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

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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.
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, Euphrydas 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 ΔAICc units of the top-ranked (lowest AICc) 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$_w$) 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 ($r_t = -0.71$, 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$_c$ for elevational trends and by AIC$_c$ 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, $\text{AIC}_c$ values were the smallest for the non-phylogenetic model and $\Delta\text{AIC}_c$ 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 $\text{AIC}_c$ 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 (±0.48) + 3.83 (±0.77) elevation − 1.73 (±0.30) elevation²], 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 (ΔQAIC<sub>c</sub> = 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 (±0.43) + 3.71 (±0.64) elevation - 1.32 (±0.23) elevation²], elevation in km; ΔQAIC<sub>c</sub> = 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
For the alternative model including annual actual evapotranspiration instead of temperature, the confidence set consisted of three models with higher AICc 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 spinip*) 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

S.B. Díez and J. Gutiérrez Illán assisted with fieldwork, A. Escudero and M. de la Cruz helped with host plant identification, C. Stefanescu provided updated data on butterfly mobility, and Rosa M. Viejo, Risto Heikkinen and one anonymous referee made useful comments on the manuscript. The research was funded by Universidad Rey Juan Carlos/Comunidad de Madrid (URJC-CM-2006-CET-0592), the Spanish Ministry of Economy and Competitiveness (REN2002-12853-E/GLO, CGL2005-06820/BOS, CGL2008-04950/BOS, CGL2011-30259, CGL2013-48277-P and CGL2014-57784-P), the British Ecological Society and the Royal Society. Research permits were provided by Comunidad de Madrid, Parque Nacional de Guadarrama, Parque Natural de Peñalara, Parque Regional de la Cuenca Alta del Manzanares, Parque Regional del Curso Medio del Río Guadarrama, Patrimonio Nacional and Ayuntamiento de Cercedilla.

(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


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


University Press, Oxford, UK.


Determinants of northerly range limits along the Himalayan bird diversity gradient.


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; \( \text{AIC}_c \): Akaike Information Criterion for small sample size; \( \Delta \text{AIC}_c \): difference in \( \text{AIC}_c \) between current and 'best' model; \( \text{AIC}_{cw} \): Akaike weight. Host plant part and mobility are categorical variables with ‘leaves’ and ‘low mobility’ as reference levels.

<table>
<thead>
<tr>
<th>a) Models for butterfly prevalence</th>
<th>( K )</th>
<th>( R^2 )</th>
<th>( \text{AIC}_c )</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( \text{AIC}_{cw} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host plant prevalence + mobility + butterfly abundance</td>
<td>6</td>
<td>0.80</td>
<td>-34.40</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>b) Models for butterfly maximum elevation</th>
<th>( K )</th>
<th>( R^2 )</th>
<th>( \text{AIC}_c )</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( \text{AIC}_{cw} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host plant maximum elevation + host plant part + butterfly abundance + minimum butterfly range temperature</td>
<td>6</td>
<td>0.70</td>
<td>16.57</td>
<td>0</td>
<td>0.36</td>
</tr>
<tr>
<td>Host plant maximum elevation + host plant part + minimum butterfly range temperature</td>
<td>5</td>
<td>0.68</td>
<td>16.87</td>
<td>0.30</td>
<td>0.31</td>
</tr>
<tr>
<td>Host plant maximum elevation + butterfly abundance + minimum butterfly range temperature</td>
<td>5</td>
<td>0.68</td>
<td>17.07</td>
<td>0.50</td>
<td>0.28</td>
</tr>
<tr>
<td>Host plant maximum elevation + minimum butterfly range temperature</td>
<td>4</td>
<td>0.63</td>
<td>20.93</td>
<td>4.37</td>
<td>0.04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>c) Models for butterfly minimum elevation</th>
<th>( K )</th>
<th>( R^2 )</th>
<th>( \text{AIC}_c )</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( \text{AIC}_{cw} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Butterfly abundance + maximum butterfly range temperature</td>
<td>4</td>
<td>0.49</td>
<td>-17.20</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

Parameter estimates (± adjusted SE) for the model averaged confidence sets are:

a) Butterfly prevalence = -0.09 (±0.05) + 0.34 (±0.08) host plant prevalence + 0.09 (±0.05)
medium mobility + 0.32 (±0.06) high mobility + 0.29 (±0.06) butterfly abundance

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

c) Butterfly minimum elevation = 4.39 (±0.60) - 0.23 (±0.07) butterfly abundance - 0.19 (±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.

