

**Asymmetric constraints on limits to species ranges influence consumer-resource richness over an environmental gradient**

David Gutiérrez<sup>1</sup>, Roger Vila<sup>2</sup> and Robert. J. Wilson<sup>3</sup>

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

Email: david.gutierrez@urjc.es

<sup>2</sup> Institut de Biologia Evolutiva (CSIC-Univ. Pompeu Fabra), Passeig Marítim de la Barceloneta 37, Barcelona, ES-08003, Spain. Email: roger.vila@csic.es

<sup>3</sup> College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, UK.

Email: R.J.Wilson@exeter.ac.uk

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Corresponding author: David Gutiérrez, Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, Madrid, ES-28933, Spain. Phone: +34 914888160. Fax: +34 916647490. Email: david.gutierrez@urjc.es

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## **A ABSTRACT**

**Aim** There is little consensus about the relative roles of biotic *versus* abiotic factors in setting limits to species distributions, or in generating geographic patterns of species richness.

However, despite the likely importance of host availability in governing the distributions and diversity of consumers, few studies have simultaneously tested the effects of resource distributions and diversity on consumer ranges and richness patterns.

**Location** Sierra de Guadarrama, central Spain.

**Methods** We examined the effects of biotic resource and consumer attributes, and climate, on the ranges and species richness patterns of 43 specialist butterflies at 40 sites over a 1800 m elevation gradient. Evidence for resource use was based on comprehensive field records of oviposition and larval feeding on host plants.

**Results** We show that limitation either by biotic interactions with resources (the distributions and parts eaten of the larval host plants), or by intrinsic dispersal ability, was stronger at upper than lower elevation range limits for butterflies. Both resource and consumer richness followed a unimodal, humped pattern over the elevation gradient, but host plant richness peaked 300 m lower than butterfly richness. In addition, whereas changes in butterfly species richness were roughly symmetrical around peak richness over the gradient studied, the host plants showed markedly lower species richness at high elevations (> 1750 m). Butterfly species richness increased with host plant resource diversity and relative humidity, with a steeper response to host plant richness in cooler sites (at higher elevations).

**Main conclusions** The results demonstrate the role of bottom-up control by resource availability in limiting consumer distributions and richness. Importantly, resource limitation had increasing relevance towards the coolest and most resource species-poor parts of environmental gradients, with potential consequences for ecological responses to environmental change.

## (A) INTRODUCTION

The determinants of species' geographic ranges are important for understanding global diversity patterns, and for modelling and managing responses of biodiversity to environmental change (Gaston, 2003). It has been long proposed that some antagonistic biotic interactions (competition, predation, herbivory, parasitism and disease) are more likely to impose range limits in relatively species-rich parts of a species distribution, such as at lower latitudes and elevations (MacArthur, 1972). Despite these long-standing predictions, the relative importance of biotic interactions limiting species distributions at opposing ends of ecological gradients remains largely unexplored (Sexton *et al.*, 2009; Louthan *et al.*, 2015). Recently, Cahill *et al.* (2014) suggested that abiotic factors are in fact supported more often than biotic interactions in setting species' warm range limits, in contrast to the widely held classical view stated above. Nevertheless, many of the studies reviewed focused on competition, and few have considered the role of resource availability in limiting distributions (Cahill *et al.*, 2014). In the case of consumer-resource interactions, two pieces of evidence suggest that biotic factors may increase in importance towards species-poor extremes of gradients, such as those at high latitudes and elevations, driven by bottom-up effects of resource availability on consumers. First, the 'resource diversity hypothesis' (Hutchinson, 1959) implies that consumer distributions and diversity are more limited by biotic resources moving down resource diversity gradients (Price *et al.*, 2011). Second, empirically-based recent models for consumers and their hosts provide evidence for greater resource limitation of consumer distributions at higher latitudes and elevations, under current conditions (Hanspach *et al.*, 2014), and climate warming (Schweiger *et al.*, 2012; Romo *et al.*, 2014).

Much research on geographic gradients in community richness focuses on correlations of richness with environmental factors (McCain & Grytnes, 2010). However, such an approach does not allow studies to distinguish between the hypotheses that (1) the environment imposes

limits on species richness independently of species identities (top-down hypotheses, e.g., Brown *et al.*, 2001) versus (2) the environment constrains individual species' ranges, and ranges sum to yield species richness patterns (bottom-up hypotheses, Kaufman, 1995). Top-down hypotheses assume that energy or other limiting resources impose a carrying capacity on species richness, whereas bottom-up hypotheses assume that species richness patterns are generated through mechanisms that modulate individual species niches (Boucher-Lalonde *et al.*, 2014). Although both groups of hypotheses are not mutually exclusive, evidence that individual consumer distributions are constrained by individual resource distributions would support the role of bottom-up hypotheses in accounting for consumer richness (Boucher-Lalonde *et al.*, 2014). Surprisingly, this kind of evidence has rarely been used for this purpose, even when it can be directly documented by field observations of trophic interactions such as host use (Rodríguez-Castañeda *et al.*, 2010). As further support for bottom-up hypotheses, there should be a stronger relationship between consumer and resource richness towards the most resource-limited extremes of environmental gradients.

If resources strongly limit consumer ranges, then a markedly positive interspecific relationship between their respective distributions is expected. However, this pattern has rarely been observed, and the majority of consumers only occupy a fraction of the distribution of their resource species (Quinn *et al.*, 1998). Variation in life history characteristics could lead individual data points to depart from this expected relationship, but in some cases they may provide further support for the limiting effects of resource availability on individual consumer distributions (Hopkins *et al.*, 2002). For instance, species using smaller or more ephemeral resources may occupy a smaller fraction of host patches (Rodríguez *et al.*, 1994; Hopkins *et al.*, 2002). On the other hand, abundant or dispersive consumers may occupy a larger fraction of resource patches because of higher rates of host patch colonization and reduced rates of local extinction (Hanski, 1999; Hopkins *et al.*, 2002).

In this study, we test the hypotheses that (1) resource availability limits elevational consumer distributions, with increasing importance towards the resource species-poor extreme of an environmental gradient, and (2) consumer species richness is accounted for by bottom-up mechanisms associated with resource constraints. As a model system, we use the specialist butterflies and their host plants of a Mediterranean mountain area in central Spain, where many species exhibit range limits at both high and low elevations (Gutiérrez Illán *et al.*, 2010). Butterflies represent an excellent model for testing the role of biotic interactions in determining range limits because they depend on a limited set of plant species as resources for larval development (Hanspach *et al.*, 2014). Highly-resolved field observations of butterfly abundance and host plant use, and of host plant distributions and climate data collected *in situ*, enable us to test (1) whether host plant distributions directly constrain the elevational distributions of butterflies, both at high and low elevation limits, and (2) whether specialist butterfly richness is positively related to host plant richness, and (3) whether this relationship varies over the climatic gradients associated with elevation. To explain deviations from the expected patterns in (1), we test for effects on butterfly distributions of resource size (herbaceous vs. woody host plants) and permanence (flower-fruit vs. leaf feeders), and of butterfly dispersal ability, abundance and climatic tolerance and limits.

## **(A) METHODS**

### **(B) Study system**

The Sierra de Guadarrama (central Spain) is an approximately 100 x 30 km mountain range located at 40°45' N 4°00' W. This mountain range (maximum elevation 2430 m) is bordered by two plains, the northern one with a minimum elevation of c. 700 m and the southern one with a minimum of c. 400 m. Typical vegetation types are evergreen broadleaf woodland (largely *Quercus ilex* subsp. *ballota*) below 1000 m, deciduous woodland (largely *Quercus pyrenaica*) at roughly 1000-1500 m, and coniferous woodland (*Pinus sylvestris*) at

approximately 1500-2000 m. Scrub and open grassland are present at all elevations, including above 2000 m (Rivas-Martínez *et al.*, 1987). Temperature decreases at a rate of c. 5.8°C whereas rainfall increases c. 680 mm per km increase in elevation (data for the period 1997-2003; Wilson *et al.*, 2005).

The study system includes 40 sites in and around the Sierra de Guadarrama, representing open areas occurring in natural or semi-natural habitat selected on the basis of accessibility and to provide a representative sample of all elevations in the region (Appendix S1 in Supporting Information, Fig. S1). Butterflies were sampled at 34 sites in 2006, and the full set of 40 sites in 2007 and 2008 (elevation range c. 560-2251 m) using standard methodology (Pollard & Yates, 1993) (Appendix S1). Butterfly distributions were characterized by three response variables based on 2006-2008 data: prevalence (proportion occupied sites), maximum elevational limit (maximum elevation of sites occupied), and minimum elevational limit (minimum elevation of sites occupied).

### **(B) Host plant data**

We classified butterfly species according to the trophic specialization of their larvae following Tolman & Lewington (1997): monophagous (butterflies feeding on plants of a single species), strictly oligophagous (more than one host plant species but only one host plant genus), oligophagous (host plants of various genera from the same family) and polyphagous (host plants of various families). The classification was adapted to the regional context of the study area, meaning that two species (*Cyaniris semiargus*, *Euphydryas aurinia*) classified as polyphagous at European level were classified as strictly oligophagous at regional level. Given the high diversity of potential host plants for Iberian butterflies (García-Barros *et al.* 2013), our analyses focus on a final set of 43 trophically specialized species: all monophagous, strictly oligophagous and those oligophagous butterflies feeding on two host plant genera at most (Appendix S1). In addition to those butterflies identified to genus level

(see Appendix S1), two species were excluded from analyses, *Favonius quercus*, a canopy-dwelling strictly oligophagous species whose occurrence and abundance is probably underestimated by the transect method, and *Libythea celtis*, a monophagous species with no host plant records at the study sites.

To examine the distribution and elevation range limits of potential larval host plants for specialized butterflies, we recorded the presence-absence of plant species at the 40 transect sites by carefully following the route of the 500 x 5 m transect in summer 2008 and spring 2009, with some additional records in 2010. All host plants were identified to species level excepting some taxa from genera *Thymus* and *Rubus*, which were to morphospecies (75 species were identified in total, Table S1). Host plant distributions were characterized by the same three variables as butterfly distributions (prevalence, and maximum and minimum elevations).

Fifteen and five butterfly species showed, respectively, higher maximum or lower minimum elevations than their host plants (Fig. 1, see results below). To test to what extent butterfly occurrence beyond the host plant elevational limits was the result of underrecording host plants that occurred nearby transects, we compared host plant distributions based on the standard 5-m band against those based on a wider 50-m band for five exemplar butterfly species (Appendix S1).

### **(B) Butterfly attributes**

Our first main aim was to determine to what extent range size and elevational limits of host plants govern range size and limits of their specialist herbivores. We expected positive relationships for elevational range sizes and limits between butterflies and their larval host plants. We considered six attributes that potentially contributed to possible departures of individual species from the expected relationship: host plant size (herbaceous vs. woody host plants), host plant part eaten by larvae (flower-fruit vs. leaf feeders), butterfly mobility (low,

medium and high), butterfly species abundance; and two measures of the climatic breadth and limits of each butterfly's environmental niche, based on temperature and precipitation data over the European range (Schweiger *et al.*, 2014). We represent climatic niche breadth by butterfly range temperature and precipitation SD, and climatic limits by maximum and minimum butterfly range temperature and precipitation (Schweiger *et al.*, 2014, see Appendix S1).

### **(B) Butterfly phylogeny**

Traits of related taxa may be similar due to common ancestry and therefore not statistically independent in comparative analyses (Harvey & Pagel, 1991). Ecological traits such as prevalence and elevational limits are emergent 'species-level' attributes rather than individual traits and therefore not in themselves heritable in the same way as morphological traits. However, they may be correlated to phylogeny (Kunin, 2008). To control for potential phylogenetic non-independence in the analyses (see below), a phylogenetic tree of all study species was constructed (Appendix S1, Fig. S2).

### **(B) Environmental data for species richness analysis**

Butterfly species richness is expected to be influenced by host plant richness, but abiotic factors including climate and productivity may directly influence consumer richness, and may impose constraints on the extent to which consumer richness responds to variation in host richness (McCain & Grytnes, 2010). For the period 2006-2012, hourly air temperature and relative humidity were recorded by HOBO H8 Pro temp/RH and U23 Pro v2 temp/RH loggers in semi-shaded conditions at each of the 40 sampling sites (Appendix S1). Site temperature (°C) and relative humidity (%) were calculated from HOBO field data as the average of annual mean temperature and relative humidity, respectively, in 2006-2008. As a surrogate of productivity, actual evapotranspiration was calculated as the average of annual actual evapotranspiration in 2006-2008 (Appendix S1).



## **(B) Statistical analysis**

### *(C) Cross-species analysis*

We used the information-theoretic approach (Burnham & Anderson, 2002) to model prevalence and elevational limits of butterflies following two steps. First, we assessed whether phylogenetic analysis was necessary by comparing residuals from linear models to phylogenetically-adjusted linear models. For each response variable (prevalence, and maximum and minimum elevations), we performed a standard generalized least squares (GLS) model (not accounting for phylogenetic relationships), and two phylogenetic generalized least-squares (PGLS) models using common models for evolutionary change, Brownian motion and Ornstein-Uhlenbeck models (Butler & King, 2004). PGLS adjusts for correlated error structure based on the variance-covariance matrix estimated from the phylogeny. The variance-covariance structure was selected following the general protocol for GLS using packages ‘nlme’ (R Development Core Team, 2014; Pinheiro *et al.*, 2014) and ‘ape’ (Paradis *et al.*, 2004) (Appendix S1).

Second, to select the model(s) on which inference for each response variable was based, we fitted with maximum likelihood all possible models that included different combinations of categorical (if applicable) and linear terms of explanatory variables (including butterfly attributes and host plant elevational range data; Appendix S1) and the selected variance-covariance structure found during the first step. The model confidence set consists of the best model(s) selected from the total collection of possible models fulfilling user-specified criteria (Burnham & Anderson, 2002). In our case, the criteria were (Richards, 2005): (1) select models within six  $\Delta AIC_c$  units of the top-ranked (lowest  $AIC_c$ ) model; (2) within this set, select only those models which did not have simpler, higher-ranking variants (i.e., including a smaller number of the same explanatory variables), thus avoiding over-parameterized models whilst maintaining a high probability of selecting the true best model. Following model

selection, we used model-averaging to obtain model coefficients based on the confidence sets. This incorporates model selection uncertainty whilst weighting the influence of each model by the strength of its supporting evidence. Model-averaged coefficients were derived by weighting using Akaike weights ( $AIC_cw$ ) and averaging coefficients over all models in the confidence set (i.e., coefficient values set to 0 in those models in which a variable was not included) (Burnham & Anderson, 2002; package ‘MuMIn’, Bartoń, 2012). We explored potential inter-correlations among predictor variables prior to model selection (Appendix S1, Table S2). Because minimum butterfly range precipitation and maximum butterfly range temperature were highly collinear ( $r_s = -0.86$ , Table S2), models for butterfly maximum elevation including temperature as an explanatory variable were performed separately from those including precipitation.

After identifying the model confidence sets for butterfly prevalence, and maximum and minimum elevations, hierarchical partitioning was performed to evaluate the independent and joint effects of each variable in single models containing all predictors (Mac Nally & Walsh, 2004). Standard regression and R-squared as the goodness of fit measure were used for hierarchical partitioning calculations. The statistical significance of the independent contributions was tested by a randomization routine (1000 permutations) based on  $Z$  scores (Mac Nally, 2002).

### (C) *Species richness analysis*

In order to quantify species richness for host resources and butterflies, we counted the number of potential host plant species and specialist butterflies, respectively, at each site. Elevational trends in numbers of species for both host plants and butterflies were analysed using quasi-Poisson regression by fitting linear and quadratic models including elevation only. Then, more complex models including number of host plant species, annual mean temperature, relative humidity and actual evapotranspiration in place of elevation, as well as the

interactions between number of host plant species and climate and productivity variables, were tested to explain observed numbers of butterfly species. Linear regression was used in this case because a potential positive relationship between number of butterfly and host plant species was expected. The interaction terms allowed us to test whether the relationship between numbers of butterfly and host plant species varied over climatic gradients (Fleming, 2005). Because annual mean temperature and actual evapotranspiration were highly collinear ( $r_s = -0.71$ , Table S3), models including temperature as an explanatory variable were performed separately from those including actual evapotranspiration (all the remaining correlations between predictor variables had absolute values lower than 0.7, Table S3).

