Ecological and evolutionary drivers of the elevational gradient of diversity

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Abstract

Ecological, evolutionary, spatial and neutral theories make distinct predictions and provide distinct explanations for the mechanisms that control the relationship between diversity and the environment. Here, we test predictions of the elevational diversity gradient focusing on Iberian bumblebees, grasshoppers and birds. Processes mediated by local abundance and regional diversity concur in explaining local diversity patterns along elevation. Effects expressed through variation in abundance were similar among taxa and point to the overriding role of a physical factor, temperature. This determines how energy is distributed among individuals and ultimately how the resulting pattern of abundance affects species incidence. Effects expressed through variation in regional species pools depended instead on taxon-specific evolutionary history, and lead to diverging responses under similar environmental pressures. Local filters and regional variation also explain functional diversity gradients, in line with results from species richness that indicate an (local) ecological and (regional) historical unfolding of diversity–elevation relationships.

Introduction

Diversity-environment relationships have been the subject of considerable research in ecology. Among these relationships, the elevational gradient of diversity is one of the most frequently documented and controversial. These gradients are found in all mountains, yet there is little agreement on the mechanisms behind them and the spatial scales at which these mechanisms operate (Ricklefs 2004; Rahbek 2005; Graham *et al.* 2014). Most of these mechanisms also operate along another striking biogeographic pattern, the latitudinal gradient of diversity, although researchers concur that this pattern mostly results from large scale processes controlling the production and extinction of species (Ricklefs 2006). Because of differences in the rates and times of evolutionary diversification along latitude, the decline in species richness towards the poles is strongly linked to the decline in γ (regional) diversity, and not to variation in α (local) community richness (Stevens & Willig 2002; Hillebrand 2004; Ricklefs 2004; Witman *et al.* 2004). This clearly underscores the role of local effects, such as upper limits to niche packing or minimum viable population sizes, as deterministic drivers of the spatial variation of diversity along environmental gradients (Lambers *et al.* 2002). No quantitative test along elevation has analysed the dependence of α -species richness on regional patterns, a crucial step for distinguishing between ecological assembly mechanisms at the local scale and evolutionary and spatial processes operating at larger scales (Srivastava 1999; Kraft *et al.* 2011).

Multiple processes operating at multiple scales determine the number of species coexisting in communities on mountainsides (Laiolo *et al.* 2017). On the one hand, ecological limitations at the local scale impose a ceiling to local species richness by actively filtering species through biotic interactions, abiotic stress, productivity and habitat heterogeneity. Temperature and productivity-driven processes, for instance,

often underlie monotonic declines of species richness with elevation (McCain & Grytnes 2010; Peters *et al.* 2016a). Variation in local abundance can mediate these relationships: energetic limitations constrain population sizes, enhancing extinction probabilities and reducing the chance of sampling rare species (energy-abundance relationship and increased population size hypotheses; Evans *et al.* 2005). Variation at the community level, however, also recapitulates processes operating at larger scales. Spatial or topographic mechanisms such as area, isolation and geometric constraints, together with broad scale environmental turnover, may affect regional species pool diversity through their effects on colonization, extinction, and speciation (sampling from regional species pools; Ricklefs 2004). Linear or unimodal diversity clines along elevation, for instance, may be explained by land area alone, with the richest species pools occupying the gradient sections with the largest area (species-area relationship; Bertuzzo *et al.* 2016). Mid-peaks of diversity are also expected if species ranges are randomly distributed within geographically limited land domains (mid domain effect, Colwell *et al.* 2004). High mountain endemic species, often originating in glacial refugia in the lower and unglaciated parts of mountain chains, significantly contribute to local diversity patterns (speciation hypothesis; Kessler 2002; Jiménez-Alfaro *et al.* 2014). Eventually, if lineages retain their niche characteristics over evolutionary time, taxa are expected to cluster at optimal, taxon-specific, sets of biotic or abiotic conditions along broader gradients (e.g., climate constraint hypothesis; Peters *et al.* 2016a).

The functional identity of community members, representing the range of activities in which organisms engage in communities and ecosystems (Petchey & Gaston 2006), is also the result of phenotypic diversification within ancestral zones of origin combined with occasional adaptive shifts associated with range expansion (Ricklefs 2006). Geographic gradients of functional diversity, a metric accounting for

the amount of difference between species' adaptive traits, may therefore arise because of the differential colonization of preadapted forms or evolutionary shifts within species already inhabiting an area (Emerson & Gillespie 2008). Local deterministic processes, however, also control the co-occurrence of different phenotypes. Many adaptive traits, especially in animals, do not have direct ecosystem functions but operate locally, determining which among many candidate species are recruited into communities (Grime & Pierce 2012). These community processes may fuel functional diversity variation: competitive exclusion among similar species in lowlands, and selection against certain forms in highlands, cause negative elevation clines of community functional diversity (Chun & Lee 2018). Thus, functional diversity also varies locally and regionally, although what drives its relationship with the environment is even less clear than for species richness, be it present local filters or previous diversification somewhere else.

