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RESEARCH ARTICLE

Stuck on top of a mountain: Consequences of dispersal limitations for alpine diversity

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Abstract

Aim: The future of biodiversity in increasingly warmer mountains may be poorly predicted by climate variation if dispersal affects ecological change. We assessed the influence of dispersal limitations in the assembly of mountaintop communities, focusing on the relationship between proxies of flight abilities and species diversity in insects.

Location: Cantabrian Mountains, Spain.

Taxon: Grasshoppers (Orthoptera, Acrididae) and bumblebees (Hymenoptera, Apidae, Bombinae).

Methods: We analysed the magnitude of variation in the relative wing length of individuals, species and communities along elevation by means of phylogenetic multilevel and generalized least square models, to assess the environmental fit of this morphological trait. Then we analysed whether wing length variation among assemblages affected species diversity and the biotic interchange between foothills and mountaintops, and between nearby mountaintops, by means of linear models and metrics quantifying dispersal.

Results: Grasshoppers and bumblebees converged in the evolution of shorter wings at higher elevations. The effects of this adaptation scaled to the community level and affected diversity patterns. Mountaintop assemblages were richer (grasshoppers) or shared more species with lowlands (bumblebees) when the average wingspan of their member species was larger. The species composition of mountaintops was significantly affected by dispersal processes and their species richness was more strongly correlated with that of their foothills than that of nearby mountains.

Main Conclusions: These results show a wingspan reduction in upland insects, the role of dispersal in improving species richness and reducing beta diversity, and the dependence of mountaintop diversity from the species pools of foothills. In these settings, we can envisage that upward movements of long-winged species will be favoured and increase the species richness and nestedness of upland biotas as climate warms. However, the fate of upland inhabitants will depend on how they tackle novel biotic and abiotic pressures, given the constraints to peak-to-peak displacement.

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KEYWORDS
community assembly, community-weighted means, global warming, insects, life-history trade-offs, mountain biodiversity, traits

1 | INTRODUCTION

The low species richness of mountaintops is a global phenomenon that is receiving considerable attention now that many species are moving their ranges upwards (Parmesan & Yohe, 2003). Climate harshness and its temporal variation (e.g. glacial cycles) are major causes of this trend, which is, or is expected to be, subject to reshuffle as climate warms (Laiolo et al., 2018; Pauli et al., 2012). Irrespective of climate, however, the reduction of land area and increased isolation also contribute to the biotic impoverishment of summits, by fuelling stochastic processes of species extinction and reducing immigration (Jiménez-Alfaro et al., 2021). Given the differential capability of organisms to disperse across landscapes (Giersch et al., 2017) and the complex population dynamics at range boundaries (Sexton et al., 2009), spatial constraints can become key pieces of information to improve our understanding of climate change effects at these elevations. In a context in which upslope shifts are unfeasible, it is imperative to assess whether movements between peaks are possible, and, in non-plant taxa, even to assess whether species from lower elevations can colonize and establish on summits.

According to biogeographical theory, increasing isolation will most strongly affect species with low dispersal ability (Gillespie et al., 2012). Therefore, it could be argued that its adverse effects on species richness should be strongest among less mobile species. Proxies of mobility such as wing size or muscle mass in animals have been shown to be relevant for species distributional patterns (Sheard et al., 2020), but their community-wide consequences have been poorly addressed (Hanski, 1998; Hendrickx et al., 2009). Yet, these traits may acquire special importance in high elevation or insular communities, where the reduction of wing size is a frequent adaptation, especially in insects (Gutiérrez & Menéndez, 1997; Leihy & Chown, 2020). Among the proposed explanations for this phenomenon, the most general involve an energy trade-off between flight and reproduction: When temperatures or wind conditions are rarely favourable for flight activity, it may be more advantageous allocating resources to reproduction than to dispersal and wing development (Hodkinson, 2005). In fragmented habitats, dispersal enhances species diversity and reduce turnover among nearby patches (Hendrickx et al., 2009; Mouquet & Loreau, 2003). In mountains, this factor may determine whether biotas are quasi-independent from lowlands (island-colonization model) or net importers from lowland biotas (foothill dependence model).

