Thermophilization and reshuffling of montane leaf beetle communities over a two decade period

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Abstract

Given the sensitivity of mountain biodiversity to human pressure, it is essential to quantify changes in montane biological communities and contrast them with expectations based on potential drivers of change. This need is particularly pressing for biological groups representing important but little-studied fractions of biodiversity, such as insects. We analyze the temporal changes (between 1998 and 2015) of leaf beetle communities in an altitudinal gradient in the Sierra de Ancares (NW Spain). Our results show temporal changes in the composition of local communities, with a tendency to assemblage thermophilization, as well as a homogenization of the spatial turnover pattern, mostly driven by an increased similarity between communities at the lower and intermediate altitudes. These temporal changes in community composition and in the spatial structure of biodiversity were associated with upward shifts of the upper altitudinal limit of warm-adapted species, and with downward shifts of the lower altitudinal limit of cold-adapted species. While this upward shift is consistent with expectations of climate change effects, the observed downward shift suggests a land use change effect. Our results point to the joint effect of multiple factors (climate and land-use change) behind temporal changes of these leaf beetle communities, which result in compositional reorganization and biotic homogenization, rather than a mere coherent displacement towards higher altitudes. More generally, we show that understanding temporal change of biodiversity requires assessing multiple community-level metrics (e.g., variation in assemblage composition and/or changes in spatial turnover) for the detection of tendencies among the species-specific signals (e.g., altitudinal range shifts).

Keywords: Coleoptera, community homogenization, community reshuffling, elevational shift, insects, temporal beta diversity, temporal turnover, thermophilization, upward range shift

1. Introduction

Climate warming is a major driver of biodiversity change in montane ecosystems (Guisan et al., 2019). Tracking of their suitable climates along environmental gradients is causing species to shift their distribution ranges (Parmesan & Yohe, 2003; Parmesan, 2006; Chen et al., 2011; Lenoir & Svenning, 2015) and species range shifts, in turn, are causing the reconfiguration of communities and ecosystems (Sundqvist et al., 2013). Although climate warming is expected to cause upward range shifts, empirical assessments have proven this to be more a tendency than an ubiquitous response, showing complex and varied responses among species (Freeman et al., 2018; Rumpf et al., 2019). In fact, not all species are expected to shift their ranges (Parmesan, 2019), as some may alternatively cope with raising temperatures through physiological mechanisms, behavioral thermoregulation and/or phenological shifts (Bellard et al., 2012; Pinsky et al., 2022). Moreover, climate change interacts with other processes, such as land use change, which is also another major driver of biodiversity loss (Jaureguiberry et al., 2022). Therefore, a key question is how land use and climate-driven range shifts at the species level aggregate into changes of biological communities at the local and regional scale. Such local and regional changes, occurring at short time periods and scales, are of special relevance as they may reflect global biodiversity changes happening in the near future (Parmesan, 2019).

Biodiversity change has many dimensions (McGill et al., 2015) that provide different insights into how communities are being restructured (Dornelas et al., 2023). For instance, species richness may be insufficient to detect temporal changes in community composition (i.e., temporal turnover) that may affect the dynamics and functioning of communities and ecosystems (Dornelas et al., 2014; McGill et al., 2015; Magurran et al., 2019). Beyond temporal turnover, the assessment of other important dimensions of diversity, such as temporal variation in spatial turnover, should also be incorporated in studies of biodiversity change (McGill et al., 2015; Hillebrand et al., 2018). While highly interconnected, measures of temporal turnover do not quantify temporal changes in spatial turnover (Baselga et al., 2015a), as either regional community homogenization (i.e., decrease in spatial turnover among localities) or differentiation could result from local processes of temporal turnover (Dornelas et al., 2023). Thus, a comprehensive understanding of changes in diversity patterns along altitudinal gradients should account for changes at the species level (i.e., range shifts), changes in local community composition (i.e., species richness and temporal turnover in species composition) and changes in the spatial structure of communities (i.e., temporal changes in spatial turnover).