Here, we studied the patterns and drivers of diversity variation along a 2.6 km elevation gradient in the westernmost range with alpine zonation of Europe, the Cantabrian Mountains in NW Spain. We centred on variation in species richness within communities (spatial scale of a few hundred meters) and regional species pools (spatial scale of a few hundred kilometres) in bumblebees, grasshoppers and birds, which were extensively surveyed from the seacoast to mountaintops. With the same approach, we addressed the diversity of traits that condense crucial biological information of animal communities, such as resource use patterns, dominance and population dynamics, and that reflect the variety of organismal adaptive strategies along elevation (Grime & Pierce 2012; Laiolo & Obeso 2017). We analysed the influence of environmental, spatial and evolutionary drivers on elevation clines of species richness and functional diversity, testing predictions of the major hypotheses of diversity variation: sampling

effects from local and regional pools, mid-domain effect, and species richness-area, - isolation, -heterogeneity, -climate, -speciation, -plant diversity relationship (Table 1). We used a hierarchical approach for distinguishing among direct effects on community diversity from indirect ones, i.e. mediated by regional species pools and the local abundance of individuals (Table 1). For evolutionary theories of diversity gradients to be supported, we predict that regional-scale effects should be important and diversity should increase with the diversity of regional species pools and its determinants, irrespective of deterministic or sampling processes at the local scale. A significant contribution of the latter would instead indicate a local (ecological) control that, if mediated by local abundance, would point to energetic constraints to population persistence. Finally, null spatial models would be supported by diversity depending exclusively on regional spatial predictors.

Methods

Species data

The study was performed in an area of 18,000 km² including the Cantabrian Mountains, one of the main mountain systems of mainland Spain. The complete elevation gradient was sampled, from the Atlantic coast at sea level to the highest summits at over 2600 m a.s.l. Hymenoptera Apidae Bombinae (bumblebees), Orthoptera Caelifera (grasshoppers, locusts and groundhoppers, hereafter grasshoppers), and Aves (birds) were surveyed in 92, 189 and 2345 circular plots of 100 m radius, respectively (Fig. S1). We visited the prevailing natural and semi-natural habitats of the region, represented by grasslands, deciduous forests, rock outcrops and shrub formations. We avoided highly anthropogenic habitats, i.e. plantations, urban and intensive agricultural areas, so that plots were generally characterized by low levels of human disturbance.

The abundance of each bird species was recorded during 10 min counts, while bumblebees and grasshoppers were collected for 1 hr, following standard procedures for these taxa as detailed in Supplementary Methods. Overall, we recorded 18147 individuals of 114 breeding bird species of 84 genera, and collected 8277 individuals of 37 grasshopper species of 20 genera, and 2322 individuals of 30 bumblebee species of 2 genera (Tab. S1).

The elevational gradient was divided into 26, 100-m elevation, bands. The spatial scale of the local community referred to here is that of the plot, in which all the species could encounter each other and interact. The scale of the regional species pool is that of the elevational band, 5.5 to 8.6 orders of magnitude larger (depending on distribution of areal extent among bands), which includes the species that could potentially colonize a location. Even if movements across elevation occur, species replacement along elevation is marked and assemblages inhabiting the same 100 m elevational band tend to affect local communities more strongly, and thus are better proxies of regional influences than assemblages from broader elevational ranges (Tab. S2). Therefore, in each band and for each taxonomic group, we calculated the average species richness per plot (species density or α -species richness, S_α), the average abundance per plot (individual density, A), and the overall species richness per band (regional species pool or γ -species richness). This approach reduces pseudoreplication, since there is a single local richness value (mean), a single local abundance value (mean), and a single regional richness value per band. A concern about testing the impact of regional scale processes on community diversity is that regional and local species richness values are not drawn from independent samples. This may enhance autocorrelation and lead to spurious relationships between these two variables (Srivastava 1999). We used two different approaches to check for spurious relationships. First, we used rarefaction

methods to calculate the expected α -species richness under the null hypothesis of local species richness being randomly drawn from the assemblage of the rest of the plots at that elevation, given local abundances. We used the R package *rareNMtests* for this purpose (details in Supplementary material). Expected (random) and observed α -species richness were strongly correlated even when drawn from different samples (bumblebees: $t_{90} = 11.6$, $P < 0.001$; grasshoppers: $t_{187} = 5.7$, $P < 0.001$; birds: $t_{2344} = 72$, $P < 0.001$). Alternatively, we partitioned our taxa datasets into two subsets each, one used for calculating α -species richness and the other half for γ -species richness. We found significant relationships between local and regional species richness in all taxa but no effect of the type of data (complete vs. partitioned dataset) on its slope (γ -species richness $\times$ type of data: bumblebees: $F_{1,46} = 0.04$; $P = 0.84$; grasshoppers: $F_{1,46} = 0.72$, $P = 0.40$; birds: $F_{1,48} = 0.02$, $P = 0.89$). These results show that local-regional relationships are not spurious, and that the complete dataset does not bias estimates and may therefore be used in analyses.