In this study, we analysed the variation along elevation in insect wing size relative to body size, and its relationships with mountaintop species richness and compositional differentiation, in a mountain chain, the Cantabrian Mountains (N Spain), in which extensive information is available on insect species distribution (Laiolo et al., 2020). Wing span is a useful indicator of dispersal for interspecific analyses, especially when dealing with large numbers of species about which other sources of information are not readily available (Sekar, 2012). Here, we tested whether wing length influences species diversity while controlling for the effects of major drivers of species richness (temperature, area, isolation) (Laiolo et al., 2018), and for the dependence of mountain assemblages from the species pools of nearby massifs or foothills. We addressed these issues in bumblebees (Hymenoptera, Apidae), which are considered good flyers among insects (Makinson et al., 2019) and grasshoppers (Orthoptera, Acrididae), which include apterous, micropterous, brachypterous and fully winged species (Illera et al., 2019; Ma et al., 2012; Ortego & Knowles, 2022). In spite of their differences in biology, grasshoppers and bumblebees are typical inhabitants of montane and alpine habitats in different part of the world (Mani, 1968). They provide an opportunity to test organismal responses to the selection pressures in these habitats, and the effects that convergent evolution may have on contemporary diversity. If adaptations are maintained along elevation at an optimum by stabilizing selection, and dispersal is a costly strategy, we expect that the relative wing length of individuals and species will decline with the average elevation of their distribution and, in keeping with the flight—reproduction trade-off, with indices of reproductive allocation. If limitations to dispersal contribute to the distribution of diversity in mountain systems, we expect that assemblages of longer winged species to have, and share, more species, that is, have higher species richness and lower beta diversity. If mountaintops are net importers of lowland species pools, we expect limited compositional differences from lowland assemblages, and high levels of nestedness at increasing elevations.

2 | MATERIALS AND METHODS

We surveyed insect communities in >400 circular plots of 100 m radius along the entire elevation gradient of the Cantabrian Mountains (0–2848 m a.s.l.) during 2011–2021 (Figure S1; Table S1). These mountains host 35 grasshopper species and 24 non-cuckoo bumblebee species (Laiolo et al., 2020), including high-elevation endemic grasshoppers (*Podisma cantabricae*, *P. carpetana*, *Chorthippus cazurroi*) and mountain bumblebees (*Bombus monticola*, *Mendacibombus mendax*) (Illera et al., 2019; Laiolo et al., 2018; Pato et al., 2019) (Table S1). In the Cantabrian range, the surface above 1900 m is entirely covered by open habitat (Jiménez-Alfaro et al., 2014) and only constitutes 3% of land area. We targeted diversity patterns in these highland patches, hereafter defined as 'mountaintop islands'.

As a proxy of dispersal capabilities, we measured the relative wing length of the collected specimens (Table S1) as the distance from the axial region to the apex of the forewing divided by a proxy of body size. The latter was total body length in grasshoppers (Laiolo

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et al., 2013) and thorax width or intertegular distance in bumblebees (Peat et al., 2005) (Figure S2). Wing length was highly correlated to overall wing area (data from Laiolo et al., 2013; Ploquin, 2013). Given the correlation between wing measurements of the sexes (grasshoppers: Pearson's $R_{31} = 0.93$; bumblebees: $R_{22} = 0.71$, all $p < 0.001$), and the importance of females in the establishment of populations, we present here only results obtained for grasshopper females (32 species with wing data) and bumblebee queens (23 species with wing data) (see Table S2 for sample sizes). From individual measurements, we obtained an average value of relative wing length for each species. From species averages, we calculated the community relative wing length and the relative wing length of mountaintop assemblages. The former was estimated by averaging the wing length of species found in each plot, either weighting or not for species abundance (community-weighted mean and community mean, respectively). The relative wing length of mountaintop assemblages was calculated by averaging the wing length of species occurring in each mountaintop island, which may include more than one plot. Abundance data were not available at the large scale of mountaintop islands and therefore means were not weighted.

We measured reproductive allocation as the size of the largest ovarioles (when they get the size of eggs at laying), measured in 26 out of the 32 grasshopper species of our sample, and 16 out of the 23 bumblebee species (Figure S2; Table S1). We calculated egg volume as $V = 1/6 \cdot \pi \cdot (\text{egg width}^2) \cdot \text{egg length}$ (Laiolo et al., 2018). We counted ovarioles to estimate clutch size in grasshoppers, as their number greatly varies among species (Stauffer & Whitman, 1997), while all bumblebees have eight ovarioles (Cumber, 1949). The relationship between species relative wing length and reproductive allocation (egg volume and number in grasshoppers, egg volume in bumblebees) was analysed by fitting generalized least square models, controlling for body size, weighting for the variance in species relative wing length, and including a correlation structure based on species phylogeny obtained from cytochrome c oxidase subunit I (COI) gene sequences by Laiolo et al. (2021) (grasshoppers) and Hofmann et al. (2019) (bumblebees) (Figure S3). The *gls* function of the R package 'nlme' (Pinheiro et al., 2017) was used, fitting two alternative correlation structures (Brownian and Pagel) with the package 'ape' (Paradis et al., 2004).