Our knowledge of how biological diversity responds to climate change is biased towards some biological groups and regions (Pilotto et al., 2020). For instance, insects are expected to be highly affected by climate change (Harvey et al., 2023), but our empirical knowledge is limited and based on a few taxonomic groups (McCain & Garfinkel, 2021), such as lepidopterans and some particular pest species, for which long-term monitoring data are available (e.g., Cannon, 1998; Pöyry et al., 2009; Wilson & Maclean, 2011; De Grandpré et al., 2018; Halsch et al., 2021). However, heat tolerance largely varies among individuals, populations, and species (Colinet et al., 2015; González-Tokman et al., 2020) and hence, extrapolation from one taxonomic group to another is compromised. Moreover, in the case of highly specialized herbivore species, such as leaf beetles (Coleoptera: Chrysomelidae), their response will be highly mediated by the response of their host plants, which will be affected by climate warming but also by the associated drought stress and, particularly, by land use change. While current efforts to compile temporal data on insect communities (van Klink et al., 2021) will likely ameliorate our knowledge gap, we still need to empirically document changes of the less studied groups. This is particularly important in the context of global insect declines (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020), as Román-Palacios & Wiens (2020) suggested that more than half of insect species many not be able to adjust their distributions rapidly enough to avoid extinction. This may be exacerbated by the interaction with other global change drivers, such as land-use changes, that are also affecting insect trends (Neff et al., 2022).

We here study (i) the temporal changes in the species' altitudinal upper and lower limits, (ii) the temporal changes in species richness and community composition (temporal turnover) and (iii) the temporal changes in spatial turnover, for a hyper-diverse family of beetles (leaf beetles, Coleoptera: Chrysomelidae) in a mountainous system at the interface of the Eurosiberian and Mediterranean regions over a ca. two decade period (from 1998 to 2010-2015). While empirical observations limit the attribution of biodiversity change (Gonzalez et al., 2023), it is still important to document patterns of change and contrast them with expectations based on main potential drivers. For instance, climate change is expected to cause an upward shift trend in species altitudinal ranges, while land use change could cause shifts in any direction of the altitudinal gradient, depending on how the mosaic of habitats has changed over time. Even in the case of upward altitudinal shifts, we need to focus separately on both the upper and lower range boundaries because there is an expectation that climate warming would produce upward shifts of either the upper limit (leading edge expansions) or the lower limit (rear edge contractions), depending on the thermal niche position and breadth of each species. An analogous expectation of asymmetrical patterns has been formulated for latitudinal gradients (Parmesan, 2019). In particular, we can predict that upward shifts in the upper limit should be more marked in warm adapted species, as higher sites become warmer and hence within their thermal niche. In contrast, upward shifts in the lower limit should be more marked in cold adapted species, as lower sites become too warm and hence out of their thermal niches.

2. Material and Methods

2.1. Community data

The Sierra de Ancares is a mountain range of the Galician Massif in the NW of the Iberian Peninsula. Altitude ranges from 400 to nearly 2000 meters and the natural vegetation is dominated by Pyrenean oaks (*Quercus pyrenaica* Willd.) at low to middle altitudes, and sessile oaks (*Q. petraea* (Matt.) Liebl) and Iberian white birch (*Betula celtiberica* Rothm. & Vasc.) at higher altitudes. These forests are interspaced by chestnuts (*Castanea sativa* Miller), human managed grasslands and meadows, shrubs dominated by *Cytisus multiflorus* (L´Hér.) Sweet and *Genista florida* L., and heathlands dominated by *Erica australis* L., which occupy large extensions at higher altitudes. Large areas have been planted with Scots pine (*Pinus sylvestris* L.) but were not sampled in this study. The climate has suffered a warming tendency, as estimated from historical climatic data (1980-2020) from close meteorological stations (AEMET, Lugo and Ponferrada): mean annual temperature has increased at a rate between 0.031ºC (Lugo) and 0.037ºC (Ponferrada) per year (Figs. S1-S2 in Supporting Information). In turn, precipitation has not shown any significant trend. In parallel, land use changes associated with the abandonment of traditional agriculture and extensive livestock systems have led the transformation of grasslands into heathlands and woodlands (Álvarez-Martínez et al., 2014).