The effect of independent variables on number of butterfly species was examined following the information-theoretic approach using the same protocol as for cross-species analyses. Models were ranked by QAIC<sub>c</sub> for elevational trends and by AIC<sub>c</sub> for the more complex models for number of butterfly species. The effect of spatial autocorrelation of butterfly data was examined using correlograms and they suggested that this phenomenon was negligible (Appendix S1). We also used hierarchical partitioning to evaluate the independent and joint effects of each variable on number of butterfly species (main effects only) in single models containing all predictors following the same protocol as above.

## **(A) RESULTS**

We recorded 64142 individuals from 97 species (plus 4 genera not identified to species level) across all 40 sites and 3 years. The 43 study species (specialists,  $n = 23780$  individuals) had on average lesser prevalence, and attained lower maximum and higher minimum elevations than the remaining 54 species (all Mann-Whitney tests,  $P = 0.05-0.02$ ). Butterfly prevalence for the 43 study species ranged from 0.025 (3 species) to 1 (2 species). Butterfly maximum elevation ranged from 558 m (the lowest site elevation; 1 species) to 2251 m (the highest site elevation; 11 species) (Fig. 1). Butterfly minimum elevation showed less variability than

maximum elevation, ranging from 558 m (the lowest site elevation; 9 species) to 1445 m (1 species).

There were 15 and five butterfly species that showed, respectively, higher maximum or lower minimum elevations than their host plants (Fig. 1). Upper elevational limits for butterflies were more likely to exceed those of their host plants in high mobility species (6/10 species) than medium and low mobility species (9/33 species).

### **(B) Cross-species analysis**

We tested one non-phylogenetic and two different models of evolutionary change for butterfly prevalence, and for maximum and minimum elevations (with two model sets for maximum elevation excluding alternatively maximum butterfly range precipitation and minimum butterfly range temperature). In the four cases,  $AIC_c$  values were the smallest for the non-phylogenetic model and  $\Delta AIC_c$  exceeded 2 in the evolutionary models (Ornstein-Uhlenbeck model did not converge for butterfly maximum and minimum elevation) (Table S4). This suggested that phylogenetic correction was not appropriate (subject to the evolutionary models considered) for cross-species analyses.

For butterfly prevalence, the confidence set consisted of just one model (Table 1), and indicated that butterfly prevalence increased with increasing host plant prevalence, butterfly mobility index (particularly for high mobility) and abundance (Fig. 2). Including an additional interaction term for ‘host plant prevalence x mobility’ increased the  $AIC_c$  value by 5.72 units relative to the best model (Table 1), suggesting a common slope for butterfly-host plant prevalence relationships for species differing in mobility.

For butterfly maximum elevation (excluding the predictor maximum butterfly range precipitation), the confidence set consisted of four models (Table 1). The final averaged model indicated that butterfly maximum elevation increased with increasing host plant maximum elevation and increasing butterfly abundance, and decreased for flower-fruits eaters

and with increasing minimum butterfly range temperature (Figs 2 and S3). Including interaction terms for 'host plant maximum elevation x host plant part eaten' and 'minimum butterfly range temperature x host plant part eaten' increased  $AIC_c$  values by 2.74 and 0.84 units, respectively, relative to a model containing the four main terms with no interactions: this suggested a common slope for butterfly-host plant maximum elevation relationships and butterfly maximum elevation-minimum range temperature relationships for species differing in host plant part eaten. The effect of host plant maximum elevation on butterfly maximum elevation could partly arise because herbivore and resource will inevitably coincide at the highest elevations in species living near the top of the gradient. Excluding the 14 butterfly species occurring above 2000 m produced a confidence set consisting of two simpler models that explained less variance but maintained the effects of host plant maximum elevation and butterfly minimum temperature (Table S5). All models for butterfly maximum elevation excluding minimum butterfly range temperature from the predictor set had higher  $AIC_c$  values than those excluding maximum butterfly range precipitation (Tables 1 and S5), suggesting that temperature was more important than precipitation in accounting for butterfly upper elevational limits (see also hierarchical partitioning analyses below).

For butterfly minimum elevation, the confidence set consisted of one model including negative effects of butterfly abundance and maximum butterfly range temperature (Table 1), indicating that species with greater abundance or greater tolerance of high temperatures reached lower elevations (Fig. 2). Excluding the 19 species occurring below 750 m generated a confidence set of two models that explained more variance, maintained the effects of abundance and maximum butterfly range temperature and also included the effect of butterfly mobility (Table S5).

The results from hierarchical partitioning analyses mostly supported results from the information-theoretic approach (Appendix S1, Fig. S4), showing significant effects of host

plant prevalence, butterfly mobility and abundance on prevalence; and significant effects of host plant and environmental niche temperature limits on upper and lower elevation limits.

### **(B) Species richness analysis**

Number of host plant species showed a unimodal relationship with elevation (number of host plant species =  $\exp[1.05 (\pm 0.48) + 3.83 (\pm 0.77) \text{ elevation} - 1.73 (\pm 0.30) \text{ elevation}^2]$ , elevation in km), with a mid-elevational peak in predicted number of species at 1105 m (Fig. 3). This model had a much smaller QAIC<sub>c</sub> than the linear and the null (intercept-only) models ( $\Delta\text{QAIC}_c = 37.87$  and  $74.13$ , respectively), strongly supporting the unimodal pattern. Based on the model, the predicted number of host plant species for the lowest site (558 m) was c. 14 species, with only c. 2.4 host plant species estimated for the highest site (2251 m). Number of specialist butterfly species represented on average 37% (range 15-46%) of species in an assemblage (excluding taxa identified to genus level), and showed a unimodal relationship with elevation (number of butterfly species =  $\exp[0.42 (\pm 0.43) + 3.71 (\pm 0.64) \text{ elevation} - 1.32 (\pm 0.23) \text{ elevation}^2]$ , elevation in km;  $\Delta\text{QAIC}_c = 35.86$  and  $33.94$  for the linear and null models, respectively) (Fig. 3). The number of butterfly species predicted by the model peaked c. 300 m higher in elevation (1404 m) than the number of host plant species.

Annual mean temperature was highly negatively correlated with elevation, whereas annual actual evapotranspiration and mean relative humidity were positively correlated with elevation, but relative humidity showed a decreasing pattern above 1700 m (Fig. S5). For the more complex model for number of butterfly species considering number of host plants, temperature and relative humidity, the confidence set consisted of three models (Table 2). The final averaged model included number of host plant species, annual mean temperature and their interaction, and annual mean relative humidity as explanatory variables (Table 2). Thus, the magnitude of the positive relationship between number of butterfly and host plant species was largely dependent on temperature, with an increasing slope as temperature decreased

(Fig. 4). For the alternative model including annual actual evapotranspiration instead of temperature, the confidence set consisted of three models with higher  $AIC_c$  than for the set including temperature, and the final averaged model included the three variables with no interactions (Table S6). The results from hierarchical partitioning analyses (including main effects only) showed that number of host plant species and relative humidity were significantly related to number of butterfly species (Fig. S6).

## **(A) DISCUSSION**

Our results show that host plants had strong effects on both the species distributions and richness patterns of specialist butterflies over an elevational gradient, supporting the hypothesis of bottom-up control of herbivore diversity. The results suggest that consumer richness tracked the environment to a large extent through the sum of effects of resource constraints on individual species ranges. Nevertheless, host plant limitations were more important towards the highest part of the elevational gradient, suggesting that the effects of consumer-resource interactions were context dependent (Meier *et al.*, 2011).

Host plant distributions imposed limits on butterfly ranges, but mostly through constraints on upper elevational limits (Fig. 2), as inferred using distribution models for a similar system elsewhere in Europe (Hanspach *et al.*, 2014). Estimated maximum and minimum temperature tolerances, inferred from the geographic ranges of the study species, appeared to influence lower and upper elevation range limits respectively; but host plant elevational limits only influenced the upper elevation limits of the butterflies. We do not have data to test whether the effects of competition and predation were stronger at lower elevations, and the biogeographically inferred temperature tolerances of species could mask the effects of species interactions on geographic ranges, but our results suggest that biotic interactions are more important in limiting ranges at cooler than at warmer parts of species' distributions (but see MacArthur, 1972). These results are consistent with more detailed research on the species

*Aporia crategi* in the same area, which suggested that climatic limitation was the most likely explanation for the lower elevational limit, whereas the absence of host plants from high altitudes set the upper limit (Merrill *et al.*, 2008).

Our multi-species approach allowed us to show joint elevational patterns of species richness for consumers and resources (which have rarely been reported before: e.g., Rodríguez-Castañeda *et al.*, 2010), showing typical peaks in numbers of species at medium elevations for both taxa (McCain & Grytnes, 2010). We found a peak in number of species at c. 1400 m for the specialist butterflies, consistent with the pattern previously shown for the whole species pool (Gutiérrez Illán *et al.*, 2010). Nevertheless, two major points emerged when comparing host plant and butterfly richness patterns. First, host plant species richness was particularly low at the highest locations (Fig. 3), supporting (along with the results for individual species) the idea that butterfly elevational ranges were constrained by host plant distributions at the part of the gradient with lower resource diversity, as reported for Himalayan birds (Price *et al.*, 2011). Second, the species richness peak for plants was c. 300 m lower than that for butterflies. Hence there was a mid-elevation section (1100-1400 m) with relatively low numbers of species of butterflies for the diversity of host plants occurring there.

Elevational species richness gradients may be influenced by patterns of human impact, which is usually more intensive at low elevations (Nogués-Bravo *et al.*, 2008). Although, based on land cover, we estimated that human impact was higher in the adjacent habitat to the lowest sites, we also found that, on average, fairly large areas of natural and semi-natural habitat remain at all elevations (> 90%, Appendix S1), suggesting that species richness patterns represent robust relationships of butterfly diversity with host plant species richness and climatic variables.

The relatively congruent elevational pattern of both taxa resulted in a strongly positive relationship between numbers of species of butterflies and host plants (Fig. 4), supporting the



'resource diversity hypothesis' (Hutchinson, 1959). Previous work on consumer assemblages has identified resource diversity as a strong predictor of species numbers (Kissling *et al.*, 2007; Menéndez *et al.*, 2007). However, it has also been shown that correlations between consumer and resource diversity can result from both groups responding to similar environmental variables and not from a causal inter-relationship (Hawkins & Porter, 2003a). Based on the results for the elevational distributions of each butterfly species and their host plants (see above) and hierarchical partitioning, the most plausible hypothesis is that the relationship between numbers of butterfly and host plant species was due to trophic dependency, and hence consumer richness would result from bottom-up control.

Once the effects of number of host plant species were accounted for, butterfly species richness tended to be greater in cooler sites (Fig. 4), and in sites with higher relative humidity. Butterfly species richness also responded more positively to number of host plant species in cooler sites, corresponding to higher elevation sites in the study system. To our knowledge, geographical differences in the strength of the relationship between consumer and resource diversity have until now not been studied over a given environmental gradient. Two potential processes could be responsible for such a pattern (Fleming, 2005): (1) between-site differences in the strength of bottom-up control of animal diversity by plant diversity; and (2) between-site differences in the degree of specialization of ecological interactions (Novotný *et al.*, 2006). Given that our study concentrated on butterflies that were relative host plant specialists, it is unlikely that the second process contributed much to the pattern. This fact, along with the apparently greater effect of host plant distribution in limiting upper than lower limits of butterfly elevational ranges, suggests that the steepness of the relationship between consumer and resource richness could be due to differences in the strength of bottom-up control. The most plausible explanation is that butterfly richness is tied most closely to number of host plant species in locations where other biotic (e.g., host plant nutritional

quality, natural enemies, habitat connectivity) or abiotic factors (e.g., limits to thermal tolerance or growing season) are least restrictive to colonization and survival. Our results suggest that direct (non-host related) environmental constraints were strongest in the hotter, drier, lower elevation parts of the study system (Fig. S5), which also had the lowest values for actual evapotranspiration. Indeed, an alternative model to that using temperature suggested that butterfly richness was positively related to actual evapotranspiration. This observation, combined with the positive effect of relative humidity, suggests that butterfly species richness could be influenced by water stress, either directly, or through effects on host plant nutritional quality (Hawkins & Porter, 2003b; Stefanescu *et al.*, 2011).

Our cross-species analyses provide evidence for the role of ecological traits in governing the strength of the relationship between the distributions of consumers and their resources. More dispersive and abundant species were more likely to occupy a larger fraction of their host elevational range, presumably because of higher rates of host patch colonization and reduced rates of local extinction (Hanski, 1999; Hopkins *et al.*, 2002). Host plant part eaten also affected butterfly distribution: as expected, species whose juvenile stages feed on flower-fruits had lower upper elevational limits than species feeding on leaves. The more ephemeral availability of flowers and fruits, and their high temporal variability (Thompson & Gilbert, 2014) may increase the chance of asynchrony with consumers, and drive reduced survival and consequently reduced occupancy relative to leaf feeders (Rodríguez *et al.*, 1994).

Some butterfly species presented elevational ranges that exceeded the distribution of their larval resources (Fig. 1). There are three potential non-exclusive explanations for this pattern: (1) seasonal elevational migrations, (2) incomplete sampling of known host plants, and (3) cryptic species and unknown host plant species. (1) The best known case in our study area is *Gonepteryx rhamni*, which undergoes seasonal elevational migrations in summer up to 750 m above the highest elevation of host plants (Gutiérrez & Wilson, 2014); it is possible that

similar migratory phenomena explain why 6/10 of high mobility species showed higher upper elevational limits than their host plants. The variance associated with seasonal migrations is expected to be partly captured by including butterfly mobility and abundance as explanatory variables in the cross-species analyses. (2) Our tests based on comparing host plant elevational ranges based on 5- and 50-m bands for five exemplar butterfly species suggest that, in some cases, there could have been unrecorded nearby host plants outside the 5-m transect band: this could explain the fact that the *Frangula-Rhamnus* feeding species (*Gonepteryx* spp. and *Satyrium spini*) represented three of the five species whose *lower* elevational limits were lower than that of their host plants. (3) Recent studies suggest that cryptic species (those overlooked due to their morphological similarity, but sometimes displaying different ecologies including larval host plant taxonomic identity) can be commoner than expected in butterfly taxa. While the incidence of this factor in our dataset is most probably minor, it could explain specific cases such as the low mobility species *Spialia sertorius*, for which the existence of two deeply diverged mitochondrial lineages in the Iberian Peninsula has been documented (Dincă *et al.*, 2015). Points (2) and (3) represent additional sources of variance that might influence our model selection process, but there is no reason to suspect any systematic bias in their incidence relative to butterfly species attributes. Nevertheless, the fact that some butterfly species occurred at higher elevations than their host plants, may potentially contribute to the differences observed in host plant and butterfly richness patterns.

Our results were based on a subset of specialist consumers, for which resource diversity could be more constraining than for generalist species (Menéndez *et al.*, 2007). It would be interesting to know whether generalist species show a similar pattern, but obtaining the necessary data for polyphagous butterflies and their host plants at similar scale and resolution would represent a major challenge. We thus advocate wider exploration of consumer-host

relationships over elevational gradients to provide further evidence of the role of biotic interactions in limiting species distributions and influencing patterns of diversity.

The study suggests that the effect of resources on consumer distributions and diversity can be asymmetric over environmental gradients, with variation in the strength of bottom-up biotic limitation. In this case, resource limitation showed greater importance towards upper than lower elevation limits. Increasing limitation by resource availability at the cool range margins of specialist consumers has been inferred from models of butterfly distributions under current (Hanspach *et al.*, 2014) and future climatic conditions (Schweiger *et al.*, 2012; Romo *et al.*, 2014): here, we provide fine-resolution empirical evidence of how host-plant use already constrains species distributions at cool range margins, suggesting that biotic interactions can play an increasing role in determining consumer diversity toward the coolest and most resource species-poor parts of a geographic gradient.

#### **(A) ACKNOWLEDGEMENTS**

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#### **(A) SUPPORTING INFORMATION**

Appendix S1 Supplementary methods and results.

### (A) BIOSKETCHES

**David Gutiérrez** is a senior lecturer in ecology at the Universidad Rey Juan Carlos, Spain.

He is a specialist in metapopulation dynamics of butterflies in fragmented landscapes, and in the biogeography of insect communities in mountain systems in the context of climate change.