The fit of wing length along elevation was studied between and within species. Between species, we run generalized least square models to regress species' average relative wing length on the average elevation of species distribution. As above, we weighted models for the variance in species relative wing length to control for intraspecific variability, and fitted a correlation structure based on the phylogenies mentioned above. To analyse variation along elevation within species, we modelled variation in specimen relative wing length in response to the elevation of sampling. We used phylogenetic Bayesian multilevel models with the 'brms' R package (Bürkner, 2017), which permits handling multiple observations per species and controlling for phylogenetic relationships between species. We built a multilevel model in which we added to the regression model (trait value on elevation) both the phylogenetic variance–covariance matrix, which permits varying intercept over species, and species variable as random factors, to account for any specific effect that would be independent of phylogenetic relationships. If the 95% credible intervals of the population-level coefficient (elevation slope) do not overlap with zero after controlling for species-level variation and phylogenetic relationships, we can assume a significant intraspecific elevation cline. Prior to running these models, wing length and elevation were scaled to zero mean and unit standard deviation. Then, we investigated the elevation cline at the community level, testing whether elevation conditioned the whole community trait composition. We regressed community average wing length on plot elevation through generalized least square models fitted with the *gls* function. For presence–absence data, we weighted the above model for community wing length variance.

We then assessed whether differences between mountaintop assemblages in wing length could explain the differences in species richness among summits, as well as in the compositional (species) differences between neighbour islands and between islands and their lowlands. Compositional differences were expressed in terms of beta diversity between pairs of the nearest mountaintop islands and between these islands and their foothills up to 500 m below. Foothill assemblages were located at elevations of 1400–1900 m, in the same massif of their respective mountaintops but at lower elevations. At these elevations in the montane belt, species diversity is the largest (Figure S1; see also Laiolo et al., 2018). Beta diversity was calculated as Sørensen index with the function *beta* of the R package 'BAT' (Cardoso et al., 2015) on the presence–absence data of island assemblages. We tested for mountaintop diversity variation with respect to wing values by means of general linear models, controlling for other important determinants of mountain diversity (Laiolo et al., 2018). Thus, in models regressing species richness or beta diversity on assemblage relative wing length, we accounted for the richness of the nearest mountaintop island and the richness of their respective foothills, for mountaintop island area and topographic isolation from large mountaintop islands (distance from the nearest island with a surface of at least 100 ha). We also controlled for the average annual temperature of survey plots, given that larger islands were higher and plots were also set at colder temperatures (correlation area-plot temperature: $r_{65} = -0.57$, $p < 0.001$; temperature variance had no effect on diversity and was not considered to avoid overfitting). By accounting for temperature, the elevation variable was not considered further, as it was highly correlated to temperature (see also Laiolo et al., 2018). In grasshoppers, only mountaintops in which at least two plots were surveyed were considered in the analysis of species richness, given that this sample size guaranteed the independence of species richness from survey effort (correlation of log-species richness on plot number, Pearson $R = 0.20$, $p = 0.35$, $n = 21$ mountaintop islands). In the case of bumblebees, one survey was enough to describe mountaintop species richness ($R = 0.22$, $p = 0.25$, $n = 20$ mountaintop islands) (Figure S4). While lowland species composition was surveyed for most target mountaintops, this information was not available for some of the nearest neighbour mountaintops. Therefore, two sets of general linear models were run