Observed α -species richness and abundance were used in analyses, since sampling area and time were standardized during surveys, and raw values were then averaged per band. On the other hand, γ -species richness was derived by pooling plot data, and thus critically depends on the number of plots and individuals sampled per band. We estimated the completeness of sampling per band with the R package *iNEXT* (details in Supplementary material), which indicated a range from 67 to 100 % in bumblebees (average sampling coverage: $94 \% \pm 1.5$ SE), from 95 to 100% in grasshoppers ($99 \% \pm 0.02$ SE), and from 87 to 100% in birds ($98 \% \pm 0.06$ SE). Differences among bands were thus reduced by rarefying γ -species richness (S_{γ}), by randomly sub-sampling the minimum observed number of individuals per band with the R package *vegan* (details in

Supplementary material). These rarefied values were considered in all analyses as a measure of richness standardized for regional abundances.

As for species richness, we calculated the average functional diversity per plot for each elevational band (local community or α -functional diversity), and the overall functional diversity of the species pool of each band (regional or γ -functional diversity). We accounted for dissimilarities among co-occurring species in traits associated with niche breadth, body mass, dispersal capacity, life cycle duration and life history trade-offs, all features important for individual performance that may affect community assembly processes. Information on traits, obtained from literature or generated by this study, is provided in Table 2, and in more detail, in the Supplementary Methods and Table S1. The use of a single trait value per species was justified by the fact that, in these taxa, the magnitude of changes due to species turnover largely exceeds intraspecific variation along elevation (Laiolo *et al.* 2013; Laiolo *et al.* 2015b; Laiolo & Obeso 2017; Peters *et al.* 2016b). The scaled values of functional traits served to calculate Gower dissimilarities among species and an index of functional diversity per plot and per band: the standardized effect size of mean pairwise functional dissimilarity among species (mean FD_α and FD_γ). The R package *picante* was used to calculate this index, which is standardized for species richness, weighted for abundance, and corrected for the expected diversity under random functional assembly. The reliability and stability of functional diversity metrics was tested by comparing functional diversity values based on increasingly larger numbers of traits, from two to six (details in Supplementary Methods), and by using three randomization procedures. We alternatively shuffled (i) species identity in functional dissimilarity matrices, (ii) the survey data matrix maintaining sample species richness and abundance with the trial swap algorithm, and (iii) the survey data matrix maintaining species richness alone.

Environmental, spatial and evolutionary predictors

Climate information for each sampling plot and for the entire elevational band was obtained from the digital layers of the Climate Atlas of the Iberian Peninsula (200 m resolution; Ninyerola *et al.* 2005). Annual temperature and accumulated precipitation were chosen as proxies of climatic conditions in plots (mean T_a and P_a) and bands (T_γ and P_γ) because variation in these variables represented that of a large set of climatic parameters (e.g., minimum and maximum temperatures, temperatures of the coldest and warmest months, precipitation of the driest and wettest months - all $r > 0.87$). We also estimated two indices of net primary productivity, the normalized difference vegetation index and the average annual actual evapotranspiration (Fig. S2). These indices were however, highly correlated with temperature both at the band ($r = 0.97$, $t_{24} = 20.6$, $P < 0.001$, and $r = 0.94$, $t_{24} = 14.7$, $P < 0.001$, respectively) and at the plot level (all taxa: $0.92 < r < 0.98$, $11.5 < t < 23.2$, $P < 0.001$, and $0.65 < r < 0.90$, $4.2 < t < 10.4$, $P < 0.001$, respectively). The correlation with precipitation was lower ($r < 0.34$), an indication of the lack of water limitation in a region with a prevailing Atlantic climate. Therefore, while precipitation and temperature are nearly independent from each other (at the plot and band levels: average $r = 0.10$), gradients of primary productivity cannot be considered as independent predictors of diversity given their high collinearity with temperature (average $r > 0.90$) (Loreau 2000). Thus, we did not consider further productivity indices and accounted instead for temperature, a key component of species niche and a driver of species distribution and productive energy (Laiolo *et al.* 2015a; Kearney & Porter 2009). Indices of habitat heterogeneity of plots (mean HET_a), and of bands (HET_γ), were calculated as $1 - \sum_{i=1}^N p_i^2$, where p_i is the proportional cover of the i th habitat type and N is the number of habitat types. The cover of natural habitat types in