**Roger Vila** is a CSIC Scientist at Institute of Evolutionary Biology (CSIC-UPF) in Barcelona, Spain, where he leads the Butterfly Diversity and Evolution Lab. He uses butterflies as a model to study large-scale biodiversity patterns, spanning from speciation to conservation biogeography.

**Robert J. Wilson** is a senior lecturer at the University of Exeter, UK. His research examines the ecological effects of climate change and habitat fragmentation, with particular focus on the distributions and dynamics of species near their geographic range margins.

### (A) REFERENCES

Bartoń, K. (2012) Multi-model inference. R package, version 1.6.6. Available at:

<http://CRAN.R-project.org/package=MUMIn>. Last accessed 19 January 2012.

Boucher-Lalonde, V., Kerr, J.T. & Currie, D.J. (2014) Does climate limit species richness by limiting individual species' ranges? *Proceedings of the Royal Society B*, **281**, 20132695.

Brown, J.H., Ernest, S.K.M., Parody, J.M. & Haskell, J.P. (2001) Regulation of diversity: maintenance of species richness in changing environments. *Oecologia*, **126**, 321-332.

Burnham K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. Springer, New York, NY, USA.

Butler, M.A. & King, A.A. (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *American Naturalist*, **164**, 683-695.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu,

- H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., & Wiens, J.J. (2014) Causes of warm-edge limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, **41**, 429-442.
- Dincă, V., Montagud, S., Talavera, G., Hernández-Roldán, J., Munguira, M., García-Barros, E., Hebert, P. & Vila, R. (2015) DNA barcode reference library for Iberian butterflies enables a continental-scale preview of potential cryptic diversity. *Scientific Reports*, **5**, 12395.
- Fleming, T.H. (2005) The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos*, **111**, 556-562.
- García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives Moreno, A. (2013) *Lepidoptera Papilionoidea*. Fauna ibérica vol. 37 (ed. by M.A. Ramos *et al.*), pp. 1-1213. Museo Nacional de Ciencias Naturales, CSIC, Madrid.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford, UK.
- Gutiérrez, D. & Wilson, R.J. (2014) Climate conditions and resource availability drive return elevational migrations in a single-brooded insect. *Oecologia*, **175**, 861–873.
- Gutiérrez Illán, J., Gutiérrez, D. & Wilson, R.J. (2010) Fine-scale determinants of butterfly species richness and composition in a mountain region. *Journal of Biogeography*, **37**, 1706–1720.
- Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Hanspach, J., Schweiger, O., Kühn, I., Plattner, M., Pearman, P.B., Zimmermann, N.E. & Settele, J. (2014) Host plant availability potentially limits butterfly distributions under cold environmental conditions. *Ecography*, **37**, 301-308.
- Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford

University Press, Oxford, UK.

Hawkins, B.A. & Porter, E.E. (2003a) Does herbivore diversity depend on plant diversity?

The case of California butterflies. *American Naturalist*, **161**, 40-49.

Hawkins, B.A. & Porter, E.E. (2003b) Water-energy balance and the geographic pattern of

species richness of western Palearctic butterflies. *Ecological Entomology*, **28**, 678-686.

Hopkins, G.W., Thacker, J.I., Dixon, A.F.G., Waring, P. & Telfer, M.G. (2002) Identifying

rarity in insects: the importance of host plant range. *Biological Conservation*, **105**, 293-307.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of

animals? *American Naturalist*, **93**, 145-159.

Kaufman, D.M. (1995) Diversity of New World mammals: universality of the latitudinal

gradients of species and bauplans. *Journal of Mammalogy*, **76**, 322-334.

Kissling, W.D., Rahbek, C. & Böhning-Gaese, K. (2007) Food plant diversity as broad-scale

determinant of avian frugivore richness. *Proceedings of the Royal Society B*, **274**, 799-808.

Kunin, W.E. (2008) On comparative analyses involving non-heritable traits: why half a loaf is

sometimes worse than none. *Evolutionary Ecology Research*, **10**, 787-796.

Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and when do species interactions

set range limits? *Trends in Ecology and Evolution*, **30**, 780-791.

Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology:

further comment of identifying important predictor variables. *Biodiversity and Conservation*, **11**, 1397-1401.

Mac Nally, R. & Walsh, C.J. (2004) Hierarchical partitioning public domain software.

*Biodiversity and Conservation*, **13**, 659-660.

MacArthur, R.H. (1972) *Geographical ecology. Patterns in the distribution of species.*

Princeton University Press, Princeton, NJ, USA.

- McCain, C.M. & Grytnes, J.A. (2010) *Elevational gradients in species richness*. Encyclopedia of life sciences, pp. 1-10. John Wiley & Sons, Ltd, Chichester.
- Meier, E.S., Edwards Jr, T.C., Kienast, F., Dobbertin, M. & Zimmermann, N.E. (2011) Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, **38**, 371-382.
- Menéndez, R., González-Megías, A., Collingham, Y., Fox, R., Roy, D.B., Ohlemüller, R. & Thomas, C.D. (2007) Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology*, **88**, 605-611.
- Merrill, R.M., Gutiérrez, D., Lewis, O.T., Gutiérrez, J., Díez, S.B. & Wilson, R.J. (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, **77**, 145-155.
- Nogués-Bravo, D., Araújo, M.B., Romdal, T. & Rahbek, C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–220.
- Novotný, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G.D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*, **313**, 1115-1118.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.
- Pinheiro, J., Bates, D., Debroy, S. & Sarkar, D. (2014) Linear and nonlinear mixed effects models: package ‘nlme’. R package, version 3.1-118. Available at: <http://cran.r-project.org/web/packages/nlme/index.html>. Last accessed 3 December 2014.
- Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation*. Chapman & Hall, London, UK.
- Price, T.D., Mohan, D., Tietze, D.T., Hooper, D.M., Orme, C.D.L. & Rasmussen, P.C. (2011)



- Determinants of northerly range limits along the Himalayan bird diversity gradient. *American Naturalist*, **178**, S97-S108.
- Quinn, R.M., Gaston, K.J. & Roy, D.B. (1998) Coincidence in the distributions of butterflies and their foodplants. *Ecography*, **21**, 279-288.
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: <http://www.R-project.org/>. Last accessed 13 February 2014.
- Richards S.A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, **86**, 2805-2814.
- Rivas-Martínez, S., Fernández González, F. & Sánchez-Mata, D. (1987) *El Sistema Central: de la Sierra de Ayllón a Serra da Estrela*. La vegetación de España (ed. by M. Peinado Lorca and S. Rivas-Martínez), pp. 419-451. Universidad de Alcalá de Henares, Alcalá de Henares.
- Rodríguez, J., Jordano, D. & Fernández Haeger, J. (1994) Spatial heterogeneity in a butterfly-host plant interaction. *Journal of Animal Ecology*, **63**, 31-38.
- Rodríguez-Castañeda, G., Dyer, L.A., Brehm, G., Connahs, H., Forkner, R.E. & Walla, T.R. (2010) Tropical forests are not flat: how mountains affect herbivore diversity. *Ecology Letters*, **13**, 1348-1357.
- Romo, H., García-Barros, E., Márquez, A.L., Moreno, J.C. & Real, R. (2014) Effects of climate change on the distribution of ecologically interacting species: butterflies and their main food plants in Spain. *Ecography*, **37**, 1063-1072.
- Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, J. & Settele, J. (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, **21**, 88-99.

- Schweiger, O., Harpke, A., Wiemers, M. & Settele, J. (2014) CLIMBER: Climatic niche characteristics of the butterflies in Europe. *ZooKeys*, **367**, 65-84.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics*, **40**, 415-436.
- Stefanescu, C., Carnicer, J. & Peñuelas, J. (2011) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography*, **34**, 353-363.
- Thompson, K. & Gilbert, F. (2014) Phenological synchrony between a plant and a specialised herbivore. *Basic and Applied Ecology*, **15**, 353-361.
- Tolman, T. & Lewington, R. (1997) *Butterflies of Britain and Europe*. HarperCollins Publishers, London, UK.
- Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138-1146.

Table 1. Confidence sets of regression models for (a) prevalence, (b) maximum elevation (excluding maximum butterfly range precipitation from the predictor set), and (c) minimum elevation of butterflies.  $n = 43$  species in all cases.  $K$ : number of parameters (includes a parameter for regression variance);  $R^2$ : coefficient of determination;  $AIC_c$ : Akaike Information Criterion for small sample size;  $\Delta AIC_c$ : difference in  $AIC_c$  between current and 'best' model;  $AIC_{cw}$ : Akaike weight. Host plant part and mobility are categorical variables with 'leaves' and 'low mobility' as reference levels.

a) Models for butterfly prevalence	$K$	$R^2$	$AIC_c$	$\Delta AIC_c$	$AIC_{cw}$
Host plant prevalence + mobility + butterfly abundance	6	0.80	-34.40	0	1
b) Models for butterfly maximum elevation					
Host plant maximum elevation + host plant part + butterfly abundance + minimum butterfly range temperature	6	0.70	16.57	0	0.36
Host plant maximum elevation + host plant part + minimum butterfly range temperature	5	0.68	16.87	0.30	0.31
Host plant maximum elevation + butterfly abundance + minimum butterfly range temperature	5	0.68	17.07	0.50	0.28
Host plant maximum elevation + minimum butterfly range temperature	4	0.63	20.93	4.37	0.04
c) Models for butterfly minimum elevation					
Butterfly abundance + maximum butterfly range temperature	4	0.49	-17.20	0	1

Parameter estimates ( $\pm$  adjusted SE) for the model averaged confidence sets are:

a) Butterfly prevalence =  $-0.09 (\pm 0.05) + 0.34 (\pm 0.08)$  host plant prevalence +  $0.09 (\pm 0.05)$

medium mobility + 0.32 ( $\pm 0.06$ ) high mobility + 0.29 ( $\pm 0.06$ ) butterfly abundance

b) Butterfly maximum elevation = 0.95 ( $\pm 0.18$ ) + 0.43 ( $\pm 0.11$ ) host plant maximum elevation (km) - 0.17 ( $\pm 0.13$ ) flower-fruits + 0.14 ( $\pm 0.12$ ) butterfly abundance - 0.05 ( $\pm 0.02$ ) minimum butterfly range temperature

c) Butterfly minimum elevation = 4.39 ( $\pm 0.60$ ) - 0.23 ( $\pm 0.07$ ) butterfly abundance - 0.19 ( $\pm 0.03$ ) maximum butterfly range temperature

Table 2. Confidence sets of regression models for number of butterfly species including number of host plant species, annual mean temperature and annual mean relative humidity as predictor variables ( $n = 40$  sites). Codes as in Table 1.

Model	$K$	$R^2$	$AIC_c$	$\Delta AIC_c$	$AIC_{cw}$
Number of host plant species + annual mean temperature + (number of host plant species x annual mean temperature)	5	0.60	230.59	0	0.82
Number of host plant species + annual mean temperature	4	0.53	234.51	3.92	0.11
Number of host plant species + annual mean relative humidity	4	0.51	235.50	4.91	0.07

Parameter estimates ( $\pm$  adjusted SE) for the model-averaged confidence set are:

Number of butterfly species = 5.04 ( $\pm 12.47$ ) + 1.40 ( $\pm 0.57$ ) number of host plant species - 0.04 ( $\pm 0.75$ ) annual mean temperature - 0.09 ( $\pm 0.04$ ) (number of host plant species x annual mean temperature) + 0.04 ( $\pm 0.15$ ) annual mean relative humidity

## FIGURE LEGENDS

Fig. 1. Elevational range for 43 butterfly species (black) and their host plants (grey). Circles (butterflies) and diamonds (host plants) represent mean elevation of occupied sites. Butterfly species classified by mobility (three categories) and ordered by their mean elevation (lowest to highest) within mobility categories. Asterisks indicate species feeding on flower-fruits. The dashed thin lines represent 750 m and 2000 m in elevation used as reference to exclude those species living at the bottom and the top of the gradient (see Results for further details).

Fig. 2. Relationship between (a) butterfly prevalence and host plant prevalence, (b) butterfly maximum elevation and host plant maximum elevation, and (c) butterfly minimum elevation and maximum butterfly range temperature. Different symbols and lines represent (in a) species differing in mobility (low mobility: open symbol, dotted line; medium mobility: crossed symbol, dashed line; high mobility: filled symbol, solid line), and (in b) host plant part eaten (leaves: circles, thick line; flowers-fruits: squares, thin line). The lines of best fit represent the equations in Table 1, based on linear regression applied (in a and c) to species of average  $\ln(\text{abundance})$ , and (in b) to species of average  $\ln(\text{abundance})$  and minimum butterfly range temperature ( $n = 43$  species).

Fig. 3. Relationship between (a) number of host plant species, (b) number of butterfly species, and elevation. Different symbols in (b) represent sites sampled over 2 (open symbol) and 3 (filled symbols) years. The lines of best fit represent the equations in the text, based on quasi-Poisson regression ( $n = 40$  sites). Vertical dashed thin lines represent the elevation of maximum predicted number of butterfly (a) and host plant species (b).

Fig. 4. Relationship between number of butterfly species and number of host plant species for

40 sites. For illustrative purposes, different symbols represent 13 sites with annual mean temperatures below 8°C (triangles), 13 sites with temperatures between 8 and 11°C (diamonds), and 14 sites with temperatures above 11°C (circles) sampled over 2 (open symbol) and 3 (filled symbol) years. The lines of best fit represent the equation in the text, based on linear regression applied to the average temperature of sites included in each interval: 6.5°C (solid line), 9.2°C (dashed line), and 12.4°C (dotted line). Lines only extend over the range of number of host plant species at sites in each temperature interval. Annual mean relative humidity averaged for all 40 sites was 71.6%.