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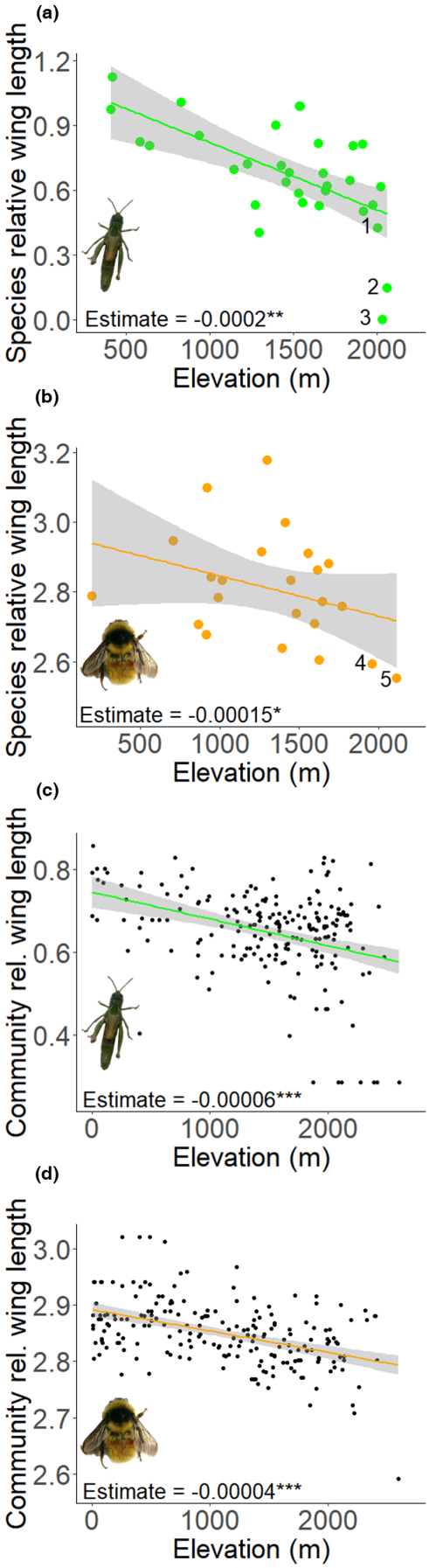

FIGURE 1 Species- and community-level variation in female relative wing length along elevation in insects from the Cantabrian Mountains. Regression estimates are also shown, together with trend lines and 95% CI. (a) Relationship between relative wing length and average elevation in 32 grasshopper species (each dot is a species; numbers highlight high elevation endemics: 1 *Chorthippus cazzuroi*, 2 *Podisma carpetana*, 3 *Podisma cantabricae*). (b) Relationship between relative wing length and average elevation in 23 bumblebee species (each dot is a species; numbers highlight high mountain species: 4 *Bombus monticola*, 5 *Mendacibombus mendax*). (c) Relationship between the average relative wing length of communities and survey plot elevation, as recorded in 202 plots in grasshoppers. (d) Relationship between the average relative wing length of communities and survey plot elevation, as recorded in 204 plots in bumblebees. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

to analyse the drivers of mountaintop species richness, one to assess the influence of species richness of the neighbour islands and the other with the rest of descriptors mentioned above, with the *dredge* function of the R package 'MuMIn' (Barton & Barton, 2015) to select the best models on the basis of AICc value. Land area, isolation and temperature were calculated as detailed in Figures S1 and S5; species richness values, area and isolation were log-transformed.

To assess whether mountaintops were sink habitats for diversity, we used paired *t*-tests and one-way analyses of variance to assess the difference in beta diversity between the nearest neighbour mountaintops and between mountaintops and their foothills. These tests were also used to assess the compositional differences in terms of (i) species gain and loss or (ii) replacement between foothill and mountaintops. These components of beta diversity were estimated with the packages 'BAT' (replacement and richness-difference) and 'betapart' (Baselga & Orme, 2012) (replacement and nestedness-resultant). Finally, to establish the relevance of dispersal over niche processes in the assembly of mountaintop assemblages, we estimated the dispersal–niche continuum index (DNCI; Vilmi et al., 2021) with the R *PerSIMPER* function (Gibert & Escarguel, 2019). This index expresses the deviation of the observed taxon distribution within sets of sampled assemblages (here mountaintop islands) from the expected distribution under null models of dispersal-driven assembly, niche-driven assembly and dispersal- plus niche-driven assembly (Vilmi et al., 2021). Dispersal is supposed to be a stronger drive of species composition than niche processes when DNCI is negative and its 95% confidence intervals do not overlap 0, while the opposite is expected for positive values not overlapping 0. We entered in the analyses only mountaintops with at least four survey sites as the DNCI is sensitive to the number of sampling units (Vilmi et al., 2021).