Phytophagous beetle communities were intensively sampled at three different sites of the NW slope of the mountain range on two consecutive days in 2010 (20-21 of June) and three consecutive days in 2015 (28-30 of May): (i) low-altitude site: Liber (Navia River), 450 m; (ii) intermediate-altitude site: Os Cabaniños, 1000 m; and (iii) high-altitude site: Degrada, 1300 m (see Figure 1). At each site, beetle communities were sampled by one (2010) or two collectors (2015) with entomological sweeping nets in 30-minute periods (hereinafter, samples), with the number of samples ranging from 20 to 24 per day. A total of 88 samples (20 in 2010 and 68 in 2015) were collected: 32 in the low-altitude site, 38 in the intermediate-altitude site, and 18 in the high-altitude site. All specimens were preserved in 96^{o} ethanol and stored in a -20^{o}C freezer until sample processing for species sorting and identification.

Community profiling was focused on leaf beetles (Coleoptera: Chrysomelidae), which were separated from other families and identified to the species level using a stereo microscope (Nikon 212734). Specimens were identified using the keys provided in the taxonomic monographs for the European (Warchalowski, 2003) and the Iberian (Petitpierre, 2000; Petitpierre, 2019) leaf beetle faunas. Taxonomic identification was confirmed with the sequencing of the *cox1*-5’ for all specimens collected in 2010 as part of a community phylogeography study (Baselga et al., 2015b). Regarding specimens collected in 2015, DNA-based identification was only used for specimens belonging to the genera *Aphthona*, *Psylliodes*, and *Longitarsus* (see Appendix S1 in Supporting Information). After identification, we built a presence/absence table of leaf beetle species in the three sample sites.

To assess temporal changes in diversity patterns, 2010-2015 leaf beetle communities were compared to those of 1998 (Baselga & Novoa, 2000). This dataset was built from an extensive, non-systematic survey in the Ancares mountain range from February to October 1998 (Figure 1). Previous analyses have shown this inventory to be complete (Baselga & Novoa, 2006). The collecting method was identical (sweeping nets), but instead of the intensive, standardized sampling performed in 2010 and 2015, multiple sites were loosely visited multiple times over a longer time period. From this 1998 dataset we built two community tables. The first one consisted of the species presence/absence table for the 20 sites below or at 1300 m in the NW slope of the mountain range. This dataset was used to compare elevational shifts within the same altitudinal range sampled in 2010-2015. The second one consisted of the aggregation of some of these localities (listed below) into low, intermediate and high-altitude sites in order to compare them with the communities sampled in 2010-2015. Because the sampling campaign in 1998 was extensive and non-systematic, presence data for the low and high-altitude sites were complemented with records from nearby localities at similar altitude. Thus, low-altitude data included Cancelada, Higón, Líber, Vilapún and Vilasante sampling sites (Baselga & Novoa, 2000; all between 500 and 550 m a.s.l.), intermediate-altitude data included the same sampling site (Os Cabaniños), which was thoroughly sampled in 1998, and the high-altitude data included Cabana Vella, Campa de Brego and Degrada (all 1300 m a.s.l.). This presence/absence table was used to quantify the differences in species richness and composition (temporal turnover) between 1998 and 2010-2015, as well as to assess the changes in spatial turnover patterns between both time periods.

2.2. Data analysis

To assess how leaf beetle communities have changed over time (1998 *versus* 2010-2015) we measured, at the community level, (i) the temporal changes in species richness and community composition (temporal turnover), (ii) the temporal changes in spatial turnover and, at the species level, (iii) the temporal changes in the species' altitudinal upper and lower limits. Temporal and spatial differences in community composition were quantified with dissimilarity indices that independently account for species replacement between sites (i.e., species turnover) and nestedness (in which the species in the poorest sites are subsets of the ones in the richest sites). We have used presence/absence data and the Sorensen's family of indices to partition total beta diversity (Sorensen's index, β_{sor}) into turnover (Simpson index, β_{sim}) and nestedness-resultant (β_{sne}) components following the framework introduced by Baselga (2010) and implemented in *betapart* (Baselga & Orme, 2012), with function beta.pair().