plots (woodland, shrubland, grassland, rocks and bare ground) was visually estimated during surveys, while the overall cover of these habitats in elevational bands was derived from CORINE land-cover data (<http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012>). As a measure of heterogeneity, we also considered the overall richness of vascular plant taxa (SP_{γ}). This was obtained, for each elevational band, from the complete floristic catalogue of the Picos de Europa area, which covers mid- and eastern-Cantabrian Mountains and hosts 1395 species of vascular plants (Felpete *et al.* 2011). Plant diversity has an asymmetric unimodal distribution with a peak in the low-half of the gradient in the study area (Fig. S3), analogous to other mountainous systems in which the complete gradient was studied (Himalaya: Grytnes & Vetaas 2002; Pyrenees: Nogués-Bravo *et al.* 2008).

Among the spatial drivers of regional species richness patterns, we considered area, isolation and an index quantifying the mid-domain effect. These predictors were estimated for each 100-m elevational band, as they primarily operate at scales larger than the plot (Lomolino 2001). Digital elevation models of 100 m resolution were used to calculate land area (distribution of areal extent; AR) and topographic isolation (the mean nearest neighbour distance of patches located within the same 100-m elevational band; I) in QGIS 2.18.3 (Quantum GIS Development Team, 2012). In our study area, the largest land area is concentrated, not at low, but at middle elevations (Fig. S3), a common pattern in mountain landscapes shaped by fluvial erosion (e.g., Alps: Bertuzzo *et al.* 2016). Moreover, the distance between adjacent peaks does not increase monotonically with elevation, given that summits are concentrated into massifs, as typical of non-conic systems (Fig. S3). Mid-domain effect models were used to generate the expected number of species per band based on a null model of increasingly higher number of species in bands toward the centre of each taxon's sampling domain (MID_{γ})

(Rahbeck *et al.* 2007; Peters *et al.* 2016a). The R package *RangemodelR* was used for this purpose (Supplementary material; Fig. S4).

Most bumblebee and bird species have broad Palearctic distributions. Thus, biogeographic dispersal, colonization and extinction are the most probable drivers of regional diversity patterns in these groups. On the other hand, grasshoppers include two stenoendemics, i.e. species with a global distribution restricted to a few Cantabrian peaks (*Podisma cantabricae* and *Chorthippus cazurroi*) with close congeners also inhabiting these mountains (Laiolo *et al.* 2013; Laiolo & Obeso 2015). Grasshoppers are, therefore, the sole group in which cladogenesis (*in situ* speciation) may have enhanced the species richness of the region. The number of stenoendemic species per band (END_{γ}) was thus entered into models of diversity variation as a direct indicator of the potential for cladogenesis along the gradient (Steinbauer *et al.* 2016).

Data analysis

We considered each taxonomic group as a coherent biological and functional unit, performing all analyses at the level of single taxa. Prior to analyses, we standardized all variables to allow diversity trends to be compared among taxa and parameter estimates (standardized β) to be compared among predictors measured in different units.

We performed an initial exploration of variation in species richness and functional diversity along elevation bands by means of generalized additive models with a Gaussian distribution of errors, with the R package *mgcv* (Supplementary material). We allowed up to five dimensions of the smoothing function to prevent an overparameterization of models (Peters *et al.* 2016a). For hump-shaped richness trends, we first checked the correlation between the observed and expected γ -species richness by mid-domain effect models. We then estimated the elevation at which inflection points occur by means of the R package *segmented* (Supplementary material).

In the next step, we tested the support for different hypotheses on diversity trends by analysing, by means of path analyses, the direct and indirect influence of the above-described predictors on species richness and functional diversity (Tab. 1). In this way, we could explicitly test the contribution of each predictor, as an alternative to analysing, indirectly and separately, the shape of local-regional diversity relationships (Srivastava 1999) and abundance-richness relationships (Evans *et al.* 2005). When sample size is naturally constrained, reliable path model estimates can be obtained even with moderate sample size if the magnitude of effects is large and simple models with no latent variables are selected (Peters *et al.* 2016a; Laiolo 2017). Thus, we analysed the direct and indirect (mediated by abundance) contribution of local predictors on α -species richness, and the indirect (mediated by γ -species richness) contribution of regional predictors on α -species richness. Similarly, we analysed the direct and indirect contribution of local and regional (mediated by γ -functional diversity) predictors on α -functional diversity. We previously evaluated models defined by the possible variable combinations listed in Table 1 with the dredge function of the R package *MuMIn*. From the set of models with the lowest AICc we built path models with the R package *lavaan* (Supplementary material), again selecting the best paths based on their AICc (considering as equally probable models with $\Delta\text{AICc} < 2$) and model performance. The latter was assessed by means of the root mean square error of approximation and χ^2 statistics, which tests whether the estimated covariance matrices are not significantly different from the actual covariance matrix. The importance of predictor combinations in explaining species diversity variation was assessed by means of the multiple coefficient of determination r^2 , while the importance of single predictors is given by standardized path β -coefficients, proportional to variable weights.