3 | RESULTS

There was a significant trade-off between relative wing length and egg volume in grasshoppers (regression slope = -0.49 ± 0.22, $p = 0.039$; Figure S6). This relationship was affected by phylogeny but not by species body size or egg number; thus ceteris

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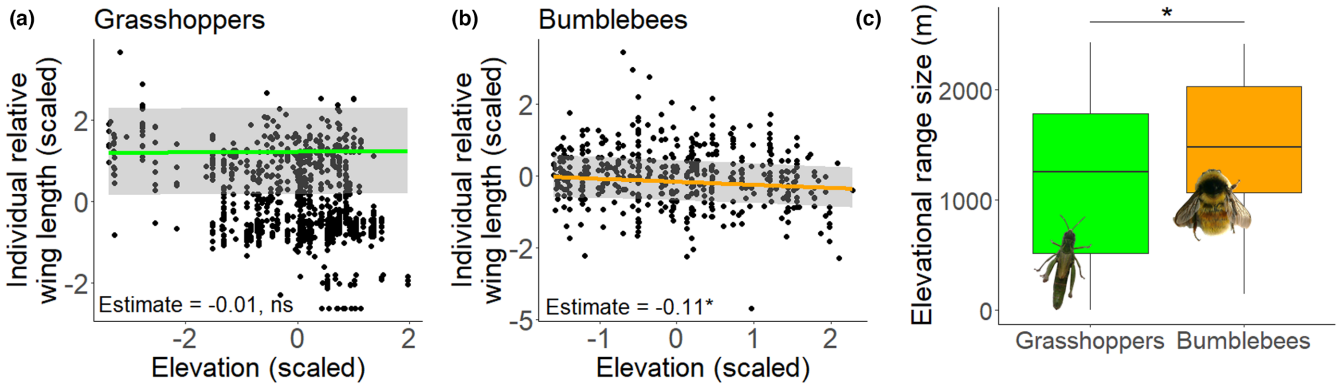

FIGURE 2 Population-level variation in female relative wing length along elevation in insects from the Cantabrian Mountains, and average range sizes of species. The slope (estimate) of the trend line shows the conditional effects of elevation (i.e. predicted wing values) at the population level, ruling out species and phylogenetic effects; 95% credible intervals are also shown. (a) Relationship between individual relative wing length and elevation of the collection site in grasshoppers (each dot is an individual). (b) Relationship between individual relative wing length and elevation of the collection site in bumblebees (each dot is an individual). (c) Boxplots depicting the average elevational range size (maximum minus minimum elevation) of grasshoppers (green) and bumblebees (orange). $^*p < 0.05$.