To complement the temporal analysis at the community level, we measured changes in species altitudinal ranges between 1998 and 2010-2015. Altitudinal ranges are predicted to change differently in cold adapted species (upward shift of their lower latitudinal limit) than in warm adapted species (upward shift of their upper altitudinal limit). Because we lack physiological measurements of the climatic niches of leaf beetle species, we approximate them by characterizing their geographical distributions and assigning them to one of the following chorotypes: Iberian, Mediterranean (i.e., species distributed around the Mediterranean basin), Northern (i.e., species distributed in the Eurosiberian region) and Widely Distributed species (i.e., species distributed both in the Mediterranean and Eurosiberian regions). Mediterranean and Northern species can be approximated to warm and cold adapted species, respectively, based on the climatic characteristics of the Mediterranean and Eurosiberian biogeographic regions. Iberian and Widely Distributed species cannot be clearly linked to any particular climatic requirements because Iberian endemic species are usually associated with mountains of warm and cold climates, and Widely Distributed species can live both in cold and warm climates too. However, these two chorotypes are still useful as a benchmark to which compare the altitudinal shifts of Mediterranean and Northern species. Chorotype categories are based on Baselga & Novoa (2000), who established these four main categories grouping the chorotypes introduced by Vigna Taglianti et al., (1992) for the West Palaearctic fauna.

Temporal shifts in altitudinal ranges were then measured for the species that were detected in both sampling periods, quantifying the difference in minimum and maximum altitude at which each species was found in each period (i.e., ΔAlt_{min} = minimum altitude in 2010-2015 minus minimum altitude in 1998; ΔAlt_{max} = maximum altitude in 2010-2015 minus maximum altitude in 1998). From this, we estimated the distribution of altitudinal differences (ΔAlt_{min} and ΔAlt_{max}) across species within each chorotype. Negative values in in ΔAlt thus indicate that species had a tendency to shift towards lower elevations, while positive values in ΔAlt indicate a shift towards higher elevations. To assess whether altitudinal shifts in any particular chorotype (Iberian, Mediterranean, Northern, or Wide Distribution) were statistically significant, we built a null model in which the assignation of species to chorotypes was randomized, and the null altitudinal shifts for each randomized chorotype were estimated 10000 times. The null model thus produces the expected null distribution of altitudinal shifts, against which we compared the observed distribution for each particular chorotype. We also quantified the proportion of each chorotype at each altitude in 1998 and in 2010-2015, which would allow observing at the community level the effects of any systematic shift in the altitudinal ranges of particular chorotypes. All analyses were performed in R (R Core Team, 2021). The R code, metadata (Appendix S2) and data tables (Tables S1-S5) are provided as Supporting Information.

3. Results

A total of 1302 leaf beetles, belonging to 88 species, were collected in the three sites sampled in the 2010-2015 intensive survey (see Table S2 in Supplementary Information), with an average richness per site of S = 47.3 ± 22.9 (S.D.). Local richness values were slightly lower than the ones observed in 1998 (total richness, S = 99, with an average richness per altitudinal site of S = 43.3 ± 31.5 [S.D.], see Figure 2a). A total of 67 species were detected in both surveys.

The richness pattern along the altitudinal gradient in 2010-2015 differed from the one observed in 1998. The number of species at the high-altitude site was the lowest in both sampling periods (Figure 2a). However, species richness declined constantly with altitude in 1998, while it slightly increased from low to intermediate altitude in 2010-2015. The temporal beta diversity pattern evidenced that community composition at each site has changed over time (Figure 2b). The higher community turnover component (β_{sim} = 0.53) was observed in the low-altitude site, compared to the intermediate and high-altitude sites (β_{sor} ~ 0.4, see Figure 2b). In contrast, the nestedness-resultant dissimilarity was relatively high in the high-altitude site (β_{sne} = 0.22), and lower in the low and intermediate sites ($\beta_{sne} < 0.07$, see Figure 2b). The spatial turnover pattern evidenced that a marked turnover in species composition between the high-altitude and the low altitude site in both 2010-2015 and 1998 (β_{sim} = 0.44 [1998] and β_{sim} = 0.43 [2010-2015], Figure 3). The most remarkable difference over time was the decrease in species turnover between the low and intermediate sites (β_{sim} = 0.52 [1998] and β_{sim} = 0.35 [2010-2015], Figure 3), and the decrease in nestedness-resultant dissimilarity between the low-altitude and the high-altitude site (β_{sne} = 0.43 [1998] and β_{sne} = 0.27 [2010-2015], Figure 3).