Figure 1

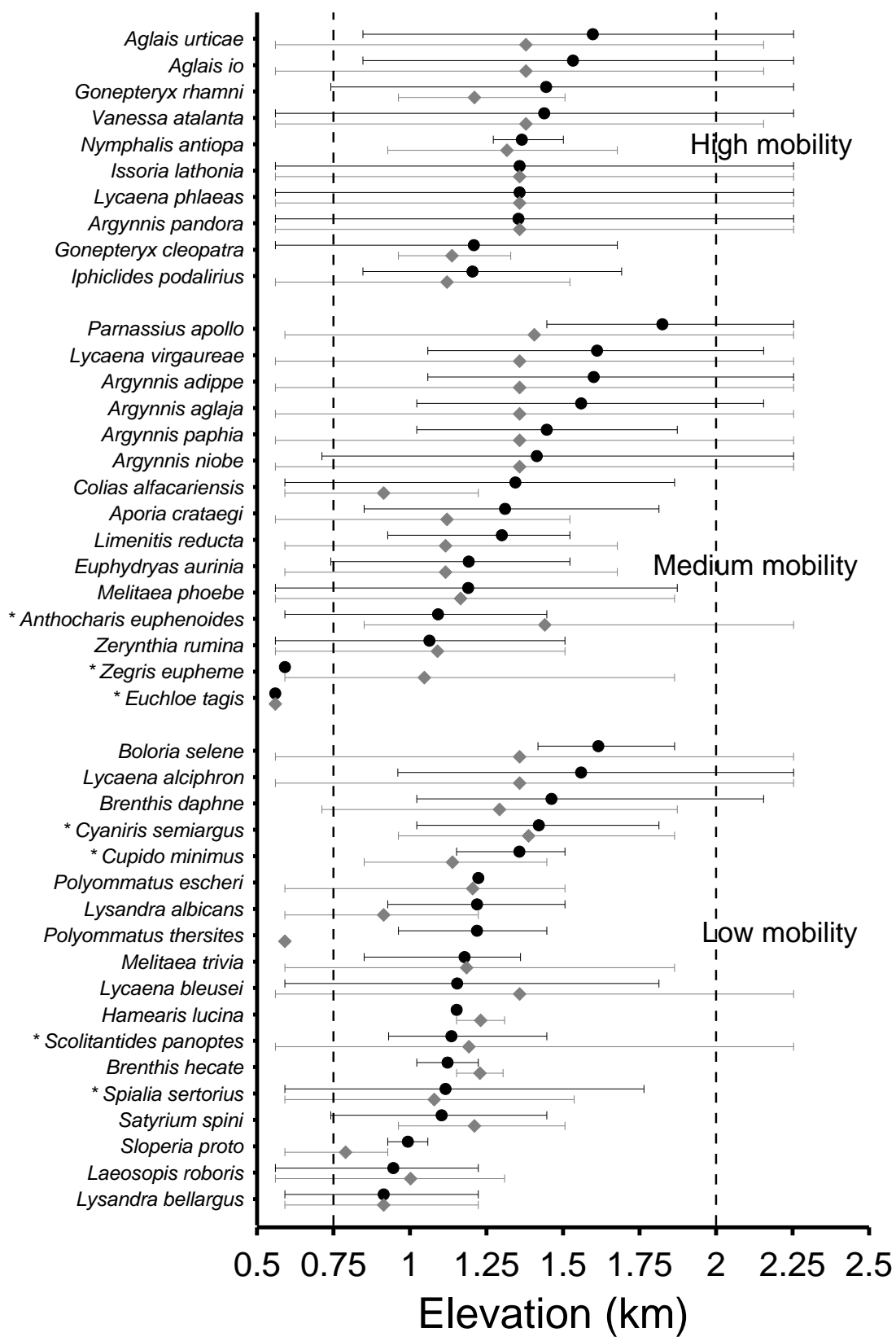




Figure 2

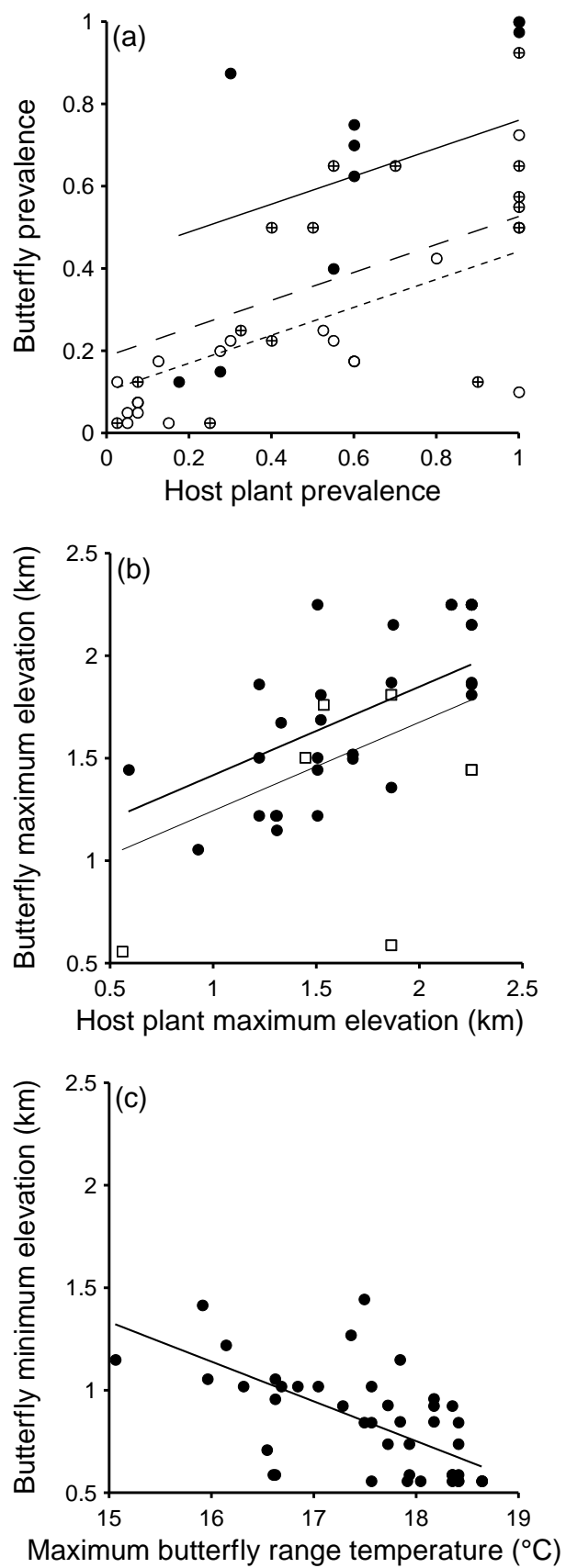


Figure 3

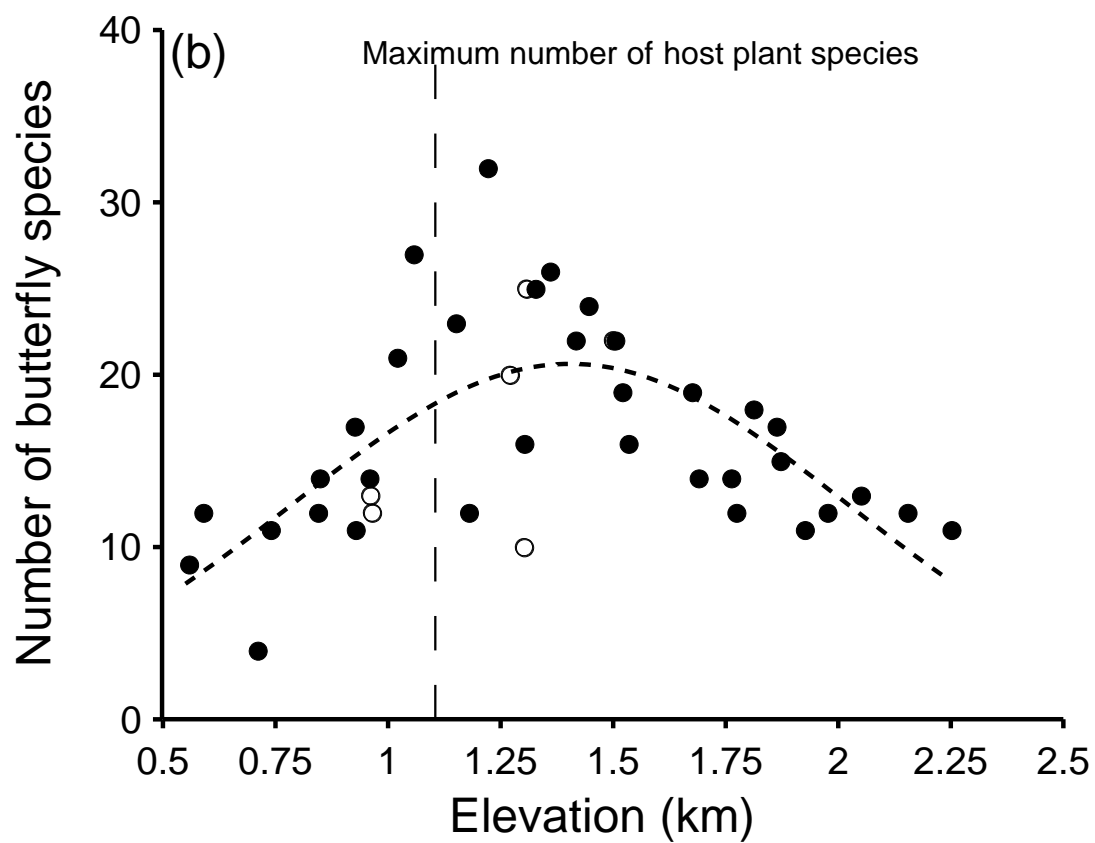
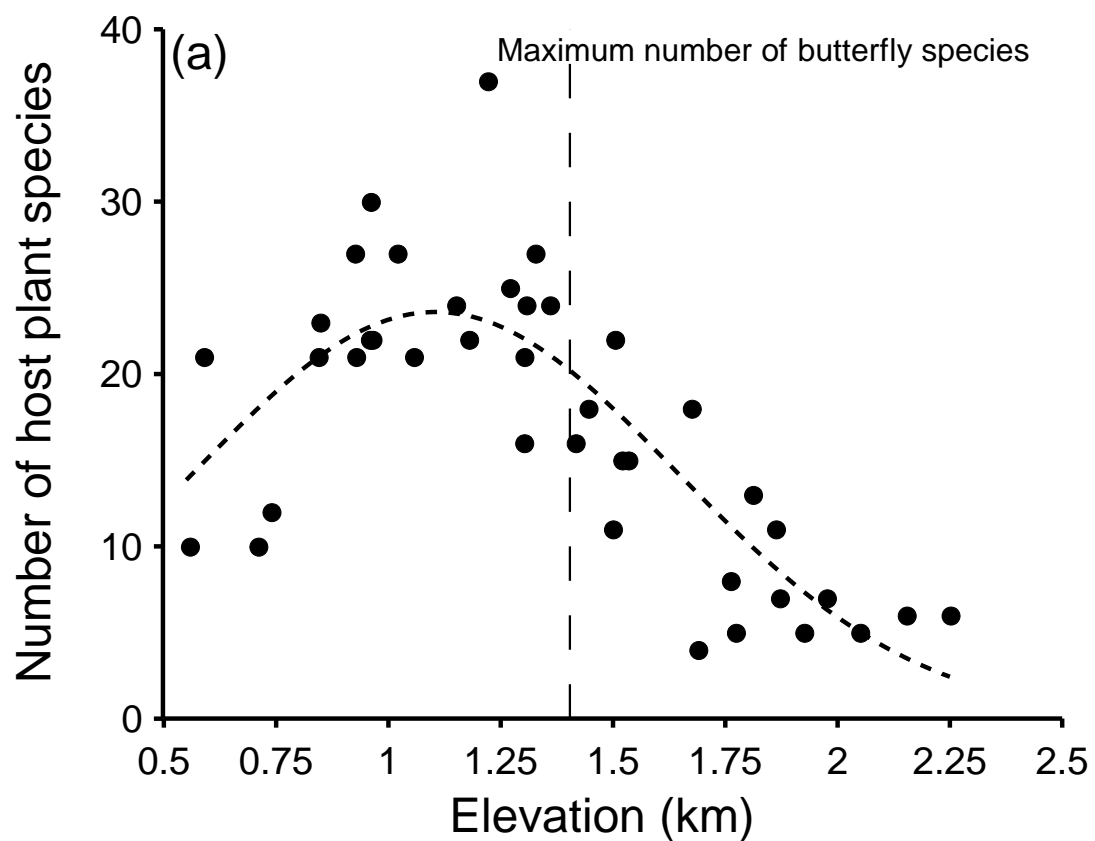
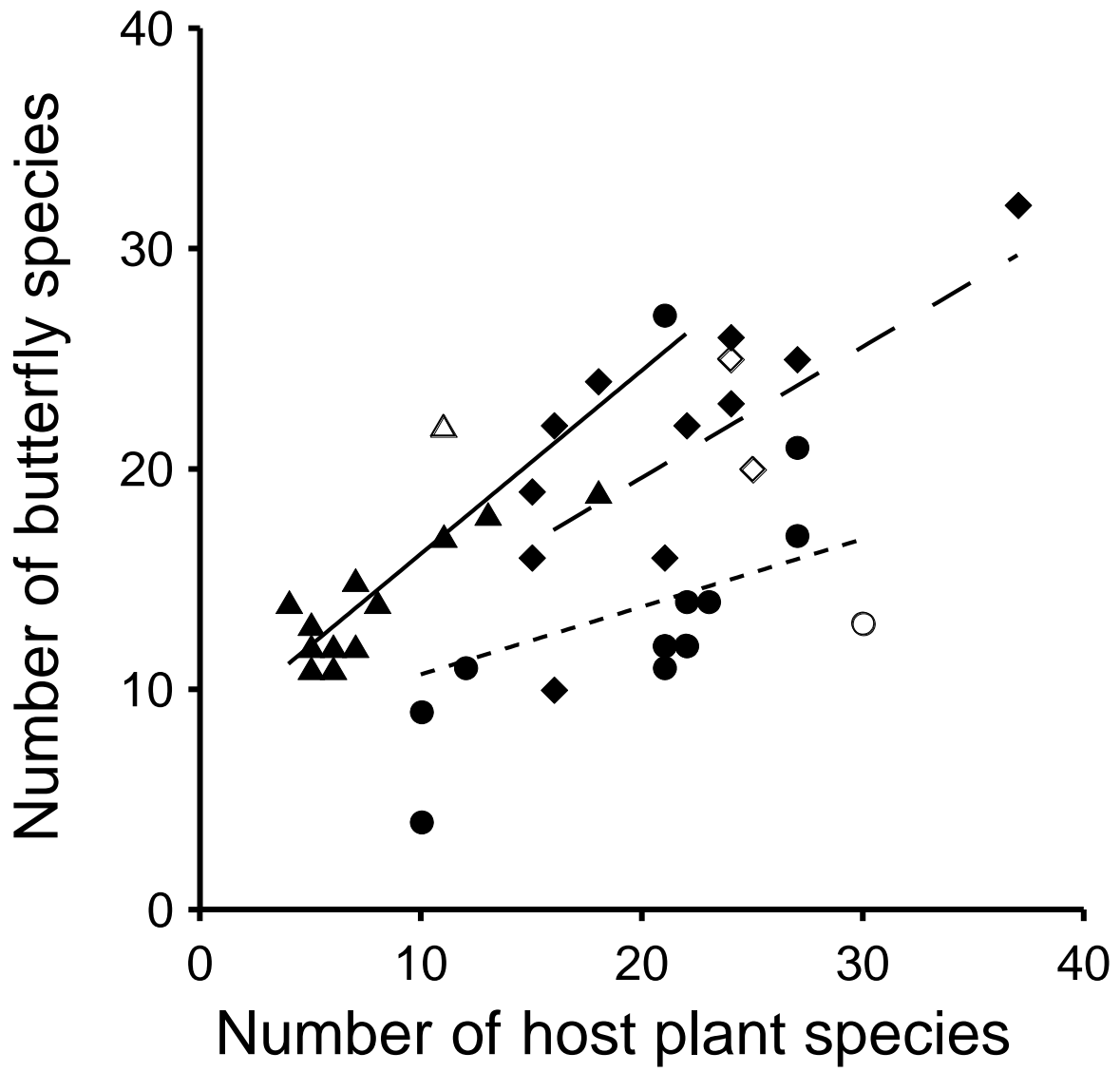


Figure 4



## **Asymmetric constraints on limits to species ranges influence consumer-resource richness over an environmental gradient**

David Gutiérrez, Roger Vila and Robert J. Wilson

### **Appendix S1. Supplementary methods and results**

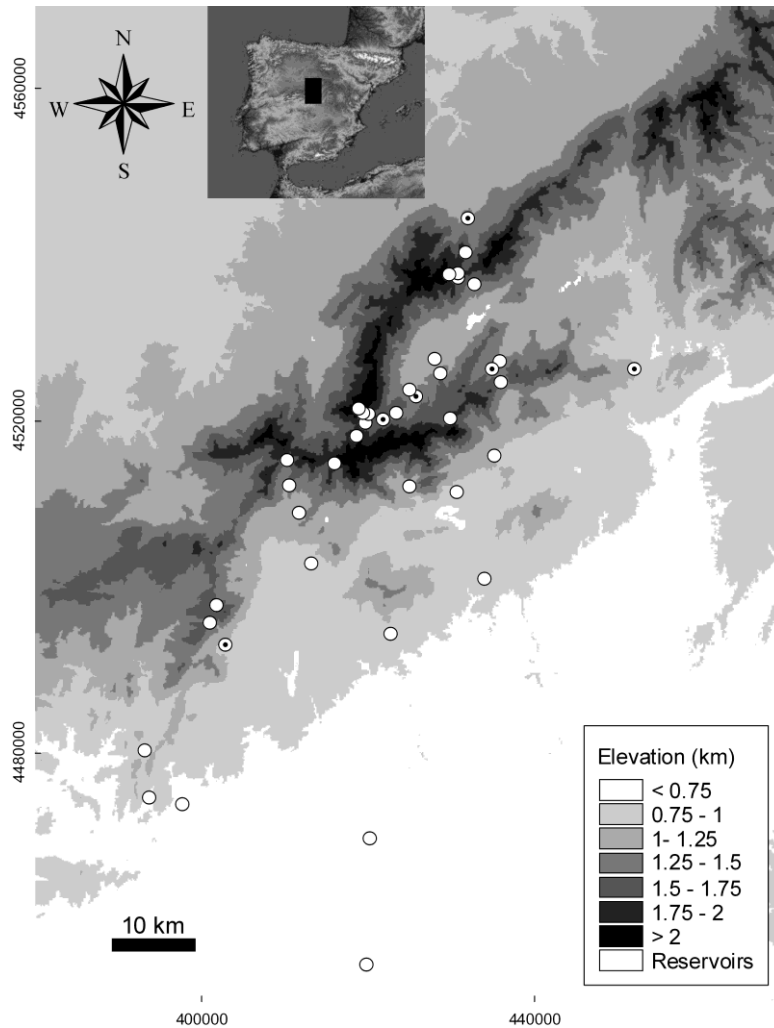
#### **METHODS**

##### **Study system**

Butterflies were sampled at 34 sites in 2006, and 40 sites in 2007 and 2008 (elevation range c. 560-2251 m) (Fig. S1). On the first visit to each site, we established a 500 m transect route, recording Universal Transverse Mercator (UTM) coordinates to the nearest metre at least every 100 m using a handheld Garmin GPS unit. The coordinates were used to plot each transect in ArcGIS 10.1 (ESRI, 2012). The average elevation of 100 m cells intercepted by transects was determined using a digital elevation model interpolated from the original c. 80 m resolution (Farr *et al.*, 2007). Standardized 500 m long x 5 m wide transects were walked at each site every two weeks during suitable conditions for butterfly activity (Pollard & Yates, 1993), from April to October in 2006, and from March to October in 2007-2008. Individuals from some species in the genera *Carcharodus* (*C. alceae*, *C. boeticus*, *C. flocciferus*), *Pyrgus* (all species), *Satyrrium* (*S. esculi*, *S. ilicis*) and *Melitaea* (*M. celadussa*, *M. deione*, *M. parthenoides*) were not easy to determine at species level in the field due to external morphological similarity and were identified to genus level (nomenclature follows García-Barros *et al.*, 2013).