<table>
<thead>
<tr>
<th>Model</th>
<th>( K )</th>
<th>( R^2 )</th>
<th>( \text{AIC}_c )</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( \text{AIC}_{cw} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of host plant species + annual mean temperature + (number of host plant species x annual mean temperature)</td>
<td>5</td>
<td>0.60</td>
<td>230.59</td>
<td>0</td>
<td>0.82</td>
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<tr>
<td>Number of host plant species + annual mean temperature</td>
<td>4</td>
<td>0.53</td>
<td>234.51</td>
<td>3.92</td>
<td>0.11</td>
</tr>
<tr>
<td>Number of host plant species + annual mean relative humidity</td>
<td>4</td>
<td>0.51</td>
<td>235.50</td>
<td>4.91</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Parameter estimates (± adjusted SE) for the model-averaged confidence set are:

Number of butterfly species = 5.04 (±12.47) + 1.40 (±0.57) number of host plant species - 0.04 (±0.75) annual mean temperature - 0.09 (±0.04) (number of host plant species x annual mean temperature) + 0.04 (±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(abundance), and (in b) to species of average ln(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 2

(a) Relationship between host plant prevalence and butterfly prevalence.

(b) Relationship between host plant maximum elevation and butterfly maximum elevation.

(c) Relationship between maximum butterfly range temperature and butterfly minimum elevation.
Figure 3

(a) Maximum number of butterfly species

(b) Maximum number of host plant species
Figure 4

Number of butterfly species

Number of host plant species
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), Satyrium (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: $r_s = 0.65, P < 0.001$).
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 Jacknife 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 ± SD (range); sites sampled two years: 0.011 ± 0.007 (0.006-0.023); sites sampled three years: 0.008 ± 0.006 (0.002-0.031); estimated sample coverage: \( U = 110, P = 0.782; \) sites sampled two years: 0.85 ± 0.07 (0.71-0.90); sites sampled three years: 0.84 ± 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 (\textsuperscript{1}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:\textsuperscript{2} unpublished data from female oviposition, egg and larvae records in the Iberian Peninsula;\textsuperscript{3} data from García-Barros \textit{et al.} (2013).