The distribution of the different chorotypes along the altitudinal range showed that, in both time periods, Widely Distributed species were relatively abundant in the three altitudes

(Figure 4). The proportion of Iberian species increased towards higher elevations in both time periods, but the patterns were different between 1998 and 2010-2015 for Mediterranean and Northern species, as the former had increased its proportion in the highest site, whereas the latter had increased its proportion in the lowest site (Figure 4). These changes, observed at the community level, can also be detected as shifts in altitudinal ranges at the species level. In most cases, range shifts (both ΔAlt_{min} and ΔAlt_{max}) were not systematic and tended to be centered around zero (Figure 5). However, the exceptions were the lower limit of the Northern species, which showed a tendency to shift towards lower elevations (p = 0.069), and particularly the upper altitudinal limit of the Mediterranean species, which showed a tendency to shift towards higher elevations (p = 0.039).

4. Discussion

This study shows species-specific altitudinal shifts over a relatively short study period (ca. 20 years), resulting in community reshuffling (i.e., temporal turnover) at all elevation sites in a mountain range in the south of Europe. Such variation in species' range dynamics would be associated with differences in their physiological and behavioural responses to a complex suite of environmental factors, likely including heat responses to climate change (González-Tokman et al., 2020) and land use change (Neff et al., 2022). Remarkably, we have observed differences in the direction of change among chorotypes, with Mediterranean species tending to move upward while the proportion of Northern species increased at lower elevations. This points to a thermophilization of assemblages at high altitudes, a result in agreement with the prediction that, under climate change, species from lower latitudes and elevations will tend to increase in abundance (Parmesan, 2019). Similar tendencies to assemblage thermophilization as a consequence of climate warming have been reported by other authors (Lajeunesse & Fourcade, 2023). In Sierra de Ancares, the most striking examples of species moving upwards were *Smaragdina concolor* (Fabricius, 1792), *Cryptocephalus vittatus* Fabricius, 1775, and

Altica ampelophaga Guerin, 1858, whose upper limits went up 750, 550 and 450 m, respectively. In 1998, these Mediterranean species were found only in the valleys (at altitudes between 450 and 550 m) but in 2010-2015 they were detected at the intermediate altitude (1000) or even the high altitude site (*S. concolor*).

Nevertheless, our results also suggest that other drivers may be at play, as the downward shift of Northern species could have been favored by land use changes and the abandonment of traditional agriculture, which have profoundly reshaped montane biodiversity in Europe (MacDonald et al., 2000) as well as caused an altitudinal redistribution of species in interaction with climate change (Guo et al., 2018). Downward movements could also be driven exclusively by climate change, as some plants may have moved their optima to lower elevations in search for water (Crimmins et al., 2011) and highly specialized herbivorous insects are expected to track their host plants even more intensely than their climatic optimum. However, we think that the latter is unlikely given that there is not an analogous change at the upper limit of the elevational range. Moreover, the most marked downward change in the lower limit of their distributions were observed in three species that are not particularly host specific: *Cryptocephalus aureolus* Suffrian, 1848, *Neocrepidodera ferruginea* (Scopoli, 1763) and *Phratora vitellinae* (Linné, 1758). The two former species are associated with meadows, feeding on several species of Asteraceae (flowers) and Poaceae, respectively. The latter species is associated with Salicaceae trees (willows and poplars). Therefore, our results seem to be more likely related to changes in land use and habitat availability, as suggested by Lenoir et al. (2010) and Bhatta et al. (2018). In particular, the abandonment of agricultural systems and the subsequent expansion of forested areas in Sierra de Ancares (Álvarez-Martínez et al., 2014) would have increased the available habitats for these cold adapted leaf beetle species.