Results

Elevation clines of diversity

The α - and γ -species richness of bumblebees and grasshoppers displayed similar, asymmetric, hump-shaped elevation trends with a steep decline towards the upper end of the gradient (Fig. 1, Tab. S3). On the contrary, bird α -species richness declined with elevation and bird γ -species richness had a low plateau distribution with a midpeak. Abundance declined with elevation in all species, more steeply in birds than in insect taxa (Fig. S5). Observed γ -species richness was significantly correlated with predicted γ -species richness by mid-domain effect models in all taxa ($0.24 < r < 0.50$; $t_{25} = 2.8$; $P < 0.01$). However, observed peaks were found to be 944 and 677 m higher than expected in bumblebees and grasshoppers, respectively (Fig. S4; Tab. S4).

The magnitude of chance effects detected in functional diversity estimates depended largely on the randomization procedure used: the number of (significant) functionally non-random communities varied from 0 to 43% (average 15%; Tab. S5). There was however agreement on other relevant issues. First, irrespective of the procedure used, the functional assortment of species was random in the majority of cases. Secondly, the most functionally diverse communities did not deviate from null expectations while the least diverse were functionally clustered (i.e. more similar than expected by chance; Fig. S6; Tab. S5). Ultimately, the shape of elevational trends matched among procedures (Fig. S7), but a variety of functional diversity patterns emerged among taxa. Bumblebee communities and assemblages were functionally poorest (clustered) at low elevations, while grasshopper and bird ones were poorest at mid-elevations (Fig. 1, Tab. S3; Fig. S6). Given the matching of functional clines among procedures, further analyses were performed with functional diversities estimated by means of the trial swap algorithm.

Drivers of diversity

The best path models fitted the data well (Tab. S6), the error terms of each independent construct were uncorrelated ($0.21 < P < 0.85$), and variable combinations explained a good proportion of diversity variance (Fig. 2). Local and regional sampling hypotheses received significant support, since the influence of environmental predictors on α -species richness and functional diversity was most often indirect and mediated by local densities (influencing α -species richness) and diversity at the largest spatial scales (influencing α -species richness and α -functional diversity) (Fig. 2; Tab. S6).

Temperature was the single predictor with the greatest direct and indirect influence on species richness and functional diversity, supporting hypotheses on climatic and energetic constraints in all taxa. This variable had, however, opposite effects on the two main drivers of local community richness in insect taxa, enhancing abundance but diminishing richness. In bumblebees, it also negatively affected functional diversity, while in birds it had opposite effects on α - and γ -functional diversity. Habitat heterogeneity was an important indirect driver of local species richness, via its positive influence on abundance (grasshoppers) and γ -species richness (birds and grasshoppers). Ultimately, paths of species richness variation in grasshoppers included the positive effect of endemics richness. Given the relatively lower support for models with the rest of predictors, the hypotheses of mid-domain effects, association with plant vascular diversity, and species-area and -isolation relationships were all poorly supported (Tab. S6).

Discussion

Explanations for biogeographic patterns, especially those of limited spatial extent such as elevational diversity gradients, are often sought in ecological processes engendered

by local physical conditions, or in stochastic processes linked to geographic constraints and species-area relationships (McCain & Grytnes 2010). Evolutionary explanations, i.e. the process of production and extinction of species within the region or in ancestral zones of lineage origin, have been less developed elevationally than latitudinally (Graham et al. 2014). Our study shows that both ecological and evolutionary explanations are necessary to understand elevational diversity gradients. We found that two common proximal mechanisms explain community diversity patterns, local abundance and regional diversity, which influence all taxa in the same direction (Fig. 2). Effects expressed through variation in abundance point to basic ecological mechanisms that operate at the level of individual organisms, determining whether they obtain sufficient energy to persist and reproduce. On the contrary, the environmental and evolutionary drivers expressed through variation in regional diversity differ markedly among taxa. The net outcome is that the response of local animal communities fails to converge under similar physical or environmental pressures along elevation, giving rise to idiosyncratic local patterns (Fig. 1).

