyommatini tribe of the Lycaenidae family, which feed mainly on calcicolous plants such as *Hippocrepis comosa* L. or *Anthyllis vulneraria* L.; C. Stefanescu, unpubl. data), suggesting a phylogenetic component on this ecological correlate of species richness. Interestingly, recent work by Shreeve *et al.* (2001) has also shown that British Polyommatini tend to co-occur in biotopes with calcareous substrates. We thus believe that further analysis taking into account the phylogenetic relationships among butterflies would reveal more complex patterns of species richness.

Finally, concerning the non-existence of a relationship between butterfly and plant richness, it should be noted that the contradictory conclusions reached by different studies (see Kremen, 1992; Hawkins & Porter, 2003) indicate that these two types of environmental variables are not necessarily correlated. In this respect, Kremen (1992) has even suggested that butterfly assemblages are poor indicators of plant diversity, and our study adds further elements in favour of a lack of a general correlated pattern between these two variables.

Concluding remarks: Mediterranean butterfly assemblages in light of global change

Over the last century, Mediterranean ecosystems have undergone important alterations as a result of extensive changes in land-use (Bacaria *et al.*, 1999; Blondel & Aronson, 1999). On the northern shores of the Basin, traditional agricultural land is being abandoned and either converted into areas of intensive agriculture or destroyed by increasing pressure from building development. More recently, climatic warming has been added to the list of factors known to be the driving forces of recorded changes (Peñuelas *et al.*, 2002; Stefanescu *et al.*, 2003).

Our findings strongly indicate that current major determinants of global change will have a negative effect on Mediterranean butterfly assemblages. First, changes in land-use are transforming and fragmenting the landscape into an inhospitable and less permeable matrix for butterflies. Secondly, the negative correlation between species richness and temperature will lead to a predictable loss of diversity over the coming years, according to the most plausible scenarios of climate change (IPCC, 2001). Overall, this represents an even more alarming situation than the scenario recently reported for northern temperate countries, in which butterfly faunas are facing overall decline because of habitat degradation, in spite of the positive effect of climate warming at higher latitudes (e.g. Warren *et al.*, 2001). Considering the high butterfly richness characterizing the Mediterranean Basin, this future trend will pose a serious threat to biodiversity.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JJBI1088/JBI1088sm.htm

Appendix S1 Butterfly species recorded in the present study, with indication of the number of sites where they were recorded.

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