<table>
<thead>
<tr>
<th>Species</th>
<th>Host plant genus in Europe\textsuperscript{1}</th>
<th>Potential and confirmed host plants</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PAPILIONIDAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parnassius apollo</td>
<td>Sedum</td>
<td>$S. \text{album}^{2,3}$, $S. \text{amplexicaule}^{2,3}$, $S.\text{brevifolium}^{2,3}$, $S.\text{forsterianum}^{2}$, other 6 species from genus Sedum.</td>
</tr>
<tr>
<td>Zerynthia rumina</td>
<td>Aristolochia</td>
<td>$A. \text{paucinervis}^{2,3}$, $A. \text{pistolochia}^{2,3}$</td>
</tr>
<tr>
<td>Iphiclides podalirius</td>
<td>Crataegus, Malus, Prunus, Pyrus, Sorbus</td>
<td>$C. \text{monogyna}^{2,3}$, $P. \text{avium}^{3}$, $P. \text{spinosa}^{2,3}$</td>
</tr>
<tr>
<td><strong>HESPERIIDAE</strong></td>
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<tr>
<td>Spialia sertorius</td>
<td>Sanguisorba</td>
<td>$S. \text{minor}^{2,3}$, $S. \text{verrucosa}^{2}$</td>
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<td>Phlomis</td>
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<td><strong>PIERIDAE</strong></td>
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<td></td>
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<tr>
<td>Gonepteryx cleopatra *</td>
<td>Rhamnus</td>
<td>$R. \text{cathartica}$</td>
</tr>
<tr>
<td>Gonepteryx rhamni</td>
<td>Frangula, Rhamnus</td>
<td>$F. \text{alnus}^{2,3}$, $R. \text{cathartica}^{2}$</td>
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<tr>
<td>Colias alfacariensis</td>
<td>Coronilla, Hippocrepis</td>
<td>$H. \text{carpetana}$, $H. \text{commutata}^{2}$</td>
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<td>Anthocaris euphenoides</td>
<td>Biscutella</td>
<td>$B. \text{valentina}^{2,3}$</td>
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<td>Zegris eupheme</td>
<td>Hirschfeldia, Isatis</td>
<td>$H. \text{incana}^{2,3}$, $Sisymbrium \text{austriacum}^{3}$</td>
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<td>Euchloe tagis</td>
<td>Iberis</td>
<td>$I. \text{ciliata}^{2}$</td>
</tr>
<tr>
<td>Aporia crataegi</td>
<td>Crataegus, Malus, Prunus, Pyrus, Sorbus</td>
<td>$C. \text{monogyna}^{2,3}$, $P. \text{avium}$, $P. \text{spinosa}^{2,3}$</td>
</tr>
<tr>
<td><strong>RIODINIDAE</strong></td>
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<tr>
<td>Hamearis lucina</td>
<td>Primula</td>
<td>$P. \text{veris}^{2}$</td>
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<td><strong>LYCAENIDAE</strong></td>
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<tr>
<td>Lycaena alciphron</td>
<td>Rumex</td>
<td>$R. \text{acetosa}^{2}$, $R. \text{acetosella}^{2,3}$, $R. \text{bucephalophorus}$, $R. \text{conglomeratus}$, $R. \text{crispus}$, $R. \text{induratus}$, $R. \text{obtusifoliu}$, $R. \text{papillaris}^{2}$, $R. \text{pulcher}$</td>
</tr>
<tr>
<td>Species</td>
<td>Host plant genus in Europe</td>
<td>Potential and confirmed host plants</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-----------------------------</td>
<td>-------------------------------------------------------------------------------------------------------</td>
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<tr>
<td>Lycaena bleusei</td>
<td>Rumex</td>
<td>( R. ) aceta(^2), ( R. ) acetasella(^2,3), ( R. ) bucephalophorus, ( R. ) conglomeratus, ( R. ) crisps(^2), ( R. ) induratus, ( R. ) obtusi folius, ( R. ) papillaris(^2,3), ( R. ) pulcher</td>
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<tr>
<td>Lycaena phlaeas</td>
<td>Rumex</td>
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</tr>
<tr>
<td>Lycaena virgaureae</td>
<td>Rumex</td>
<td>( R. ) aceta(^3), ( R. ) acetasella(^2,3), ( R. ) bucephalophorus, ( R. ) conglomeratus, ( R. ) crisps, ( R. ) induratus, ( R. ) obtusi folius, ( R. ) papillaris, ( R. ) pulcher</td>
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<td>Laesopis roboris</td>
<td>Fraxinus</td>
<td>( F. ) angustifolia(^3)</td>
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<td>Satyrium spini</td>
<td>Rhamnus</td>
<td>( Frangula ) alnus(^2,3), ( R. ) cathartica(^2,3)</td>
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<td>Cupido minimus</td>
<td>Anthyllis (A. vulneraria)</td>
<td>( A. ) vulneraria(^2,3)</td>
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<tr>
<td>Scolitantides panoptes</td>
<td>Thymus, Satureja</td>
<td>( T. ) gr. praecox, ( T. ) mastichina(^3), ( T. ) zygr(^2,3)</td>
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<td>Cyaniris semiargus</td>
<td>Trifolium (T. pratense)</td>
<td>( T. ) pratense(^2,3)</td>
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<tr>
<td>Polyommatus thersites</td>
<td>Onobrychis</td>
<td>( O. ) humilis(^3)</td>
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<tr>
<td>Polyommatus escheri *</td>
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<td>( A. ) glycyphyllos, ( A. ) hamosus, ( A. ) cancus</td>
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<td>( H. ) carpetana(^2), ( H. ) commutata(^3)</td>
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<td>Polyommatus bellargus</td>
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<td>( H. ) carpetana(^2), ( H. ) commutata(^2,3)</td>
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<td><strong>NYMPHALIDAE</strong></td>
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<tr>
<td>Libythea celtis</td>
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<td>No host plant records at study sites</td>
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<tr>
<td>Vanessa atalanta</td>
<td>Urtica</td>
<td>( U. ) dioica(^2,3), ( U. ) urens(^2,3)</td>
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<tr>
<td>Nymphalis antiopa</td>
<td>Populus, Salix</td>
<td>( P. ) nigra(^3), ( P. ) tremula(^3), ( S. ) atrocinerea(^3), ( S. ) purpurea, ( S. ) salvi folia</td>
</tr>
<tr>
<td>Aglais urticae</td>
<td>Urtica</td>
<td>( U. ) dioica(^2,3), ( U. ) urens(^3)</td>
</tr>
<tr>
<td>Aglais io</td>
<td>Urtica</td>
<td>( U. ) dioica(^2,3), ( U. ) urens</td>
</tr>
<tr>
<td>Euphydryas aurinia</td>
<td>Lonicera</td>
<td>( L. ) etrusca(^2,3), ( L. ) pericymenmen(^2)</td>
</tr>
<tr>
<td>Melitaea phoebe</td>
<td>Centaurea</td>
<td>( C. ) alba, ( C. ) calcitraps, ( C. ) cyanus, ( C. ) melitensis, ( C. ) nigra, ( C. ) ornata(^2,3), ( C. ) aristata, ( C. ) graminifolia</td>
</tr>
</tbody>
</table>