The first evidence of evolutionary constraints is provided by the significant relationship between grasshopper diversity and endemic species occurrence. In volcanic island archipelagos, species diversity is frequently associated with speciation rate, either because both phenomena are enhanced by increased population persistence times with area or because of a causal link between biotic interactions and differentiation rate (Emerson & Kolm 2005). In the case of grasshoppers and other mountain endemics, it seems that higher speciation rates are linked to increasing isolation with elevation and to the distribution of refugia during the Pleistocene glacial maxima, rather than to more intense biotic interactions (Hewitt 1996; Steinbauer *et al.* 2016). Apart from the effect of speciation rate, evolutionary history may also explain

the negative effects of temperature on regional species richness of insect taxa. Every clade has its particular zone of origin, and when most of its representatives are restricted to a particular climatic region, as in the case of bumblebees and the most speciose genus of grasshoppers, *Chorthippus*, one could parsimoniously infer that these clades originated within those climatic conditions (Ricklefs 2006). In support of this idea, phylogenetic analyses showed that these groups radiated in cool temperate and cold regions of the Palearctic and that these regions also represent the ancestral zone of origin, as they host the oldest species (Williams *et al.* 1985; Hines 2008; Bugrov *et al.* 2006). Thus, alpine communities may be richer because these taxa, due to their peculiar evolutionary history, contribute more species to the subalpine and alpine belts than to lowlands. Iberian fauna in fact comprise large proportions of boreo-alpine bumblebees and gomphocerine grasshoppers that are obligate dwellers of upland areas (Gangwere & Agacino 1970; Obeso 1992). The effect of habitat heterogeneity on regional species richness also appears to have a remote cause. Elevational bands with high habitat turnover have large cumulative numbers of species of grasshoppers and birds, two taxonomically-broad lineages that have filled multiple niches (Davidowitz & Rosenzweig 1998; Laiolo *et al.* 2015b). In contrast, bumblebees are phylogenetically homogeneous; species largely share habitat preferences and do not form habitat-specific communities (Herrera *et al.* 2014).

Unlike regional effects, local influences on species richness, mediated by abundance, converge among taxa and are related to a small set of environmental characteristics. A straightforward role is played by temperature, which is a broad indicator of the availability of energy to organisms and a strong determinant of nutrient dynamics in mountain food webs (Laiolo *et al.* 2015a). The relevance for diversity relies on the fact that the success of individual organisms in obtaining resources

ultimately determines how many individuals occur locally and, in turn, the probability of a species being present (Wright *et al.* 1983). Pure sampling effects may underlie this pattern, but deterministic explanations are also possible and, at least in the avian assemblage, they are preponderant (Seoane *et al.* 2017). In fact, an increased amount of resources elevates species richness through larger numbers of potentially viable populations of different species, or through narrower niche breadths that promote species coexistence. These effects also apply to bumblebee and grasshopper populations, since temperature strongly influences their activity (Classen *et al.* 2015). However, paradoxically and in contrast with the above result at the local scale, local species richness in insect taxa depends on regional species richness values that are depressed by temperature. These contrasting contributions of temperature are not mutually exclusive as they involve different spatial and temporal scales, of sampling or ecological dynamics on the one hand (more energy, more individuals and more species) and of historical biogeographic processes on the other (radiations in cool climates). Such temperature-driven trade-offs may also explain the shape of the richness function with elevation, which bends in the extremes of the gradient (Fig. 1). Thus far, a commonly accepted explanation for unimodal patterns with temperature or energy was that competition is driving both sides of the richness function downward (Rosenzweig & Abramsky 1993). At the low productivity end, species should compete for scarce resources and at the high end competitively dominant species should monopolize resources (Graham & Duda 2011). This competition-based explanation, however, is neither compatible with the experimental and observational evidence we obtained for the study communities (Obeso 1992; Bastianelli *et al.* 2017; Laiolo *et al.* 2017) nor with the functional diversity results of this study. There was no evidence of functionally-divergent communities supporting limiting similarity patterns. Rather, we observed

many randomly assembled communities with a few composed of functionally redundant species in coincidence with poorly diverse regional assemblages and mild conditions.

Taken together, the results of this study indicate that variation in species diversity across broad elevation gradients depends largely on sampling effects. The significant contribution of regional processes to diversity supports evolutionary theories and, partly, Hubbels's (2001) neutral theory of communities except for the lack of significant spatial effects. Ecological theories, however, cannot be dismissed because local influences are evident and convergent among taxa. Such repeated patterns are linked to basic mechanisms that determine how energy is partitioned among individual organisms and how the resulting patterns of abundance affect species incidence. This result, together with that obtained for functional diversity, confirms the predictive power of temperature in explaining diversity variation along this type of geographic gradient, which is primarily a climate gradient (Peters *et al.* 2016a). However, this variable fuels contrasting evolutionary and ecological processes in insects that may concur in positioning diversity peaks along elevation. Different forces determine the composition of regional assemblages, such as habitat turnover, past radiations and *in situ* speciation, and these indirectly drive local patterns. Therefore, although ecological forces are an important driver of the elevational patterns of species richness, the history of lineages and the inherent diversity in the tree of life is fundamental to understanding the diversity of elevational patterns and the shape of elevational clines.