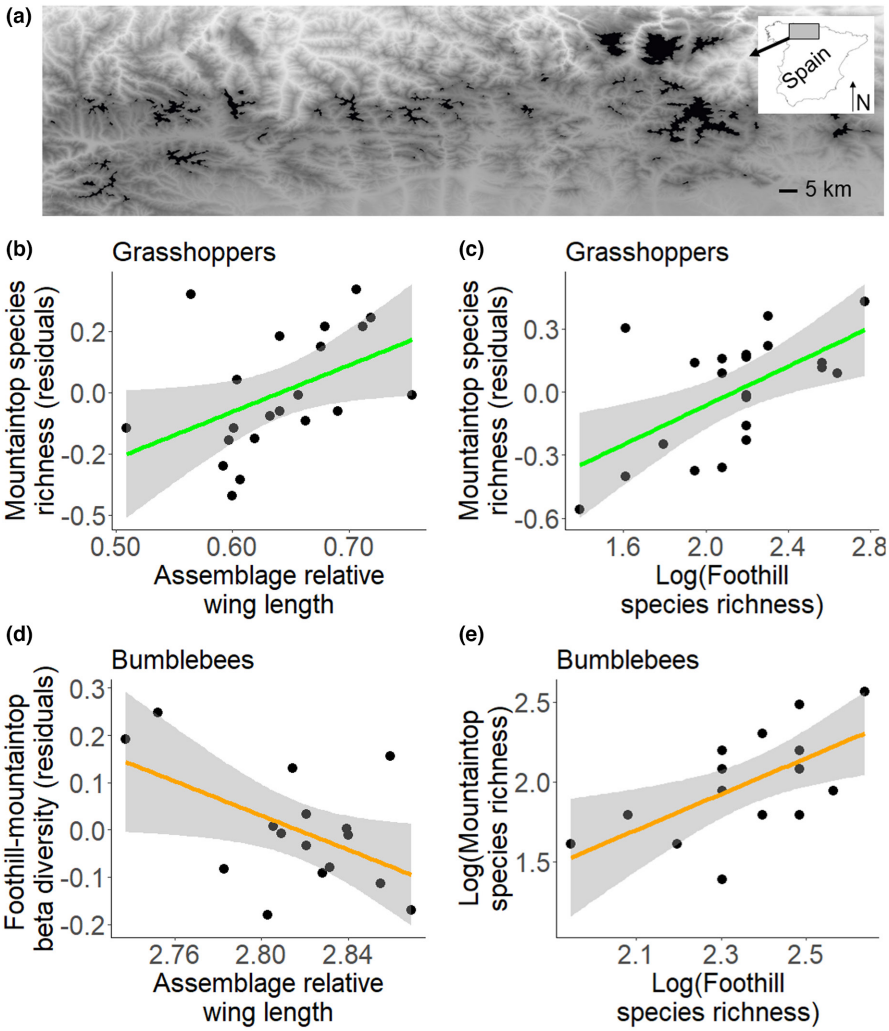

FIGURE 3 Relationship between mountaintop diversity and average assemblage wing length and foothill species richness, in 21 mountaintop islands for grasshoppers and 20 for bumblebees. (a) Distribution of mountaintop islands (black areas) in the Cantabrian Mountains, with increasing elevation represented by darker shading. The projection of the map is EPSG:4326 (WGS84). (b) Increase in mountaintop species richness with the average wing length of assemblages, after controlling for the effect of foothill species richness, in grasshoppers. (c) Increase in mountaintop species richness with foothill species richness, after controlling for the effect of the average wing length of assemblages, in grasshoppers. (d) Decline of the compositional differences between mountaintops and foothills with the average wing length of assemblages, after controlling for the effect of mountaintop species richness, in bumblebees. (e) Increase in mountaintop species richness with foothill species richness in bumblebees. Trend lines and 95% CI are also shown.

paribus the shorter the wings, the larger the allocation in egg size (Table S3). The same trend was recorded in bumblebees but the relationship was not significant (regression slope = −0.02 ± 0.03, $p = 0.58$; Table S3).

In grasshoppers, a steep decline of wing length was observed along elevation at the species and community levels (Figure 1; Table S4). At the population level, however, there was no morphological gradient (Figure 2a) and all variation along elevation appears to be due to

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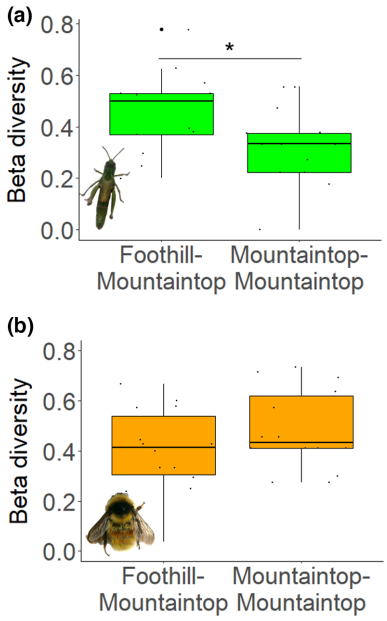

FIGURE 4 Compositional differences between mountaintops and foothills, and between nearby mountaintops. (a) Box plots of beta diversity between mountaintops and foothills, and between nearest neighbour mountaintops, in grasshopper assemblages, with significant differences marked by an asterisk (*$p < 0.05$). (b) Box plots of beta diversity between mountaintops and foothills, and between nearest neighbour mountaintops, in bumblebee assemblages.

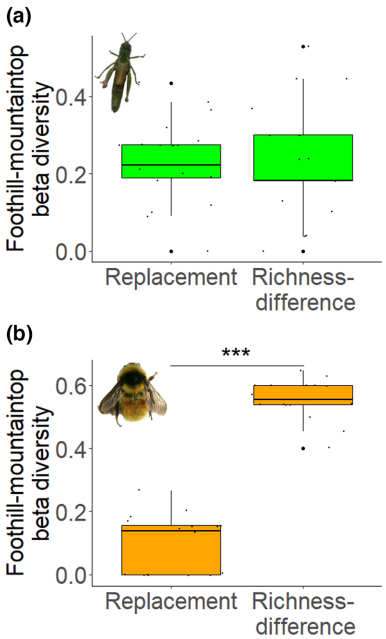

FIGURE 5 Box plots depicting the partition of mountaintop-foothill beta diversity into the richness difference and replacement components in grasshoppers (a) and bumblebees (b). Significant differences are depicted with asterisks (***$p < 0.001$).

differences among species (Figure 1; Table S4), 46% of which cannot fly (Table S2). Conversely, the relative wing length of bumblebee individuals significantly declined with elevation (Figure 2b). Bumblebees had greater opportunities of intraspecific differentiation as their elevational ranges were larger than those of grasshoppers ($t_{56} = 2.01$, $p = 0.049$) (Figure 2c). The reduction of bumblebee wing was significant at the species and community levels as well (Figure 1b,d; Table S4), although in this case all species were fully winged (Table S2).