\(^1\) Potential host plants. \(^2\) Confirmed host plants.
<table>
<thead>
<tr>
<th>Species</th>
<th>Host plant genus in Europe</th>
<th>Potential and confirmed host plants</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Melitaea trivia</em></td>
<td>Verbascum</td>
<td><em>V. pulverralentum</em>&lt;sup&gt;2,3&lt;/sup&gt;, <em>V. rotundifolium</em>, <em>V. simplex</em>, <em>V. sinuatum</em>, <em>V. thapsus</em>&lt;sup&gt;3&lt;/sup&gt;, <em>V. virgatum</em></td>
</tr>
<tr>
<td><em>Limenitis reducta</em></td>
<td>Lonicera</td>
<td><em>L. etrusca</em>&lt;sup&gt;3&lt;/sup&gt;, <em>L. periclymenum</em></td>
</tr>
<tr>
<td><em>Issoria lathonia</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>&lt;sup&gt;2&lt;/sup&gt;, <em>V. odorata</em>, <em>V. palustris</em>, <em>V. parvula</em>&lt;sup&gt;2&lt;/sup&gt;, <em>V. riviniana</em></td>
</tr>
<tr>
<td><em>Argynnis pandora</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>, <em>V. palustris</em>, <em>V. parvula</em>, <em>V. riviniana</em></td>
</tr>
<tr>
<td><em>Argynnis paphia</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>, <em>V. palustris</em>, <em>V. parvula</em>, <em>V. riviniana</em></td>
</tr>
<tr>
<td><em>Argynnis aglaja</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>&lt;sup&gt;2&lt;/sup&gt;, <em>V. palustris</em>, <em>V. parvula</em>, <em>V. riviniana</em></td>
</tr>
<tr>
<td><em>Argynnis adippe</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>, <em>V. palustris</em>, <em>V. parvula</em>, <em>V. riviniana</em>&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Argynnis niobe</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>, <em>V. palustris</em>, <em>V. parvula</em>, <em>V. riviniana</em></td>
</tr>
<tr>
<td><em>Brenthis daphne</em></td>
<td>Rubus</td>
<td><em>Rubus idaeus</em>, <em>Rubus gr. ulmifolius</em>&lt;sup&gt;2&lt;/sup&gt;, <em>Rubus sp.</em>&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Brenthis hecate</em></td>
<td>Filipendula</td>
<td><em>F. vulgaris</em>&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Boloria selene</em></td>
<td>Viola</td>
<td><em>V. canina</em>, <em>V. hirta</em>, <em>V. kitaibeliana</em>, <em>V. odorata</em>, <em>V. palustris</em>&lt;sup&gt;3&lt;/sup&gt;, <em>V. parvula</em>, <em>V. riviniana</em>&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

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 Heikkila 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 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; Hesperiidae, 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.

<table>
<thead>
<tr>
<th></th>
<th>Host plant prevalence</th>
<th>Host plant max elevation</th>
<th>Host plant min elevation</th>
<th>Host plant part</th>
<th>Butterfly mobility</th>
<th>Butterfly abundance</th>
<th>Butt range temp SD</th>
<th>Max butt range temp</th>
<th>Min butt range temp</th>
<th>Butt range precip SD</th>
<th>Max butt range precip</th>
</tr>
</thead>
<tbody>
<tr>
<td>Host plant maximum elevation</td>
<td>( r_s = 0.92^{***} )</td>
<td>( r_s = -0.64^{***} )</td>
<td>( r_s = 0.32^* )</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
</tr>
<tr>
<td>Host plant minimum elevation</td>
<td>( r_s = -0.50^{***} )</td>
<td>( r_s = -0.64^{***} )</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
</tr>
<tr>
<td>Host plant size</td>
<td>U = 208 ns</td>
<td>U = 217 ns</td>
<td>U = 217 ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
</tr>
<tr>
<td>Host plant part</td>
<td>U = 169.5 ns</td>
<td>U = 130 ns</td>
<td>U = 92.5 ns</td>
<td>ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
</tr>
<tr>
<td>Butterfly mobility</td>
<td>H = 3.72 ns</td>
<td>H = 4.23 ns</td>
<td>H = 5.14 ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
<td>Fisher ns</td>
</tr>
<tr>
<td>Butterfly abundance</td>
<td>( r_s = 0.04** )</td>
<td>( r_s = 0.07** )</td>
<td>( r_s = -0.08** )</td>
<td>U = 177 ns</td>
<td>U = 148*</td>
<td>H = 9.67**</td>
<td>( r_s = 0.03** )</td>
<td>( r_s = -0.18** )</td>
<td>( r_s = -0.49*** )</td>
<td>( r_s = 0.07** )</td>
<td>( r_s = -0.12** )</td>
</tr>
</tbody>
</table>