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Figure Captions:

Fig. 1. Elevational trends of species richness (S) and functional diversity (FD) at the local (average α) and regional (γ) scales in the Cantabrian Mountains, NW Spain.

Functional diversity is calculated as standardized effect size of trait dispersion with the trial swap algorithm (results with other randomization procedures can be found in Supplementary Material). All diversity values were standardized to zero mean and unit standard deviation for comparative purposes. Band-level values of α and γ diversity, elevation trends (continuous lines) and confidence intervals (dotted lines) are shown.

Fig. 2. Path models showing direct and indirect effects of predictor variables on species richness (S) and functional diversity (FD) at the local (α) and regional (γ) scales.

Interrupted lines indicate the effect of a variable that only enters into one of the best path models; black and grey arrows indicate positive and negative relationships, respectively. A = Local Abundance, T = Temperature, HET = Habitat heterogeneity, P = Precipitation, END = Number of endemic species. Standardized β -coefficients for each variable are highlighted in grey and multiple r^2 are highlighted in black. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Tab. 1. Main hypotheses on the origin of biodiversity gradients, together with the target dependent variable, and the main predictors considered in this study.

Dependent Variable	Hypotheses	Predictor
<i>α –species richness</i>	<u>Effect of sampling (from regional pools of species)</u> : Stochastic immigration maintains community species richness, with the actual level of local species richness determined by the size of the regional species pool (Hubbell 2001).	<i>γ –species richness</i>
	<u>Effect of sampling (from local pools of individuals)</u> : More individuals lead to more species because of more viable populations or reduced sampling biases (Increased population size hypothesis; Evans <i>et al.</i> 2005).	<i>Local abundance</i>
	<u>Heterogeneity-diversity relationship</u> : Habitat heterogeneity increases the number of ecological niches and thus of co-occurring species (MacArthur & MacArthur 1961).	<i>Local habitat heterogeneity</i>
	<u>Climate constraints</u> : Taxon-specific physiological limits and thermal or aridity tolerance determine the composition of local communities (McCain & Grytnes 2010; Peters <i>et al.</i> 2016a).	<i>Local temperature and precipitation</i>
<i>γ –species richness</i>	<u>Geographic constraints to random sampling</u> : Boundaries of land area lead to greater overlap of species ranges toward the centre of the gradient if species are randomly distributed (Colwell <i>et al.</i> 2004).	<i>Mid domain effect</i>
	<u>Heterogeneity-diversity relationship</u> : The variety of habitat patches increases turnover between sites, enhancing overall species diversity in clades that differentiated across multiple habitats (Anderson <i>et al.</i> 2006). As an extension, the diversity of primary producers supports and fuels the evolution of a diversity of consumers (Hutchinson 1959).	<i>Regional habitat heterogeneity</i> <i>Plant species richness</i>
	<u>Climate constraints</u> : Depending on the taxa's biogeographic history, a subset of the available abiotic gradient may be favoured by species (McCain & Grytnes 2010; Ricklefs 2006).	<i>Regional temperature and precipitation</i>
	<u>Energy –species richness relationship</u> : In productive and milder climates, rates of evolutionary diversification, biotic processes and interactions are higher (Allen <i>et al.</i> 2002).	
	<u>Species-Area relationship</u> : Decrease in extinction rate with land area (MacArthur & Wilson 1967).	<i>Area</i>
	<u>Species-Isolation relationship</u> : Decrease in colonization rate with isolation (MacArthur & Wilson 1967).	<i>Isolation</i>