Mountaintop assemblages of long-winged grasshoppers were significantly richer in species than those with shorter winged species and the effect of wing length ($R^2 = 0.11$) persisted when considering alternative drivers of species diversity, such as species richness of lowlands, nearby islands, area, isolation and temperature (Figure 3; Table S5a). Among these drivers, only lowland species richness was significantly and positively associated with mountaintop island species richness ($R^2 = 0.27$) (Figure 3c), with no effect of species richness of nearby mountains (Table S5a). Grasshopper beta diversity was not significantly associated with wing length and the effect of other variables was weak (Table S5b,c). In the case of bumblebees, foothill-mountaintop beta diversity was significantly correlated with wing length ($R^2 = 0.14$) when controlling for the differential species richness of mountaintops: the longer the wings of mountaintop assemblages, the lower the difference from the surrounding lowlands (Figure 3d; Table S5f). Mountaintop species richness in this insect group was solely influenced by the richness of foothills ($R^2 = 0.31$) (Figure 3e; Table S4d). Despite the lack of influence of nearby mountaintops on species richness, the nearest mountaintops tended to share more species among each other than with lowlands, at least in grasshoppers: beta diversity between mountaintop assemblages was lower than that between mountaintops and their foothills (pairwise test: $t_{12} = 2.19$, $p = 0.049$), while in bumblebees there was no significant difference ($t_{13} = 1.74$, $p = 0.10$) (Figure 4a,b). Most mountaintops (81%) hosted mountain endemic grasshoppers thus had typical assemblages of high elevation species, while significantly fewer summits (35%, $\chi^2_2 = 8.91$, $p = 0.008$) hosted high elevation bumblebees. As a consequence, bumblebee upland assemblages displayed greater differences from lowlands in species richness than in species composition (replacement) ($t_{15} = 13.3$, $p < 0.001$), as opposite to grasshoppers ($t_{20} = 0.17$, $p = 0.86$) (Figure 5). Although the relative contribution of replacement to beta diversity was greater with the 'betapart' approach, the result that bumblebees had greater nestedness than grasshoppers was shared between the methods used ($F_{1,35} = 5.53$, $p = 0.024$) (Figure S7). Finally, the overwhelming contribution of dispersal over niche processes in shaping mountaintop assemblages was corroborated by the negative DNCI values in both grasshoppers (−4.51, 95% CI = −6.71, −2.32) and bumblebees (−3.49, 95% CI = −5.70, −1.28).

4 | DISCUSSION

This study shows that two insect group separated by over 300 MYA of independent evolution (Laiolo et al., 2020) have converged in the evolution of short wings at high elevations. The decline was especially dramatic in grasshoppers, in which almost half of the species

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was flightless and concentrated at high elevations. This morphological shift was associated with an increase in investment in egg size, a result that supports the reproduction-dispersal trade-off at least when extreme variation in flying abilities occurs. In grasshoppers, this occurs both among species (this study) and within species (Steenman et al., 2015). Conversely, this relationship did not emerge when variation in wing length is less dramatic, as in bumblebees, neither among species (this study) nor within species (Levy & Nufio, 2015).

The effects of such convergent evolution scaled to the community level by influencing species diversity patterns in both insect groups, a result that suggests that this phenotypic adjustment may be critical for the future of upland insect communities. The negative values of the DNCI metric, pointing to dispersal-based mountain community assembly, and the association between wing length and the increase in species richness, or the decline of beta diversity, underscore the contribution of dispersal in the assembly of these biotas. This is a non-trivial finding for mountain ecological assemblages of mobile species, in which the focus has been traditionally set on the dichotomy between environmental vs. biotic filters overlooking this third filter to community assembly (Bryan et al., 2008; Graham et al., 2009; Staude et al., 2021).