The upward shift of altitudinal ranges that we detected for warm adapted species was asymmetrical, with significant changes in the upper limit but negligible in the lower limit. An analogous asymmetrical pattern is expected along latitudinal gradients, with faster range expansion in the leading edge and slower contraction in the trailing edge (Parmesan, 2019), given that population extinction usually lags behind the deterioration of the environment (i.e., extinction debt; Kuussaari et al., 2009). Similar increases of upper altitudinal limits have been reported for other biological groups (Freeman et al., 2018; Iseli et al., 2023), as taxa would be expanding their altitudinal ranges to recently suitable territories. At the lower elevation boundaries, lack of change could be attributed to temperature having positive effects in insects, i.e., growth stimulation and voltinism (González-Tokman et al., 2020), while still being within the thermal safety margins of most species (Deutsch et al., 2008) or compensated with behavioral thermoregulation (Sunday et al., 2014). Nevertheless, temperature-driven damage, mostly associated with heat wave exposure, may still be affecting fitness and accumulating over time (Kingsolver et al., 2013; Colinet et al., 2015) although not readily observable yet (Harvey et al., 2020). In fact, meta-analyses in other studies have shown that lower boundaries are moving upward in similar magnitude as upper boundaries over longer temporal periods (Freeman et al., 2018; Rumpf et al., 2019), thus suggesting that our time span may be too short to detect rear elevation edge shrinking. This contrasts with the few previous studies on Coleoptera, mostly on dung beetles, which suggest that this group may be tracking temperature change the most, with both upward expansions and contractions of their trailing edges (McCain & Garfinkel, 2021 and references therein). A plausible explanation would be that, given the strong trophic specialization of leaf beetles, their range dynamics may be more mediated by their host plants (Hamann et al., 2021). In fact, alteration of biotic interactions and, in particular, phenological asynchrony between host plants and insects, is one of the major climatic risks for highly specialized species (Parmesan, 2019).

Heterogeneity in range shifts among species has also driven changes in the spatial diversity pattern along the elevation gradient. The reduction in spatial turnover between the low and intermediate sites has caused biotic homogenization at the regional scale (sensu Rolls et al., 2023), as previously observed for other montane organisms (e.g., Ploquin et al., 2013;

Savage & Vellend, 2015). Similar patterns have emerged across studies of different global change effects on insect communities, thus pointing to a worrying loss of beta diversity in this taxonomic group (Gossner et al., 2023). The varying strength of homogenization along the altitudinal gradient could be driven by the tendency of low-altitude species to move upslope farther than high-altitude species (Mamantov et al., 2021) and the downward shift of cold-adapted species associated with forest expansion due to the abandonment of traditional agriculture and livestock practices (Álvarez-Martínez et al., 2014), which would also explain the higher temporal turnover observed at the low-altitude site. The replacement of distinct communities by more similar communities, as observed here, evidences the impact that climate and land use change may have on the spatial structure of biodiversity, thus compromising the integrity of biodiversity at regional and global scales (Hillebrand et al., 2018). However, this dimension of global change on biodiversity is less studied than other aspects, such as species richness or temporal beta diversity at local scale (McGill et al., 2015). While the need to account for species composition rather than aggregate metrics, like species richness, is widely accepted in studies of the effect of climate change on biological communities (Dornelas et al., 2014; Hillebrand et al., 2018), a similar argument could be made about the relevance of looking for analogous changes in the spatial structure of diversity (McGill et al., 2015; Hillebrand et al., 2018).

Altitudinal range shifts, community reshuffling or alteration of biodiversity patterns, like the ones observed here, are driven by environmental changes but mediated by a key intrinsic species attribute, dispersal ability. In other words, not all species are able to actively modify their altitudinal ranges in response to climate warming (Harvey et al., 2023). Although dispersal limitation in flying insects is negligible at the scale of this study, it may turn relevant at larger geographical scales and hence, extrapolations based on the latitude-elevation analogy (Jump et al., 2009; Sundqvist et al., 2013) should be made with caution. The steep environmental gradients in mountains make them natural laboratories to study how species may track recent temperature change (McCain & Garfinkel, 2021) but cannot answer one of the most pressing questions: will migration rates be faster than the velocity of climate change? (Loarie et al., 2009). In fact, studies of biodiversity patterns at large spatio-temporal scales suggest that the ability to track climate change in the past varied broadly across beetle taxa (Gómez-Rodríguez & Baselga, 2018) and, hence, different species may also have very different abilities to track climate in the context of current global warming. Our lack of knowledge on how dispersal ability will mediate range shifts at larger geographical scales should be also considered as one of the main shortfalls besetting our understanding of biodiversity and how it will respond to global change (Hortal et al., 2015).