The study sites represented open areas occurring in natural or semi-natural habitat. To estimate the degree of human impact on the adjacent landscape, we quantified the cover of natural and semi-natural habitats (forests, shrubland, meadows/pasture and bare rock; Gutiérrez Illán *et al.*, 2010) within circles of 0.5, 1 and 2-km radius from transect centroids using regional land-cover maps obtained in vector format at 1:50000 scale (Ministerio de Medio Ambiente, 2000, 2002a, b, 2003). Proportion cover of natural and semi-natural habitat exceeded 0.9 on average for the three different radii (mean, range; 0.5-km radius: 0.97, 0.63-1; 1-km radius: 0.95, 0.67-1; 2-km radius: 0.92, 0.45-1). Nevertheless, proportion cover of natural and semi-natural habitat was smaller at lower elevations (Spearman's rank correlation coefficient,  $r_s$ ; 0.5-km radius:  $r_s = 0.40$ ,  $P = 0.009$ ; 1-km radius:  $r_s = 0.55$ ,  $P < 0.001$ ; 2-km

radius:  $r_s = 0.71$ ,  $P < 0.001$ ;  $n = 40$  in all cases), suggesting that human impact was higher in the lowlands.



**Figure S1** Site distribution in 2006-08. Open circles show sites visited in 2006-08 ( $n = 34$ ) and filled circles sites visited in 2007-08 only ( $n = 6$ ). Nearest neighbouring sites were  $4.12 \pm 0.66$  km apart (mean  $\pm$  SE,  $n = 40$ ). Elevation bands are shown as 0.25 km increments from  $< 0.75$  km (pale grey) to  $> 2$  km (black). The inset map shows the geographical context of the study area in Spain. Georeferencing units are in UTM (30T; ED50).

To test whether number of butterfly species and composition (and hence distribution) were comparable between sites sampled over two (2007-08) and three years (2006-08), we quantified sampling effort by computing species accumulation curves and species richness estimators for each site (based on all butterfly species and genera recorded) using software EstimateS 9.1.0 (Colwell, 2013). Sample-based rarefaction based on the analytical formulas of Colwell *et al.* (2004), rescaled to number of individuals, was used to interpolate number of species per individual sampled. As a first measure of sampling effort at each site, the rate of species accumulation per individual on the final sample was used (Hortal *et al.*, 2004; Wilson *et al.*, 2007). Seven species richness estimators were calculated based on 100 randomizations of sampling order: ACE, ICE, Chao 1, Chao 2, first- and second-order Jackknife estimators, and the Bootstrap estimator (Colwell & Coddington, 1994). As a second measure of effort, the proportion of species present that had been recorded was estimated by dividing observed number of species by final extrapolated richness for each estimator, and then, as a summary estimate of sample coverage, the average for the seven values was calculated (Wilson *et al.*, 2007).

Rates of species accumulation per individual ranged 0.002-0.031, indicating that at present, collecting c. 500-32 individuals more, respectively, would result in 1 new species added. Estimated sample coverage ranged 0.71-0.94, indicating that more than two-thirds of total estimated species were detected at least at all sites. No significant differences were found in the rate of species accumulation nor in estimated sample coverage between sites sampled over two and three years, suggesting that the number and composition of species were comparable (Mann-Whitney test, rate of species accumulation:  $U = 142$ ,  $P = 0.137$ ; mean  $\pm$  SD (range); sites sampled two years:  $0.011 \pm 0.007$  (0.006-0.023); sites sampled three years:  $0.008 \pm 0.006$  (0.002-0.031); estimated sample coverage:  $U = 110$ ,  $P = 0.782$ ; sites sampled two years:  $0.85 \pm 0.07$  (0.71-0.90); sites sampled three years:  $0.84 \pm 0.06$  (0.71-0.94)).

### Host plant data

Host plant use data were obtained from egg laying, egg and larval records in the Iberian Peninsula during the period 2002-15 ( $n = 279$  records) and from García-Barros *et al.* (2013), with the use of host species confirmed in the field for 38 (88%) out of 43 butterfly species (Table S1). Two of the remaining five species (*Gonepteryx cleopatra*, *Polyommatus escheri*) were recorded in the region feeding or egg-laying on host plants that were absent from the 40 study sites, but were taxonomically very close to those found at them (Table S1). The most limited evidence of host plant use was for the genus *Argynnis*, which includes highly active butterflies that frequently oviposit on substrates other than their host plants.

Inclusion of all potential host plants, based on plant genera used at a European scale (Tolman & Lewington, 1997), made it unlikely that important food plant resources were missed for the 43 specialist butterfly species included in analyses. After the main field work of this study, we found that two butterfly species oviposited on previously unrecorded host plants, *Anthocharis euphenoides* (one record on *Arabis glabra*) and *Cyaniris semiargus* (two records on *Trifolium ochroleucon*) (c. 1% of total records), but both plants were rare at the study sites and their distributions were nearly nested within those of the main host plants (unpublished data).

To test to what extent butterfly occurrence at elevations where their host plants were not recorded was a function of the fact that the host plants were present nearby, we compared host plant distributions based on the standard 5-m band against those based on a wider 50-m band for exemplar butterfly species feeding on genera *Crataegus* and *Prunus* (*Aporia crataegi*, *Iphiclides podalirius*; Merrill *et al.*, 2008), and *Frangula* and *Rhamnus* (*Gonepteryx cleopatra*, *G. rhamni*, *Satyrium spini*; Gutiérrez & Wilson, 2014). For *Crataegus-Prunus*, maximum elevation increased from 1520 to 1534 m, and minimum elevation remained unchanged at 558 m (the lower elevation sampled) when the 5-m band was increased to 50 m. *A. crataegi* and *I. podalirius* maximum elevations (1818 and 1689 m, respectively) were greater than those of their host plants regardless of the band width used. For *Frangula-Rhamnus*, host plant maximum elevation remained unchanged at 1504 m, and minimum elevation decreased from 960 to 558 m when the 5-m was expanded to 50 m. *Gonepteryx rhamni* and *G. cleopatra* maximum elevations (2251 and 1675 m, respectively) were greater than those of their host plants regardless of the band width used, but *G. cleopatra*, *G. rhamni* and *S. spini* minimum elevations (558, 739 and 739 m, respectively) became higher than or equal to those of their host plants when using a 50-m band.

The distribution and elevational range limits of potential larval host plants was examined by recording their presence-absence at the 40 transect sites by carefully following the route of the 500 x 5 m transect in summer 2008 and spring 2009, with some additional records in 2010. This represents a slight temporal mismatch between the butterfly and host plant surveys, because butterfly transects were walked earlier in 2006-08. This potential source of variation on range limit data could affect butterfly species feeding on host plants with high temporal turnover, i.e. annual species. However, only two study butterfly species (*Cupido minimus* and *Zegris eupheme*) rely on facultatively annual host plants (data from Castroviejo *et al.*, 1986), and no butterfly species does on strictly annual host plants.



**Table S1** Study species with their host plant genera in Europe (<sup>1</sup>Tolman & Lewington, 1997) and potential host plants in the study area (from records at the 40 study sites only; additional host plants can be found more widely in the study region). Confirmed host plants from: <sup>2</sup>unpublished data from female oviposition, egg and larvae records in the Iberian Peninsula; <sup>3</sup>data from García-Barros *et al.* (2013).

Species	Host plant genus in Europe <sup>1</sup>	Potential and confirmed host plants
<b>PAPILIONIDAE</b>		
<i>Parnassius apollo</i>	<i>Sedum</i>	<i>S. album</i> <sup>2,3</sup> , <i>S. amplexicaule</i> <sup>2,3</sup> , <i>S. brevifolium</i> <sup>2,3</sup> , <i>S. forsterianum</i> <sup>2</sup> , other 6 species from genus <i>Sedum</i> .
<i>Zerynthia rumina</i>	<i>Aristolochia</i>	<i>A. paucinervis</i> <sup>2,3</sup> , <i>A. pistolochia</i> <sup>2,3</sup>
<i>Iphiclides podalirius</i>	<i>Crataegus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Sorbus</i>	<i>C. monogyna</i> <sup>2,3</sup> , <i>P. avium</i> <sup>3</sup> , <i>P. spinosa</i> <sup>2,3</sup>
<b>HESPERIIDAE</b>		
<i>Spialia sertorius</i>	<i>Sanguisorba</i>	<i>S. minor</i> <sup>2,3</sup> , <i>S. verrucosa</i> <sup>2</sup>
<i>Sloperia proto</i>	<i>Phlomis</i>	<i>P. herba-venti</i> <sup>2,3</sup> , <i>P. lychnitis</i> <sup>2,3</sup>
<b>PIERIDAE</b>		
<i>Gonepteryx cleopatra</i> *	<i>Rhamnus</i>	<i>R. cathartica</i>
<i>Gonepteryx rhamni</i>	<i>Frangula</i> , <i>Rhamnus</i>	<i>F. alnus</i> <sup>2,3</sup> , <i>R. cathartica</i> <sup>2</sup>
<i>Colias alfacariensis</i>	<i>Coronilla</i> , <i>Hippocrepis</i>	<i>H. carpetana</i> , <i>H. commutata</i> <sup>2</sup>
<i>Anthocharis euphenoides</i>	<i>Biscutella</i>	<i>B. valentina</i> <sup>2,3</sup>
<i>Zegris eupheme</i>	<i>Hirschfeldia</i> , <i>Isatis</i>	<i>H. incana</i> <sup>2,3</sup> , <i>Sisymbrium austriacum</i> <sup>3</sup>
<i>Euchloe tagis</i>	<i>Iberis</i>	<i>I. ciliata</i> <sup>2</sup>
<i>Aporia crataegi</i>	<i>Crataegus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Sorbus</i>	<i>C. monogyna</i> <sup>2,3</sup> , <i>P. avium</i> , <i>P. spinosa</i> <sup>2,3</sup>
<b>RIODINIDAE</b>		
<i>Hamearis lucina</i>	<i>Primula</i>	<i>P. veris</i> <sup>2</sup>
<b>LYCAENIDAE</b>		
<i>Lycaena alciphron</i>	<i>Rumex</i>	<i>R. acetosa</i> <sup>3</sup> , <i>R. acetosella</i> <sup>2,3</sup> , <i>R. bucephalophorus</i> , <i>R. conglomeratus</i> , <i>R. crispus</i> , <i>R. induratus</i> , <i>R. obtusifolius</i> , <i>R. papillaris</i> <sup>2</sup> , <i>R. pulcher</i>

Species	Host plant genus in Europe <sup>1</sup>	Potential and confirmed host plants
<i>Lycaena bleusei</i>	<i>Rumex</i>	<i>R. acetosa</i> <sup>3</sup> , <i>R. acetosella</i> <sup>2,3</sup> , <i>R. bucephalophorus</i> , <i>R. conglomeratus</i> , <i>R. crispus</i> <sup>2</sup> , <i>R. induratus</i> , <i>R. obtusifolius</i> , <i>R. papillaris</i> <sup>2,3</sup> , <i>R. pulcher</i>
<i>Lycaena phlaeas</i>	<i>Rumex</i>	<i>R. acetosa</i> <sup>3</sup> , <i>R. acetosella</i> <sup>2,3</sup> , <i>R. bucephalophorus</i> <sup>2</sup> , <i>R. conglomeratus</i> <sup>2</sup> , <i>R. crispus</i> <sup>3</sup> , <i>R. induratus</i> , <i>R. obtusifolius</i> , <i>R. papillaris</i> , <i>R. pulcher</i> <sup>3</sup>
<i>Lycaena virgaureae</i>	<i>Rumex</i>	<i>R. acetosa</i> <sup>3</sup> , <i>R. acetosella</i> <sup>2,3</sup> , <i>R. bucephalophorus</i> , <i>R. conglomeratus</i> , <i>R. crispus</i> , <i>R. induratus</i> , <i>R. obtusifolius</i> , <i>R. papillaris</i> , <i>R. pulcher</i>
<i>Laeosopis roboris</i>	<i>Fraxinus</i>	<i>F. angustifolia</i> <sup>3</sup>
<i>Satyrium spini</i>	<i>Rhamnus</i>	<i>Frangula alnus</i> <sup>2,3</sup> , <i>R. cathartica</i> <sup>2,3</sup>
<i>Cupido minimus</i>	<i>Anthyllis (A. vulneraria)</i>	<i>A. vulneraria</i> <sup>2,3</sup>
<i>Scolitantides panoptes</i>	<i>Thymus, Satureja</i>	<i>T. gr. praecox</i> , <i>T. mastichina</i> <sup>3</sup> , <i>T. zygis</i> <sup>2,3</sup>
<i>Cyaniris semiargus</i>	<i>Trifolium (T. pratense)</i>	<i>T. pratense</i> <sup>2,3</sup>
<i>Polyommatus thersites</i>	<i>Onobrychis</i>	<i>O. humilis</i> <sup>3</sup>
<i>Polyommatus escheri</i> *	<i>Astragalus</i>	<i>A. glycyphyllos</i> , <i>A. hamosus</i> , <i>A. incanus</i>
<i>Polyommatus albicans</i>	<i>Coronilla, Hippocrepis</i>	<i>H. carpetana</i> <sup>2</sup> , <i>H. commutata</i> <sup>3</sup>
<i>Polyommatus bellargus</i>	<i>Hippocrepis</i>	<i>H. carpetana</i> <sup>2</sup> , <i>H. commutata</i> <sup>2,3</sup>
NYMPHALIDAE		
<i>Libythea celtis</i>	<i>Celtis (C. australis)</i>	No host plant records at study sites
<i>Vanessa atalanta</i>	<i>Urtica</i>	<i>U. dioica</i> <sup>2,3</sup> , <i>U. urens</i> <sup>2,3</sup>
<i>Nymphalis antiopa</i>	<i>Populus, Salix</i>	<i>P. nigra</i> <sup>3</sup> , <i>P. tremula</i> <sup>3</sup> , <i>S. atrocinerea</i> <sup>3</sup> , <i>S. purpurea</i> , <i>S. salviifolia</i>
<i>Aglais urticae</i>	<i>Urtica</i>	<i>U. dioica</i> <sup>2,3</sup> , <i>U. urens</i> <sup>3</sup>
<i>Aglais io</i>	<i>Urtica</i>	<i>U. dioica</i> <sup>2,3</sup> , <i>U. urens</i>
<i>Euphydryas aurinia</i>	<i>Lonicera</i>	<i>L. etrusca</i> <sup>2,3</sup> , <i>L. periclymenum</i> <sup>2</sup>
<i>Melitaea phoebe</i>	<i>Centaurea</i>	<i>C. alba</i> , <i>C. calcitrapa</i> , <i>C. cyanus</i> , <i>C. melitensis</i> , <i>C. nigra</i> , <i>C. ornata</i> <sup>2,3</sup> , <i>C. aristata</i> , <i>C. graminifolia</i>

Species	Host plant genus in Europe <sup>1</sup>	Potential and confirmed host plants
<i>Melitaea trivia</i>	<i>Verbascum</i>	<i>V. pulverulentum</i> <sup>2,3</sup> , <i>V. rotundifolium</i> , <i>V. simplex</i> , <i>V. sinuatum</i> , <i>V. thapsus</i> <sup>3</sup> , <i>V. virgatum</i>
<i>Limenitis reducta</i>	<i>Lonicera</i>	<i>L. etrusca</i> <sup>3</sup> , <i>L. periclymenum</i>
<i>Issoria lathonia</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> <sup>2</sup> , <i>V. odorata</i> , <i>V. palustris</i> , <i>V. parvula</i> <sup>2</sup> , <i>V. riviniana</i>
<i>Argynnis pandora</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> , <i>V. palustris</i> , <i>V. parvula</i> , <i>V. riviniana</i>
<i>Argynnis paphia</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> , <i>V. palustris</i> , <i>V. parvula</i> , <i>V. riviniana</i>
<i>Argynnis aglaja</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> <sup>2</sup> , <i>V. palustris</i> , <i>V. parvula</i> , <i>V. riviniana</i>
<i>Argynnis adippe</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> , <i>V. palustris</i> , <i>V. parvula</i> , <i>V. riviniana</i> <sup>2</sup>
<i>Argynnis niobe</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> , <i>V. palustris</i> , <i>V. parvula</i> , <i>V. riviniana</i>
<i>Brenthis daphne</i>	<i>Rubus</i>	<i>Rubus idaeus</i> , <i>Rubus</i> gr. <i>ulmifolius</i> <sup>2</sup> , <i>Rubus</i> sp. <sup>2</sup>
<i>Brenthis hecate</i>	<i>Filipendula</i>	<i>F. vulgaris</i> <sup>3</sup>
<i>Boloria selene</i>	<i>Viola</i>	<i>V. canina</i> , <i>V. hirta</i> , <i>V. kitaibeliana</i> , <i>V. odorata</i> , <i>V. palustris</i> <sup>3</sup> , <i>V. parvula</i> , <i>V. riviniana</i> <sup>3</sup>

Species names are arranged following the checklist in García-Barros *et al.* (2013).