Wing reduction, by fitting upland conditions, apparently did not limit the directional species exchange from foothills, as highlighted by the correlation between lowland and highland species diversity (Figure 3c,e). Similar dispersal patterns have been observed in mountain flora, where colonizers display wing-aided dispersal favoured by specific diaspore morphologies (Matteodo et al., 2013). The upward movements of long-winged insects will almost certainly be favoured by climate warming and contribute to improve upland species richness. However, the interchange between nearby massifs might be prevented by the dispersal limitations of local fauna, for which mountaintops are similar to true islands (Illera et al., 2019). Even in taxa that possess roughly continuous alpine communities, such as grasshoppers in our study, the ranges of most alpine specialists have been eroding since the last glacial maximum and are now much more fragmented than in the past (Ortego & Knowles, 2022). Warmer climate will change conditions for life for these range-restricted high-elevation specialists, but given the infeasibility of upslope shifts from the summits and the constraints to stepping-stone movements for flightless species, we expect that they will be increasingly confined in spots with favourable micro-environmental conditions within their massifs. The strategy of investing in egg size, here highlighted in flightless grasshopper species, can increase reproductive success via offspring survival (Laiolo & Obeso, 2015), which, in turn, may contribute to growth rate and population persistence on mountaintops (Laiolo & Obeso, 2017). Apart from these demographic aspects, selection on wingspan is expected to be released in increasingly warmer mountains. This trait has great evolvability in insects (Roff, 1986) and bumblebees may present such evolvability, or plasticity, since shorter winged individuals inhabit higher elevations than longer winged ones within species (Figure 2b). In Orthoptera, long- and short-winged morphs frequently occur within populations (Steenman et al., 2015), but our study grasshoppers displayed little intraspecific variation (Figure 2a). They were in fact less exposed than bumblebees to both low and high elevation conditions, as their ranges were smaller (Figure 2c). Whether shifting climate can trigger this or other evolutionary pathways that rescue mountain populations therefore remain an open question for future research. Obtaining this knowledge is especially pressing in highland grasshoppers, given the apparently relict nature of their populations (Illera et al., 2019; Ortego & Knowles, 2022).

In spite of some parallelism between grasshoppers' and bumblebees' results, relevant differences emerged, as expected for two taxa that differ in many aspects of their biology, the most evident being that only half of grasshopper species can to some extent fly while all bumblebees are good flyers. Brachypterous, micropterous and apterous grasshoppers are flightless and their soft body makes improbable the dispersal (and posterior survival) mediated by flying predators (Illera et al., 2019). For bumblebees, wing reduction with elevation has been observed within and among species (Lozier et al., 2021; Peters et al., 2016), and although we cannot prove consequences for dispersal as for flightless grasshoppers, a study by Mountcastle et al. (2016) points this way. The experimental shortening of wingspan did not compromise manoeuvring efficiency in bumblebees, but it did reduce directional flight power. When scaling to community effects, grasshopper and bumblebee diversity patterns appeared to sit in-between the island-colonization model and the foothill dependence model. In grasshoppers, mountaintops shared their independent species pools more frequently than with lowlands in support of the island-colonization model (Figure 4a), but rich lowland species pools contributed to the diversity of mountaintops in support of the foothill dependence model (Figures 3c and 5a). Bumblebees had fewer alpine representatives and their assemblages were more frequently importer of the diverse communities at immediately lower elevations than were grasshopper assemblages (Figures 3e and 5). The nestedness of bumblebee communities suggests that many species are filtered out by mountaintop conditions, a result that may be tied to the lack of reproductive benefits as observed in grasshoppers. In general terms, it seems that taxa that are better dispersers contribute more significantly to community nestedness, while endemicity and small ranges increase turnover, as also observed in plants (Staude et al., 2021).

In conclusion, our results suggest that alpine insect diversity depend on aspects of species dispersal, which, in turn, depends on the environment and on traits, which, in turn, can evolve. This scenario involves several levels of the biological organization and anticipates complex outcomes in response to climate change, involving both ecological and evolutionary responses. Since climate warming will open new habitats for species from lower elevations, we should expect an increase in the species richness in upland habitats, which will become vital remnants for animal species tracking their climate niche (Ploquin et al., 2013). On the other hand, given the difficulties for migration of alpine specialists, their fate will depend on the capability to tackle novel biotic and abiotic pressures in situ.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The dataset is freely available at https://doi.org/10.20350/digitalCSIC/14717.

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BIOSKETCHES

Paola Laiolo is interested in community assembly mechanisms, the dynamics of populations and communities along elevation gradients, and the evolution of phenotypic traits.

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Author contributions: Paola Laiolo designed the study; Paola Laiolo, José Ramón Obeso and Juan Carlos Illera performed the field and laboratory work; Paola Laiolo analysed the data and drafted the manuscript with inputs from José Ramón Obeso and Juan Carlos Illera. All authors read and approved the final manuscript.

SUPPORTING INFORMATION

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