\( r_s \), Spearman’s rank correlation coefficient (two continuous variables); \( U \), Mann-Whitney 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. ns \( P > 0.1 \); * \( P < 0.1 \); ** \( P < 0.05 \); *** \( P < 0.01 \); **** \( P < 0.001 \).
Species richness analysis

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

<table>
<thead>
<tr>
<th></th>
<th>Number of host plant species</th>
<th>Annual mean temperature</th>
<th>Annual mean relative humidity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual mean temperature</td>
<td>0.53***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual mean relative humidity</td>
<td>0.09ns</td>
<td>-0.57***</td>
<td></td>
</tr>
<tr>
<td>Annual actual evapotranspiration</td>
<td>-0.57***</td>
<td>-0.71***</td>
<td>0.37*</td>
</tr>
</tbody>
</table>

ns P > 0.1 ; + P < 0.1 ; * P < 0.05; ** P < 0.01; *** P < 0.001.

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

Cross-species analysis

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

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model</th>
<th>Parameter</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Butterfly prevalence</td>
<td>No phylogenetic correction</td>
<td>n.a.</td>
<td>19.44</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Brownian motion</td>
<td>n.a.</td>
<td>44.05</td>
<td>24.61</td>
</tr>
<tr>
<td></td>
<td>Ornstein-Uhlenbeck</td>
<td>α = 48.50</td>
<td>23.07</td>
<td>3.63</td>
</tr>
<tr>
<td>Butterfly maximum elevation (excluding maximum butterfly range precipitation)</td>
<td>No phylogenetic correction</td>
<td>n.a.</td>
<td>50.62</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Brownian motion</td>
<td>n.a.</td>
<td>65.21</td>
<td>14.60</td>
</tr>
<tr>
<td></td>
<td>Ornstein-Uhlenbeck</td>
<td>α = n.a.*</td>
<td>n.a.*</td>
<td>n.a.*</td>
</tr>
<tr>
<td>Butterfly maximum elevation (excluding minimum butterfly range temperature)</td>
<td>No phylogenetic correction</td>
<td>n.a.</td>
<td>66.88</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Brownian motion</td>
<td>n.a.</td>
<td>76.56</td>
<td>9.68</td>
</tr>
<tr>
<td></td>
<td>Ornstein-Uhlenbeck</td>
<td>α = n.a.*</td>
<td>n.a.*</td>
<td>n.a.*</td>
</tr>
<tr>
<td>Butterfly minimum elevation</td>
<td>No phylogenetic correction</td>
<td>n.a.</td>
<td>40.59</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Brownian motion</td>
<td>n.a.</td>
<td>52.96</td>
<td>12.37</td>
</tr>
<tr>
<td></td>
<td>Ornstein-Uhlenbeck</td>
<td>α = n.a.*</td>
<td>n.a.*</td>
<td>n.a.*</td>
</tr>
</tbody>
</table>

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

* no convergence was found for butterfly maximum and minimum elevation using the Ornstein-Uhlenbeck model.
Figure S3 Relationship between butterfly maximum elevation and minimum butterfly range temperature. Different symbols and lines represent species differing in 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 to species of average ln(abundance) and host plant maximum elevation ($n = 43$ species).
Table S5  Confidence sets of regression models for (a) butterfly maximum elevation (all species, \(n = 43\)), (b, c) butterfly maximum elevation of species occurring below 2000 m \((n = 29)\), and (d) butterfly minimum elevation of species occurring above 750 m \((n = 24)\).

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

Parameter estimates (± adjusted SE) for the model averaged confidence sets are:
(a) Butterfly maximum elevation = 0.44 (±0.24) + 0.53 (±0.12) host plant maximum elevation - 0.29 (±0.13) flower-fruits + 0.05 (±0.12) butterfly abundance + 0.0002 (±0.0001) maximum butterfly range precipitation.