Nomenclature of host plant species follows Castroviejo *et al.* (1986).

\* recorded host plants that were absent at the 40 study sites but were taxonomically very close to those found at them: *G. cleopatra*: *Rhamnus alaternus*<sup>2,3</sup>, *R. lycioides*<sup>2</sup>; *P. escheri*: *Astragalus monspessulanus*<sup>2,3</sup>.

### **Butterfly attributes**

We considered six attributes that potentially contributed to possible departures of individual species from the expected relationship between butterfly and host plant elevational range size and limits: host plant size, host plant part eaten by larvae, butterfly mobility, butterfly abundance, and two measures of butterfly climatic breadth and limits. Host plant size was defined using a binary variable: herbaceous versus woody plants (trees, shrubs and vines). Butterfly species reported to feed on at least one tree, shrub or vine species were classified as woody-plant feeders (11 species), whereas all other species only reported to feed on herbs and grasses were classified as herbaceous-plant feeders (32 species). Host plant part eaten was described by one binary variable, leaf feeders (larvae feeding on leaves over their entire life; 36 species) and flower-fruit feeders (larvae feeding on flowers and/or fruits over at least part of their life; 7 species).

Butterfly mobility was classified in four categories (Stefanescu *et al.*, 2011; C. Stefanescu, unpublished data): 1, species living in metapopulations with relatively little dispersal between populations (low mobility, 18 species); 2, species living in metapopulations with relatively high dispersal between populations (medium mobility, 15 species); 3, species living in patchy populations with non-seasonal migration; and 4, species living in patchy populations with seasonal migration. Because there was only one species with mobility index 4, it was included in index 3 (high mobility, 10 species in total). Butterfly species abundance was a continuous variable obtained from transect data. To estimate abundance for each species, we first calculated the mean abundance (over 2006-08) for each site when species occurred on two-weekly transects, and then we calculated the average where occupied across space (i.e., excluding zero counts). By including only count data greater than 0 we avoided potential artefactual positive effects of abundance on prevalence resulting from mean abundances being a direct function of the number of sites at which species did not occur (e.g., Gaston *et al.*, 1997).

Butterfly climatic breadth and limits were based, respectively, on the standard deviation (SD) and maximum and minimum values of two climate variables (mean annual temperature and annual precipitation sum) across the geographic range of each species in Europe (Schweiger *et al.*, 2014). We considered these variables (butterfly range temperature and precipitation SD, and maximum and minimum butterfly range temperature and precipitation henceforth) because they represent the two major climatic gradients associated with elevation over the study area (Wilson *et al.*, 2005). These components of the environmental niche for each species have been calculated from monthly interpolated climate data for the period 1971-

2000 over occupied 50 x 50 km grid squares in Europe, and values are available from Schweiger *et al.* (2014). It is worth taking into account that the variables used are surrogates of climatic breadth and limits inferred from the geographic ranges of species in the absence of experimental data, and that they will be partly influenced by other environmental variables and dispersal limitations.

Elevational distributions, particularly upper limits, can be influenced by hill-topping behaviour, a mating strategy of some insect species in which males occupy prominent topographic features due to female scarcity (e.g., Carneiro *et al.*, 2014). However, there were just three species reported to use this strategy in our study (*I. podalirius*, *V. atalanta* and *M. trivia*, García-Barros *et al.*, 2013) and therefore hill-topping was not considered as an additional butterfly attribute.

### **Butterfly phylogeny**

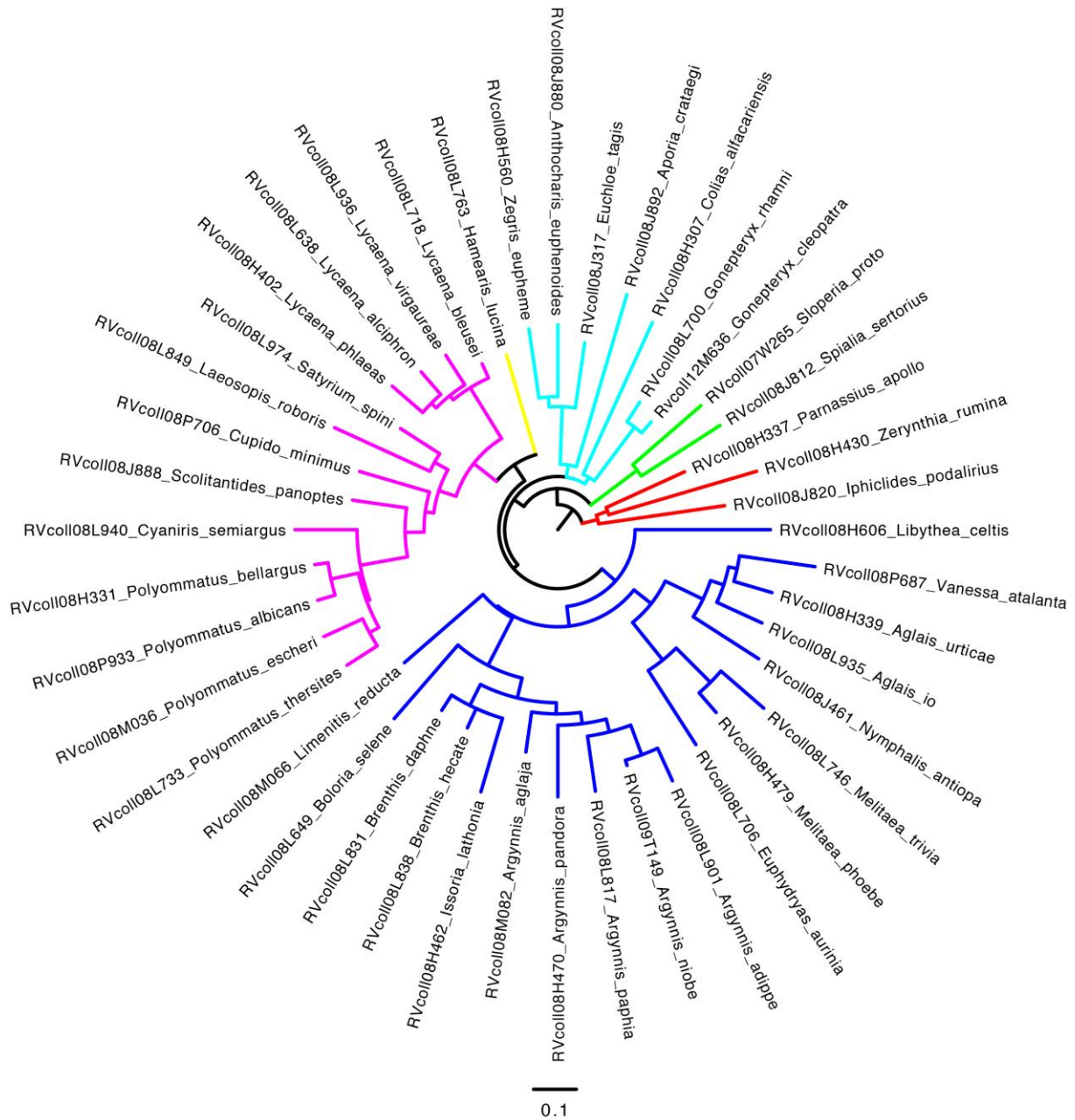
In order to account for potential phylogenetic non-independence in the analyses, a molecular phylogenetic tree of all species included in our study was constructed using maximum likelihood reconstruction based on COI sequences (658 bp). Sequences were obtained from Dincă *et al.* (2015) and correspond to representative specimens collected in the central Iberian Peninsula. The tree was inferred with RAxML with a gamma model of rate heterogeneity and topological constraints at the levels of family and subfamily following the butterfly phylogeny published in Heikkilä *et al.* (2012) (Fig. S2).

### **Environmental data for species richness analysis**

For the period 2006-12, hourly air temperature and relative humidity were recorded by HOBO H8 Pro temp/RH and U23 Pro v2 temp/RH loggers in semi-shaded conditions at each of the 40 sampling sites. Twenty data loggers were deployed at sites and started recording data in spring 2004, and the remaining twenty in spring 2006. Mechanical failure or damage to some loggers generated gaps of variable duration in the data, with daily temperature and relative humidity completeness averaging, respectively, 91% and 79% per logger (ranges 69-100% and 28-100%, respectively) for the period 2004-12. Daily average temperatures and relative humidity were interpolated for missing periods using linear regressions of temperature and relative humidity data from the site in question with the site giving the most quantitatively consistent temperature and relative humidity time series (for further details, see Gutiérrez & Wilson, 2014).

Actual evapotranspiration is a measure of water-energy balance and was used as a surrogate of productivity. The elevations with the warmest-wettest conditions should be the

most productive, and therefore, the pattern of evapotranspiration over the elevational gradient will be dependent on the specific climate regime of the mountain (McCain & Grytnes, 2010). Actual evapotranspiration was calculated using the Granger-Gray formula (Granger & Gray, 1989; McMahon *et al.*, 2013) with package 'Evapotranspiration' (Guo *et al.*, 2016). The Granger-Gray equation requires as input daily measured weather variables (temperature, relative humidity, solar radiation and wind speed) and the albedo for a given site. Daily temperature and relative humidity were obtained from data loggers as specified above, and daily solar radiation was estimated by implementing the Solar Radiation tool in ArcGIS 10.1 (ESRI, 2012), which estimates the incoming radiation to a grid cell using the slope, aspect, curvature, elevation and shading effects from surrounding topography. Topographic data were derived from a digital elevation model of the area (Fig. S1), which was obtained at c. 80 x 80 m resolution and interpolated to 100 x 100 m (Farr *et al.*, 2007). Because wind speed data were not available for any of the study sites, the average value of  $2 \text{ m s}^{-1}$  from c. 2000 stations over the globe was used in the Granger-Gray equation (Valiantzas, 2006). Albedo data for the major land covers surrounding each data logger in the field were obtained from tabulated values (McMahon *et al.*, 2013). Another alternative recent equation to estimate actual evapotranspiration, the Szilagyi-Jozsa model, generated many negative daily evapotranspiration estimates (particularly in winter, see McMahon *et al.*, 2013) and therefore was not considered.



**Figure S2** Maximum likelihood reconstruction based on COI sequences (658 bp) for the 44 specialist butterfly species found in the study system (including *Libythea celtis*, which was excluded from analysis because host plants were absent from the study sites). The different families are represented by different colours (Papilionidae, red; Hesperiiidae, green; Pieridae, cyan; Riodinidae, yellow; Lycaenidae, magenta; Nymphalidae, blue).

## Statistical analysis

### *Cross-species analysis*

For each response variable (butterfly prevalence, and maximum and minimum elevations), we performed a standard generalized least squares (GLS) model (not accounting for phylogenetic relationships), and two PGLS models (Grafen, 1989) using common models for evolutionary change, Brownian motion and Ornstein-Uhlenbeck models (e.g., Butler *et al.*, 2000; Butler & King, 2004). Brownian motion is used to approximate neutral drift or selection with a randomly changing selection gradient. Ornstein-Uhlenbeck is the simplest approximation for an evolutionary process with selection. The main difference is that, with the Brownian motion model, phenotypic similarity between species is expected to decrease linearly with time, whereas with the Ornstein-Uhlenbeck model it is expected to decrease much faster (exponentially). In the Ornstein-Uhlenbeck model, parameter  $\alpha$  measures the strength of selection: increasing values reflect increasing stabilizing selection and the model is reduced to a Brownian model when  $\alpha = 0$  (Butler & King, 2004).

Full models that included linear terms for all potential explanatory variables fitted with restricted maximum likelihood, were used to test the different variance-covariance structures (following the general protocol for GLS by Zuur *et al.*, 2009). The variance structure was selected based on the model with the lowest value of Akaike Information Criterion corrected for small sample size ( $AIC_c$ ) if the  $AIC_c$  difference ( $\Delta AIC_c$ ) between the 'best' and the following model was  $> 2$ . If there was no clear 'best' model ( $\Delta AIC_c < 2$ ), the GLS model (that with the simplest variance-covariance structure) was retained (e.g., Kharouba *et al.*, 2014).

### Correlations between independent variables

To explore inter-correlations among predictor variables, we performed Spearman's rank correlations (for continuous variable comparisons), Mann-Whitney and Kruskal-Wallis tests (for continuous-categorical variable comparisons) and Fisher's exact tests for contingency tables (for categorical variable comparisons). There were high pair-wise correlations (in absolute value) between continuous independent variables for host plant maximum elevation and prevalence, and minimum butterfly range temperature and temperature SD (Table S2), but these variables were not included in the same analyses. Between the continuous predictor variables included in the same analyses, only maximum butterfly range precipitation was highly correlated with minimum butterfly range temperature; all the remaining Spearman's rank coefficients had absolute values well lower than 0.7 (0.37-0.53; Table S2), the most commonly applied threshold for collinearity (Dormann *et al.*, 2013). Between the pair-wise



comparisons including at least one categorical independent variable, there were significant effects of host plant part eaten on butterfly abundance and butterfly range precipitation SD (species feeding on leaves were more abundant and showed higher precipitation SD on average than those feeding on flower-fruits; Table S2), and butterfly mobility on minimum butterfly range precipitation (species with high mobility showed lower minimum precipitation values on average than those with medium and low mobility; Table S2).

**Table S2** Correlation table of the environmental variables included in the cross-species analysis. We used non-parametric tests to examine potential collinearity between variables.  $n = 43$  species in all cases.