	<u>In situ speciation increases species richness.</u> The presence of an endemic species, evidence of a speciation event, and the number of endemic species, a measure of diversification, enhance diversity (Steinbauer <i>et al.</i> 2016).	<i>Number of endemic species</i>
<i>Abundance</i>	<u>Heterogeneity-abundance relationship:</u> When habitats provide complementary resources, individual species' abundances increase with increasing habitat diversity (Dunning <i>et al.</i> 1992).	<i>Local habitat heterogeneity</i>
	<u>Energy –abundance relationship:</u> Low temperatures or precipitation limit productivity and individual activity, and in turn population sizes (Allen <i>et al.</i> 2002; Classen <i>et al.</i> 2015).	<i>Local temperature and precipitation</i>
<i>α –functional diversity</i>	<u>Effect of sampling (from regional pools of species):</u> Processes operating at higher scales dictate trait composition of local communities, and evolutionary limitations to phenotypic differentiation at the largest scale hamper regional functional diversity (Ricklefs 2004).	<i>γ –functional diversity</i>
	<u>Heterogeneity-diversity relationship:</u> Habitat and resource heterogeneity increases the number of ecological niches and thus consumer' functions (MacArthur & MacArthur 1961).	<i>Local habitat heterogeneity</i>
	<u>Trait overdispersion in favourable conditions, trait clustering in harsh conditions:</u> High productivity and low abiotic stress reduce constraints, or fuel competitive interactions, enhancing trait divergence (Lamanna <i>et al.</i> 2014).	<i>Local temperature and precipitation</i>
<i>γ – functional diversity</i>	<u>Heterogeneity-diversity relationship:</u> Habitat heterogeneity increases the variety of habitat patches and functional turnover among sites. Habitat heterogeneity promoted taxa phenotypic diversification (Emerson & Gillespie 2008).	<i>Regional heterogeneity Plant species richness</i>
	<u>Climate as a driver of phenotypic differentiation:</u> Climate promoted the phenotypic diversification within ancestral climatic zones of origin (Allen <i>et al.</i> 2002; Ricklefs 2006).	<i>Regional temperature and precipitation</i>
	<u>Area effects:</u> Small areas may select for certain shared niche and phenotypic traits, resulting in clustered assemblages (Emerson & Gillespie 2008).	<i>Area</i>
	<u>Isolation effects:</u> Isolated areas may select for certain shared niche and phenotypic traits, resulting in clustered assemblages (Emerson & Gillespie 2008).	<i>Isolation</i>

Table 2. Adaptive features that condense information on the ecological development, assembly and structure of animal communities.

Feature	Relevance	Target trait
<i>Mass</i>	The variability and range of body mass within communities is related to thermal and energetic constraints (climate filters, secondary production), habitat heterogeneity (locomotion), competition and predation (limiting similarity and trophic pyramid shape), consumer-driven resource dynamics (stoichiometry) (Peters 1983; Brown <i>et al.</i> 2004; Woodward <i>et al.</i> 2005).	<i>Bumblebees and birds:</i> weight <i>Grasshoppers:</i> body length (isometric with weight, Laiolo <i>et al.</i> 2013)
<i>Diet width</i>	Diet width expresses the feeding links in ecological networks and its variation is associated with environmental productivity, successional stage and interspecific dominance (Brown & Southwood 1983; McDonald 2002).	Diversity of food items
<i>Reproductive investment</i>	The variability and range of reproductive investment is related to food web position, disturbance and environmental productivity (Laiolo & Obeso 2017). It also conditions the dynamics of resources (Grime & Pierce 2012) and of populations facing environmental variation (Laiolo & Obeso 2017).	<i>Bumblebees:</i> sexual individuals' biomass per unit of queen weight <i>Grasshoppers:</i> mm of eggs per mm of female body <i>Birds:</i> egg biomass per unit of female weight
<i>Mobility</i>	Dispersal and locomotion abilities are associated with environmental variability, disturbance and spatial constraints. They condition metacommunity structure and may trade off with competitive abilities (Van Dyck & Matthysen 1999; Grime & Pierce 2012)	<i>Bumblebees:</i> wing length/thorax width <i>Grasshoppers:</i> forewing/femur length <i>Birds:</i> wing/tarsus length
<i>Sexual dimorphism</i>	Sexual dimorphism is attributable to sexual selection but also reflects adaptations for niche divergence between the sexes driven by environmental productivity, seasonal constraints and habitat spatial configuration (Van Dyck & Matthysen 1999; Laiolo <i>et al.</i> 2013).	Ratio between female and male indicators of structural body size (above)
<i>Length of the adult cycle</i>	Survival, life span and duration of the adult cycle are sensitive to environmental productivity and length of the growing and reproductive season (Laiolo & Obeso 2015, 2017; Laiolo <i>et al.</i> 2015a,b). They also condition the dynamics of resources (Grime & Pierce 2012) and of populations (see reproductive investment).	<i>Bumblebees and grasshoppers:</i> duration of the period with adult presence <i>Birds:</i> adult survival

Fig. 1.

Fig. 2.

Tested pathways of local species richness. Possible direct influences: *local species richness* influenced by *regional species richness*, *local abundance*, *local habitat heterogeneity*, *local temperature and precipitation*. Indirect local influences (via abundance): *local abundance* influenced by *local habitat heterogeneity*, *local temperature and precipitation*. Indirect regional influences (via regional diversity): *regional species richness* influenced by *area*, *isolation*, *regional temperature and precipitation*, *regional habitat heterogeneity*, *regional plant species richness*, *mid-domain effect*. Pathways of local functional diversity. Possible direct influences: *local functional diversity* influenced by *regional functional diversity*, *local habitat heterogeneity*, *local temperature and precipitation*. Indirect regional influences (via regional diversity): *regional functional diversity* influenced by *area*, *isolation*, *regional temperature and precipitation*, *regional habitat heterogeneity*, *regional plant species richness*.