(b) Butterfly maximum elevation = 1.29 (±0.24) + 0.18 (±0.12) host plant maximum elevation - 0.05 (±0.02) minimum butterfly range temperature.

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

(d) Butterfly minimum elevation = 3.67 (±0.59) + 0.08 (±0.06) medium mobility + 0.001 (±0.07) high mobility - 0.28 (±0.08) butterfly abundance - 0.15 (±0.03) maximum butterfly range temperature.

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

\( R^2 \), coefficient of determination; \( \text{AIC}_c \), Akaike Information Criterion for small sample size;

\( \Delta \text{AIC}_c \), difference in \( \text{AIC}_c \) between current and 'best' model; \( \text{AIC}_c \text{w} \), Akaike weight. Mobility is a categorical variable with ‘low mobility’ as reference level.
Hierarchical partitioning

In hierarchical partitioning, host plant prevalence, butterfly mobility and abundance showed statistically significant independent contributions for butterfly prevalence (Fig. S4). For butterfly maximum elevation, there were significant independent effects of host plant maximum elevation, butterfly abundance, minimum butterfly range temperature and maximum butterfly range precipitation when all 43 species were considered. The significant independent contributions of host plant maximum elevation and minimum butterfly range temperature remained when the 14 species occurring above 2000 m were excluded (Fig. S4). For butterfly minimum elevation, there were significant independent contributions of butterfly abundance and maximum butterfly range temperature for all 43 species and for the 24 occurring above 750 m (Fig. S4). The negative joint contributions of butterfly abundance (and to a lesser degree, host plant size and part, butterfly mobility and maximum butterfly range temperature) for lower elevational limits (Fig. S4c, e) indicate that the joint action of these variables suppresses or masks the independent contribution of other factors (Chevan & Sutherland, 1991; Mac Nally, 1996).
**Figure S4** The independent (black bars) and joint contribution (white bars) (given as a percentage of the total variance explained by the model) of the environmental variables estimated from hierarchical partitioning for (a) butterfly prevalence, (b) butterfly maximum elevation, (c) butterfly minimum elevation \((n = 43\) species in a, b and c), (d) butterfly maximum elevation for species occurring below 2000 m \((n = 29\) species), and (e) butterfly minimum elevation for species occurring above 750 m \((n = 24\) species). Asterisks indicate
significant ($P < 0.05$) independent contributions from randomization tests. Note the different y-axis scales.
Species richness analysis

**Figure S5** Relationship between elevation and (a) annual mean temperature ($r_s = -0.96, P < 0.001$), (b) annual mean relative humidity ($r_s = 0.44, P = 0.005$), (c) annual actual evapotranspiration ($r_s = 0.72, P < 0.001$) ($n = 40$ sites for all cases). Values averaged for the period 2006-08 in all cases.
Table S6 Confidence sets of regression models for number of butterfly species including number of host plant species, annual mean relative humidity and annual actual evapotranspiration as predictor variables (n = 40 sites).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>$R^2$</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$\text{AIC}_w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of host plant species + annual mean relative humidity + annual actual evapotranspiration</td>
<td>5</td>
<td>0.56</td>
<td>234.88</td>
<td>0</td>
<td>0.56</td>
</tr>
<tr>
<td>Number of host plant species + annual mean relative humidity</td>
<td>4</td>
<td>0.52</td>
<td>235.50</td>
<td>0.62</td>
<td>0.41</td>
</tr>
<tr>
<td>Number of host plant species + annual actual evapotranspiration</td>
<td>4</td>
<td>0.45</td>
<td>240.58</td>
<td>5.71</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Parameter estimates (± adjusted SE) for the model averaged confidence set are:

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

$K$, number of parameters (includes an extra parameter for the estimate of regression variance); $R^2$, coefficient of determination; $\text{AIC}_c$, Akaike Information Criterion for small sample size; $\Delta\text{AIC}_c$, difference in $\text{AIC}_c$ between current and 'best' model; $\text{AIC}_w$, Akaike weight.

Figure S6 The independent (black bars) and joint contribution (white bars) (given as percentage of the total variance explained by the model) of the environmental variables
estimated from hierarchical partitioning for butterfly species richness ($n = 40$ sites). Asterisks indicate significant ($P < 0.05$) independent contributions from randomization tests.
REFERENCES


Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M.,