	Host plant prevalence	Host plant max elevation	Host plant min elevation	Host plant size	Host plant part	Butterfly mobility	Butterfly abundance	Butt range temp SD	Max butt range temp	Min butt range temp	Butt range precip SD	Max butt range precip
Host plant maximum elevation	$r_s = 0.92^{***}$											
Host plant minimum elevation	$r_s = -0.64^{***}$	$r_s = -0.50^{***}$										
Host plant size	$U = 208^{ns}$	$U = 217^{ns}$	$U = 129.5^{ns}$									
Host plant part	$U = 169.5^{ns}$	$U = 130^{ns}$	$U = 92.5^{ns}$	Fisher <sup>ns</sup>								
Butterfly mobility	$H = 3.72^{ns}$	$H = 4.23^{ns}$	$H = 5.14^+$	Fisher <sup>ns</sup>	Fisher <sup>ns</sup>							
Butterfly abundance	<b><math>r_s = 0.48^{**}</math></b>	$r_s = 0.32^*$	<b><math>r_s = -0.46^{**}</math></b>	$U = 208^{ns}$	<b><math>U = 199^*</math></b>	$H = 1.65^{ns}$						
Butterfly range temperature SD	$r_s = 0.27^+$	$r_s = 0.23^{ns}$	$r_s = -0.16^{ns}$	$U = 138.5^{ns}$	$U = 140^{ns}$	$H = 5.32^+$	$r_s = -0.09^{ns}$					
Maximum butterfly range temperature	$r_s = -0.24^{ns}$	$r_s = -0.26^+$	$r_s = 0.03^{ns}$	$U = 113^+$	$U = 77.5^{ns}$	$H = 3.96^{ns}$	$r_s = 0.26^+$	$r_s = 0.15^{ns}$				
Minimum butterfly range temperature	$r_s = -0.46^{**}$	<b><math>r_s = -0.42^{**}</math></b>	$r_s = 0.15^{ns}$	$U = 159.5^{ns}$	$U = 85^{ns}$	$H = 4.99^+$	$r_s = -0.12^{ns}$	$r_s = -0.76^{***}$	$r_s = 0.32^*$			
Butterfly range precipitation SD	$r_s = 0.17^{ns}$	$r_s = 0.12^{ns}$	$r_s = -0.02^{ns}$	$U = 190^{ns}$	<b><math>U = 62^*</math></b>	$H = 0.40^{ns}$	$r_s = -0.04^{ns}$	<b><math>r_s = 0.53^{***}</math></b>	$r_s = -0.09^{ns}$	$r_s = -0.50^{***}$		
Maximum butterfly range precipitation	$r_s = 0.43^{**}$	<b><math>r_s = 0.37^*</math></b>	$r_s = -0.13^{ns}$	$U = 191^{ns}$	$U = 70^+$	$H = 5.19^+$	$r_s = 0.21^{ns}$	$r_s = 0.58^{***}$	$r_s = -0.30^*$	<b><math>r_s = -0.86^{***}</math></b>	$r_s = 0.65^{***}$	
Minimum butterfly range precipitation	$r_s = 0.04^{ns}$	$r_s = 0.07^{ns}$	$r_s = -0.08^{ns}$	$U = 177^{ns}$	$U = 148^{ns}$	<b><math>H = 9.67^{**}</math></b>	$r_s = 0.03^{ns}$	$r_s = -0.18^{ns}$	<b><math>r_s = -0.49^{***}</math></b>	$r_s = 0.07^{ns}$	$r_s = -0.12^{ns}$	$r_s = -0.09^{ns}$

$r_s$ , Spearman's rank correlation coefficient (two continuous variables);  $U$ , Mann-Whitney statistic (continuous-categorical variables);  $H$ , Kruskal-Wallis statistic (continuous-categorical variables); Fisher, Fisher's exact test for contingency tables (two categorical variables). Significant tests between variables within the same analysis in bold. <sup>ns</sup>  $P > 0.1$  ; <sup>+</sup>  $P < 0.1$  ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

1 *Species richness analysis*

2 **Table S3** Correlation table of the environmental variables included in the butterfly species  
 3 richness analysis (Spearman's rank correlation coefficient and  $n = 40$  sites for all cases.

	Number of host plant species	Annual mean temperature	Annual mean relative humidity
Annual mean temperature	0.53***		
Annual mean relative humidity	0.09 <sup>ns</sup>	-0.57***	
Annual actual evapotranspiration	-0.57***	-0.71***	0.37*

4 <sup>ns</sup>  $P > 0.1$  ; <sup>+</sup>  $P < 0.1$  ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

5

6 When using information theory criteria, existence of autocorrelation in the data may affect  
 7 AIC<sub>c</sub> selection, as autocorrelated data will tend to generate more complicated (i.e., with more  
 8 explanatory variables) models (e.g., Diniz-Filho *et al.*, 2008). To examine spatial  
 9 autocorrelation, we generated all-directional correlograms (Legendre & Legendre, 1998) for  
 10 the number of butterfly species by plotting values of Geary's c coefficient (recommended for  
 11 variables departing from normality) against Euclidean distances between sites. Geary's c  
 12 calculation and testing for significance were performed using 4999 Monte Carlo permutations  
 13 in Excel add-in Rookcase (Sawada, 1999). The correlogram was not globally significant,  
 14 suggesting that spatial autocorrelation in number of butterfly species data was negligible.

15

16

17 **RESULTS**18 **Cross-species analysis**

19 **Table S4** Phylogenetic generalized least-squares models for the relationships between  
 20 butterfly prevalence, maximum and minimum elevations with the prevalence and elevational  
 21 limits of their host plants, and host plant and butterfly attributes ( $n = 43$  butterfly species).  
 22 Models include all potential explanatory variables (full models, see Methods), differing only  
 23 in their phylogenetic component.

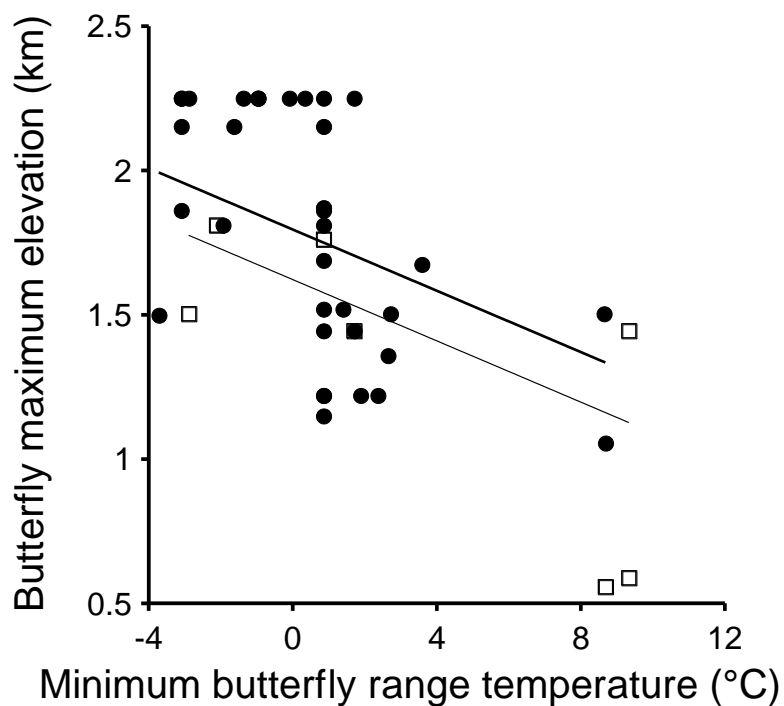
Response variable	Model	Parameter	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
Butterfly prevalence	<b>No phylogenetic correction</b>	<b>n.a.</b>	<b>19.44</b>	<b>0</b>
	Brownian motion	n.a.	44.05	24.61
	Ornstein-Uhlenbeck	$\alpha = 48.50$	23.07	3.63
Butterfly maximum elevation (excluding maximum butterfly range precipitation)	<b>No phylogenetic correction</b>	<b>n.a.</b>	<b>50.62</b>	<b>0</b>
	Brownian motion	n.a.	65.21	14.60
	Ornstein-Uhlenbeck	$\alpha = \text{n.a.}^*$	n.a.*	n.a.*
Butterfly maximum elevation (excluding minimum butterfly range temperature)	<b>No phylogenetic correction</b>	<b>n.a.</b>	<b>66.88</b>	<b>0</b>
	Brownian motion	n.a.	76.56	9.68
	Ornstein-Uhlenbeck	$\alpha = \text{n.a.}^*$	n.a.*	n.a.*
Butterfly minimum elevation	<b>No phylogenetic correction</b>	<b>n.a.</b>	<b>40.59</b>	<b>0</b>
	Brownian motion	n.a.	52.96	12.37
	Ornstein-Uhlenbeck	$\alpha = \text{n.a.}^*$	n.a.*	n.a.*

24 Models in bold represent the 'best' model. The table indicates the variance component  
 25 (Model); AIC<sub>c</sub>, Akaike Information Criterion for small sample size; ΔAIC<sub>c</sub>, difference in  
 26 AIC<sub>c</sub> between current and 'best' model; parameter  $\alpha$ , intensity of stabilizing selection in  
 27 Ornstein-Uhlenbeck model. n.a., not applicable.

28 \* no convergence was found for butterfly maximum and minimum elevation using the  
 29 Ornstein-Uhlenbeck model.

30

31



32  
 33 **Figure S3** Relationship between butterfly maximum elevation and minimum butterfly range  
 34 temperature. Different symbols and lines represent species differing in host plant part eaten  
 35 (leaves: circles, thick line; flowers-fruits: squares, thin line). The lines of best fit represent the  
 36 equations in Table 1, based on linear regression applied to species of average  $\ln(\text{abundance})$   
 37 and host plant maximum elevation ( $n = 43$  species).  
 38

39 **Table S5** Confidence sets of regression models for (a) butterfly maximum elevation (all  
 40 species,  $n = 43$ ), (b, c) butterfly maximum elevation of species occurring below 2000 m ( $n =$   
 41 29), and (d) butterfly minimum elevation of species occurring above 750 m ( $n = 24$ ).

Model	$K$	$R^2$	$AIC_c$	$\Delta AIC_c$	$AIC_{cw}$
(a) Models for butterfly maximum elevation (excluding minimum butterfly range temperature)					
Host plant maximum elevation + host plant part + maximum butterfly range precipitation	5	0.63	22.56	0	0.65
Host plant maximum elevation + butterfly abundance + maximum butterfly range precipitation	5	0.61	25.08	2.52	0.18
Host plant maximum elevation + host plant part	4	0.58	25.68	3.12	0.14
Host plant maximum elevation + maximum butterfly range precipitation	4	0.55	28.45	5.89	0.03
(b) Models for butterfly maximum elevation < 2000 m (excluding maximum butterfly range precipitation)					
Host plant maximum elevation + minimum butterfly range temperature	4	0.47	10.54	0	0.74
Minimum butterfly range temperature	3	0.38	12.58	2.04	0.26
(c) Models for butterfly maximum elevation < 2000 m (excluding minimum butterfly range temperature)					
Host plant maximum elevation + host plant part + maximum butterfly range precipitation	5	0.40	17.31	0	0.29
Host plant maximum elevation + maximum butterfly range precipitation	4	0.33	17.42	0.11	0.27
Host plant maximum elevation + host plant part	4	0.32	17.74	0.43	0.23
Maximum butterfly range precipitation	3	0.22	19.05	1.74	0.12
Host plant maximum elevation	3	0.20	19.68	2.37	0.09
(d) Models for butterfly minimum elevation > 750 m					
Mobility + butterfly abundance + maximum butterfly range temperature	6	0.65	-25.92	0	0.53
Butterfly abundance + maximum butterfly range temperature	4	0.53	-25.65	0.27	0.47

42 Parameter estimates ( $\pm$  adjusted SE) for the model averaged confidence sets are:

43 (a) Butterfly maximum elevation =  $0.44 (\pm 0.24) + 0.53 (\pm 0.12)$  host plant maximum elevation  
44 -  $0.29 (\pm 0.13)$  flower-fruits +  $0.05 (\pm 0.12)$  butterfly abundance +  $0.0002 (\pm 0.0001)$  maximum  
45 butterfly range precipitation.

46 (b) Butterfly maximum elevation =  $1.29 (\pm 0.24) + 0.18 (\pm 0.12)$  host plant maximum elevation  
47 -  $0.05 (\pm 0.02)$  minimum butterfly range temperature.

48 (c) Butterfly maximum elevation =  $0.77 (\pm 0.27) + 0.28 (\pm 0.14)$  host plant maximum elevation  
49 -  $0.13 (\pm 0.14)$  flower-fruits +  $0.0002 (\pm 0.0001)$  maximum butterfly range precipitation.

50 (d) Butterfly minimum elevation =  $3.67 (\pm 0.59) + 0.08 (\pm 0.06)$  medium mobility +  $0.001$   
51  $(\pm 0.07)$  high mobility -  $0.28 (\pm 0.08)$  butterfly abundance -  $0.15 (\pm 0.03)$  maximum butterfly  
52 range temperature.

53  $K$ , number of parameters (includes an extra parameter for the estimate of regression variance);  
54  $R^2$ , coefficient of determination;  $AIC_c$ , Akaike Information Criterion for small sample size;  
55  $\Delta AIC_c$ , difference in  $AIC_c$  between current and 'best' model;  $AIC_{cw}$ , Akaike weight. Mobility  
56 is a categorical variable with 'low mobility' as reference level.

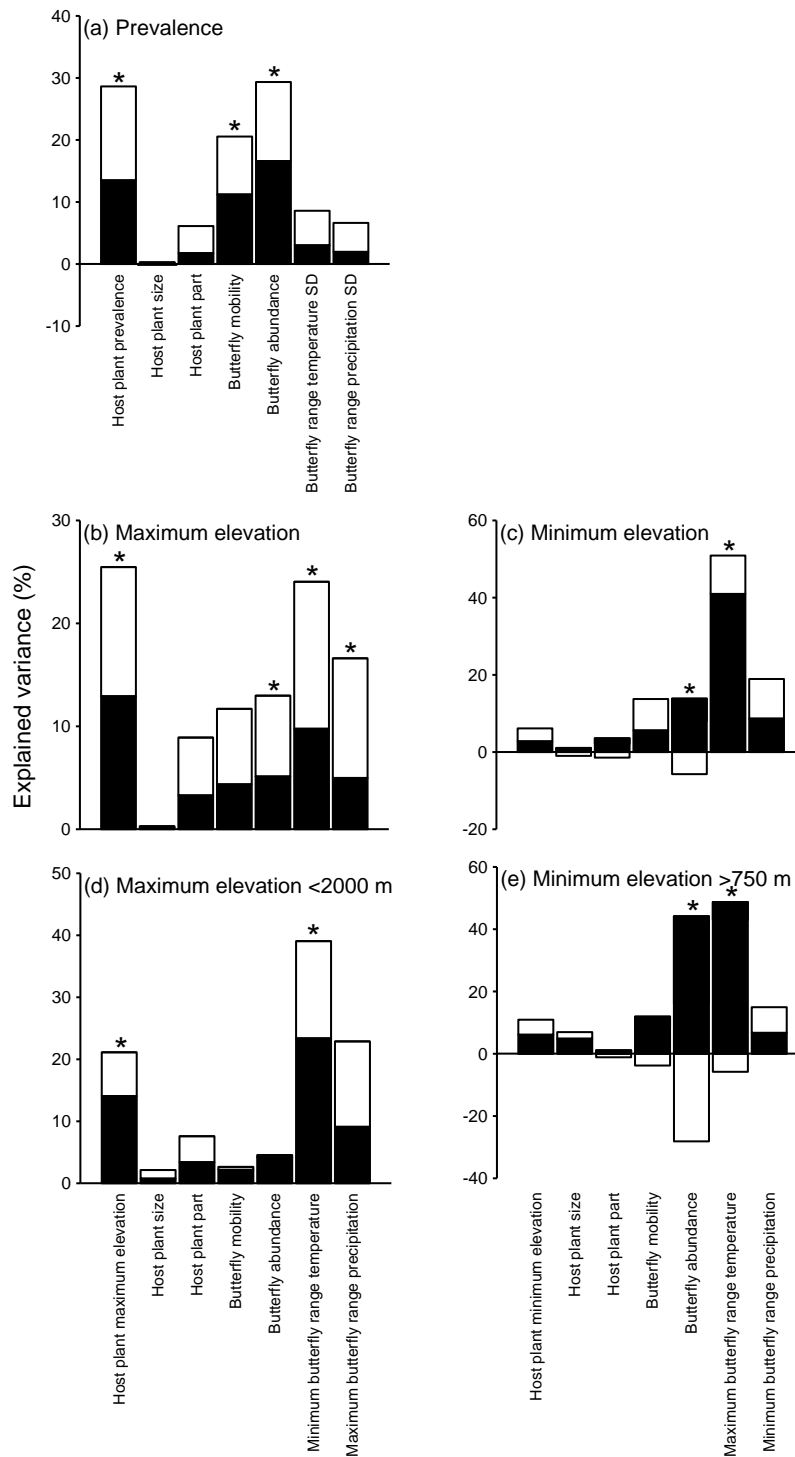
57

58 *Hierarchical partitioning*

59 In hierarchical partitioning, host plant prevalence, butterfly mobility and abundance showed  
60 statistically significant independent contributions for butterfly prevalence (Fig. S4). For  
61 butterfly maximum elevation, there were significant independent effects of host plant  
62 maximum elevation, butterfly abundance, minimum butterfly range temperature and  
63 maximum butterfly range precipitation when all 43 species were considered. The significant  
64 independent contributions of host plant maximum elevation and minimum butterfly range  
65 temperature remained when the 14 species occurring above 2000 m were excluded (Fig. S4).  
66 For butterfly minimum elevation, there were significant independent contributions of butterfly  
67 abundance and maximum butterfly range temperature for all 43 species and for the 24  
68 occurring above 750 m (Fig. S4). The negative joint contributions of butterfly abundance (and  
69 to a lesser degree, host plant size and part, butterfly mobility and maximum butterfly range  
70 temperature) for lower elevational limits (Fig. S4c, e) indicate that the joint action of these  
71 variables suppresses or masks the independent contribution of other factors (Chevan &  
72 Sutherland, 1991; Mac Nally, 1996).

73





74

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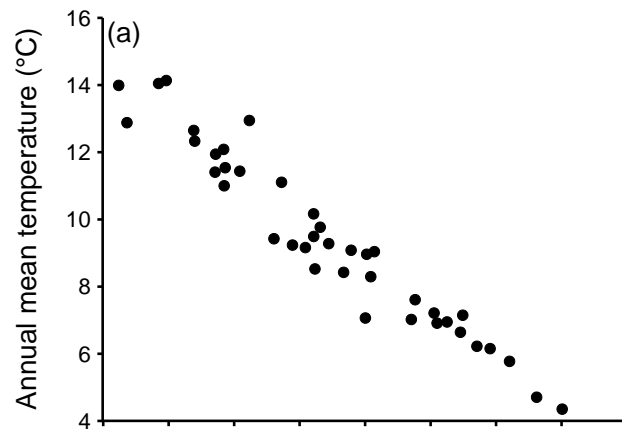
76

77 **Figure S4** The independent (black bars) and joint contribution (white bars) (given as a  
 78 percentage of the total variance explained by the model) of the environmental variables  
 79 estimated from hierarchical partitioning for (a) butterfly prevalence, (b) butterfly maximum  
 80 elevation, (c) butterfly minimum elevation ( $n = 43$  species in a, b and c), (d) butterfly  
 81 maximum elevation for species occurring below 2000 m ( $n = 29$  species), and (e) butterfly  
 82 minimum elevation for species occurring above 750 m ( $n = 24$  species). Asterisks indicate

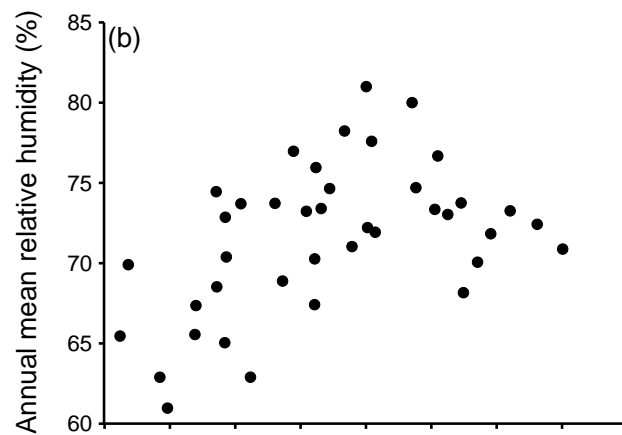
83 significant ( $P < 0.05$ ) independent contributions from randomization tests. Note the different  
84 y-axis scales.  
85

86 **Species richness analysis**

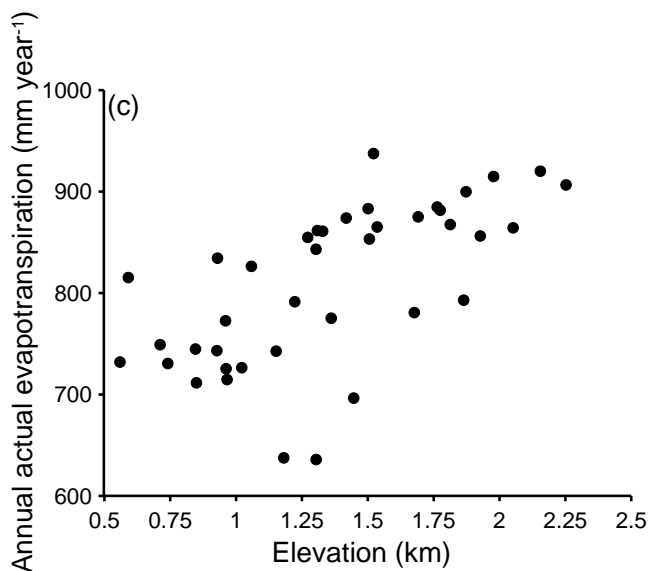
87



88



89



90 **Figure S5** Relationship between elevation and (a) annual mean temperature ( $r_s = -0.96$ ,  $P <$   
 91  $0.001$ ), (b) annual mean relative humidity ( $r_s = 0.44$ ,  $P = 0.005$ ), (c) annual actual  
 92 evapotranspiration ( $r_s = 0.72$ ,  $P < 0.001$ ) ( $n = 40$  sites for all cases). Values averaged for the  
 93 period 2006-08 in all cases.

94

95 **Table S6** Confidence sets of regression models for number of butterfly species including  
 96 number of host plant species, annual mean relative humidity and annual actual  
 97 evapotranspiration as predictor variables ( $n = 40$  sites).

Model	$K$	$R^2$	$AIC_c$	$\Delta AIC_c$	$AIC_{c,w}$
Number of host plant species + annual mean relative humidity + annual actual evapotranspiration	5	0.56	234.88	0	0.56
Number of host plant species + annual mean relative humidity	4	0.52	235.50	0.62	0.41
Number of host plant species + annual actual evapotranspiration	4	0.45	240.58	5.71	0.03

98 Parameter estimates ( $\pm$  adjusted SE) for the model averaged confidence set are:

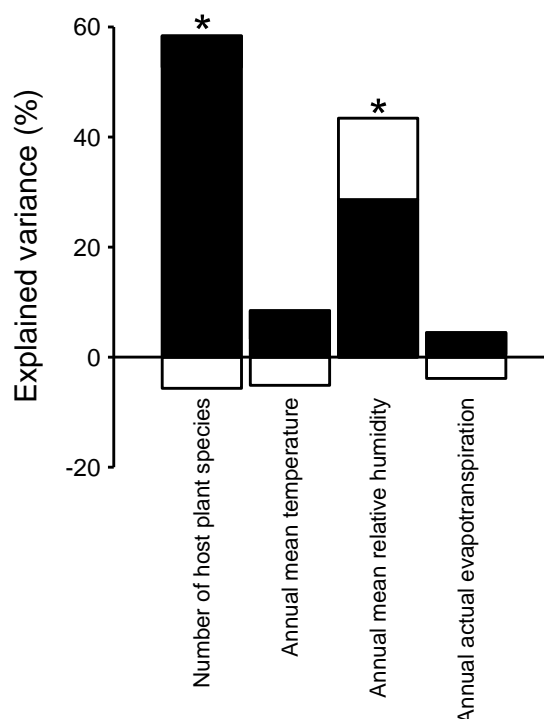
99 Number of butterfly species =  $-37.02 (\pm 12.35) + 0.45 (\pm 0.11)$  number of host plant species +  
 100  $0.51 (\pm 0.18)$  annual mean relative humidity +  $0.01 (\pm 0.01)$  annual actual evapotranspiration.

101  $K$ , number of parameters (includes an extra parameter for the estimate of regression variance);

102  $R^2$ , coefficient of determination;  $AIC_c$ , Akaike Information Criterion for small sample size;

103  $\Delta AIC_c$ , difference in  $AIC_c$  between current and 'best' model;  $AIC_{c,w}$ , Akaike weight.

104



105

106 **Figure S6** The independent (black bars) and joint contribution (white bars) (given as  
 107 percentage of the total variance explained by the model) of the environmental variables

108 estimated from hierarchical partitioning for butterfly species richness ( $n = 40$  sites). Asterisks  
109 indicate significant ( $P < 0.05$ ) independent contributions from randomization tests.  
110

111 **REFERENCES**

- 112 Butler, M.A. & King, A.A. (2004) Phylogenetic comparative analysis: a modeling approach  
 113 for adaptive evolution. *The American Naturalist*, **164**, 683-695.
- 114 Butler, M.A., Schoener, T.W. & Losos, J.B. (2000) The relationship between sexual size  
 115 dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, **54**, 259-272.
- 116 Carneiro, E., Mielke, O. H. H., Casagrande, M. M. & Fiedler, K. (2014) Community structure  
 117 of skipper butterflies (Lepidoptera, HesperIIDae) along elevational gradients in Brazilian  
 118 Atlantic forest reflects vegetation type rather than altitude. *PLoS ONE*, **9**, e108207.
- 119 Castroviejo, S. (gen. coord.) (1986-2012) *Flora Ibérica 1-8, 10-15, 17-18, 21*. Real Jardín  
 120 Botánico, CSIC, Madrid.
- 121 Chevan, A. & Sutherland, V. (1991) Hierarchical partitioning. *American Statistician*, **45**, 90-  
 122 96.
- 123 Colwell, R.K. (2013) *EstimateS: statistical estimation of species richness and shared species*  
 124 *from samples*. Version 9. Available at: <http://purl.oclc.org/estimates> (accessed 6 February  
 125 2015).
- 126 Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through  
 127 extrapolation. *Philosophical Transactions of the Royal Society of London B*, **345**, 101-118.
- 128 Colwell, R.K., Mao, C.X. & Chang, J. (2004) Interpolating, extrapolating, and comparing  
 129 incidence-based accumulation curves. *Ecology*, **85**, 2717-2727.
- 130 Dincă, V., Montagud, S., Talavera, G., Hernández-Roldán, J., Munguira, M.L., García-  
 131 Barros, E., Hebert, P.D.N. & Vila, R. (2015) DNA barcode reference library for Iberian  
 132 butterflies enables a continental-scale preview of potential cryptic diversity. *Scientific*  
 133 *Reports*, **5**, 12395
- 134 Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information  
 135 theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479-488.
- 136 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J.R.,  
 137 Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,  
 138 Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013)  
 139 Collinearity: a review of methods to deal with it and a simulation study evaluating their  
 140 performance. *Ecography*, **36**, 27-46.
- 141 ESRI (2012) *ArcGIS 10.1*. Environmental System Research Institute Inc., Redlands.
- 142 Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller,  
 143 M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M.,

- 144 Oskin, M., Burbank, D. & Alsdorf, D. (2007) The shuttle radar topography mission.  
145 *Reviews of Geophysics*, **45**, RG2004.
- 146 García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives Moreno, A. (2013) *Fauna Ibérica*  
147 *37: Lepidoptera, Papilionoidea* (ed. by M.A. Ramos, J Alba, X. Bellés, J. Gosálbez, A.  
148 Guerra, E. Macpherson, J. Serrano and X. Templado). Museo Nacional de Ciencias  
149 Naturales, CSIC, Madrid.
- 150 Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance-range size  
151 relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579-601.
- 152 Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal*  
153 *Society of London B*, **326**, 119-157.
- 154 Granger, R.J. & Gray, D.M. (1989) Evaporation from natural nonsaturated surfaces. *Journal*  
155 *of Hydrology*, **111**, 21-29.
- 156 Guo, D., Westra, S. & Maier, H.R. (2016) An R package for modelling actual, potential and  
157 reference evapotranspiration. *Environmental Modelling & Software*, **78**, 216-224.
- 158 Gutiérrez, D. & Wilson, R.J. (2014) Climate conditions and resource availability drive return  
159 elevational migrations in a single-brooded insect. *Oecologia*, **175**, 861–873.
- 160 Gutiérrez Illán, J., Gutiérrez, D. & Wilson, R.J. (2010) The contributions of topoclimate and  
161 land cover to species distributions and abundance: fine-resolution tests for a mountain  
162 butterfly fauna. *Global Ecology and Biogeography*, **19**, 159–173.
- 163 Heikkilä, M., Kaila, L., Mutanen, M., Peña, C. & Wahlberg, N. (2012) Cretaceous origin and  
164 repeated tertiary diversification of the redefined butterflies. *Proceedings of the Royal*  
165 *Society B*, **279**, 1093-1099.
- 166 Hortal, J., Garcia-Pereira, P. & García-Barros, E. (2004) Butterfly species richness in  
167 mainland Portugal: predictive models of geographic distribution patterns. *Ecography*, **27**,  
168 68-82.
- 169 Kharouba, H.M., Paquette, S.R., Kerr, J.T. & Vellend, M. (2014) Predicting the sensitivity of  
170 butterfly phenology to temperature over the past century. *Global Change Biology*, **20**, 504-  
171 514.
- 172 Legendre, P. & Legendre, L. (1998) *Numerical ecology*. 2nd English edn. Elsevier,  
173 Amsterdam.
- 174 Mac Nally, R. (1996) Hierarchical partitioning as an interpretative tool in multivariate  
175 inference. *Australian Journal of Ecology*, **21**, 224-228.
- 176 McCain, C.M. & Grytnes, J.-A. (2010) *Elevational gradients in species richness*.  
177 *Encyclopedia of life sciences (eLS)*. Wiley, Chichester.

- 178 McMahon, T.A., Peel, M.C., Lowe, L., Srikanthan, R. & McVicar, T.R. (2013) Estimating  
179 actual, potential, reference crop and pan evaporation using standard meteorological data: a  
180 pragmatic synthesis. *Hydrology and Earth System Sciences*, **17**, 1331-1363.
- 181 Merrill, R.M., Gutiérrez, D., Lewis, O.T., Gutiérrez, J., Díez, S.B. & Wilson, R.J. (2008)  
182 Combined effects of climate and biotic interactions on the elevational range of a  
183 phytophagous insect. *Journal of Animal Ecology*, **77**, 145-155.
- 184 Ministerio de Medio Ambiente (2000) *Mapa forestal de España. Escala 1:50000. Provincia*  
185 *de Madrid*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente,  
186 Madrid.
- 187 Ministerio de Medio Ambiente (2002a) *Mapa forestal de España. Escala 1:50000. Provincia*  
188 *de Ávila*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente,  
189 Madrid.
- 190 Ministerio de Medio Ambiente (2002b) *Mapa forestal de España. Escala 1:50000. Provincia*  
191 *de Guadalajara*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio  
192 Ambiente, Madrid.
- 193 Ministerio de Medio Ambiente (2003) *Mapa forestal de España. Escala 1:50000. Provincia*  
194 *de Segovia*. Organismo Autónomo de Parques Nacionales, Ministerio de Medio Ambiente,  
195 Madrid.
- 196 Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation*.  
197 Chapman & Hall, London.
- 198 Sawada, M. (1999) Rookcase: an Excel 97/2000 visual basic (VB) add-in for exploring global  
199 and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**, 231-  
200 234.
- 201 Schweiger, O., Harpke, A., Wiemers, M. & Settele, J. (2014) CLIMBER: Climatic niche  
202 characteristics of the butterflies in Europe. *ZooKeys*, **367**, 65-84.
- 203 Stefanescu, C., Carnicer, J. & Peñuelas, J. (2011) Determinants of species richness in  
204 generalist and specialist Mediterranean butterflies: the negative synergistic forces of  
205 climate and habitat change. *Ecography*, **34**, 353-363.
- 206 Tolman, T. & Lewington, R. (1997) *Butterflies of Britain and Europe*. HarperCollins  
207 Publishers, London.
- 208 Valiantzas, J.D. (2006) Simplified versions for the Penman evaporation equation using  
209 routine weather data. *Journal of Hydrology*, **331**, 690-702.



- 210 Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V.J. (2005)  
211 Changes to the elevational limits and extent of species ranges associated with climate  
212 change. *Ecology Letters*, **8**, 1138-1146.
- 213 Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J. (2007) An elevational shift in  
214 butterfly species richness and composition accompanying recent climate change. *Global*  
215 *Change Biology*, **13**, 1873-1887.
- 216 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects*  
217 *models and extensions in ecology with R*. Springer, New York.
- 218