Assessing temporal biodiversity change requires historical datasets for resurveys, which are lacking for many insect groups and regions (McCain & Garfinkel, 2021). Even when available, differences in data type and sampling may still limit our ability to document changes (Magurran et al., 2019). Although this study is based on surveys of different nature, it allows the detection of coarse tendencies in species' elevation ranges and community rearrangements. We have opted for incidence-based metrics of diversity change, rather than abundance weighted metrics, as the latter are more prone to biases due to methodological differences (McCain & Garfinkel, 2021). Our measure of change is thus conservative, unable to detect more subtle abundance shifts that may be occurring within the species' ranges (e.g., Antão et al., 2022). Likewise, the observed upward shift of warm adapted species cannot be mechanistically linked to the species' thermal tolerance (as in Birkett et al., 2018). While this precludes the unequivocal attribution of biotic responses to climate change effects (Parmesan, 2019; Gonzalez et al., 2023), it constitutes relevant empirical data which is consistent with the assumed driver of change. Moreover, while range shifts at the species level may be noisy (Rumpf et al., 2019), complementing analyses at the species and community levels unveils relevant emergent patterns of climate responses (Pinsky et al., 2022). Detecting change is not as robust as detecting trend over temporal series but it may be the only documentation possible given that long-term monitoring data is lacking for most biological groups and regions despite recent efforts to provide long-term datasets for insects (van Klink et al., 2021). While not ideal, we should not let data scarcity hamper our ability to report biodiversity changes that may be relevant in a context of global change.

While an upward shift of montane communities is the main expectation in a climate change context, species are showing idiosyncratic responses (Lenoir & Svenning, 2015; Freeman et al., 2018; Rumpf et al., 2019; McCain & Garfinkel, 2021), which may be explained by the existence of other factors driving species range shifts (Rumpf et al., 2019), such as land use change (Lenoir et al., 2010; Bhatta et al., 2018; Guo et al., 2018). In fact, while climate warming has been shown to strongly affect long-term distribution changes in insects, short-term changes have been associated with both climate changes and regional land-use changes (Neff et al., 2022). In any case, the existence of multiple factors or multiple responses points to the need of community-level assessments for the detection of tendencies among the mixed species-specific signals. Moreover, they evidence how species-specific responses result in compositional reorganization and biotic homogenization, rather than a mere displacement of assemblages towards higher altitude. The assessment of community rearrangements and compositional change has lagged behind the assessment of species loss, but it is critical to understand temporal changes in biodiversity (Magurran et al., 2019). In particular, species turnover driven by variable changes in species' range limits is rapidly creating novel assemblages (Gibson-Reinemer et al., 2015) and affecting ecosystem functioning (Pecl et al., 2017).

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Supporting Information

Figure S1. Variation of Mean Annual Temperature between 1980 and 2020 in Ponferrada (NW Spain).

Figure S2. Variation of Mean Annual Temperature between 1985 and 2020 in Lugo (NW Spain).

Appendix S1. Supplementary methods for DNA based identification of specimens of *Psylliodes*, *Aphthona* and *Longitarsus* (samples collected in 2015).

Appendix S2. Metadata describing information provided as Tables S1-S5.

R code. R code used in this study.

Table S1. Leaf beetle presence data in 1998 from Baselga & Novoa (2000).

Table S2. Leaf beetle presence data for the period 2010-2015.

Table S3. Altitude data for localities sampled in 1998.

Table S4. Altitude data for localities sampled in the period 2010-2015.

Table S5. Chorotypes assigned to species observed in this study. Chorotypes are based on Baselga & Novoa (2000), who established four main categories grouping the chorotypes introduced by Vigna Taglianti et al., (1992) for the West Palaearctic fauna.

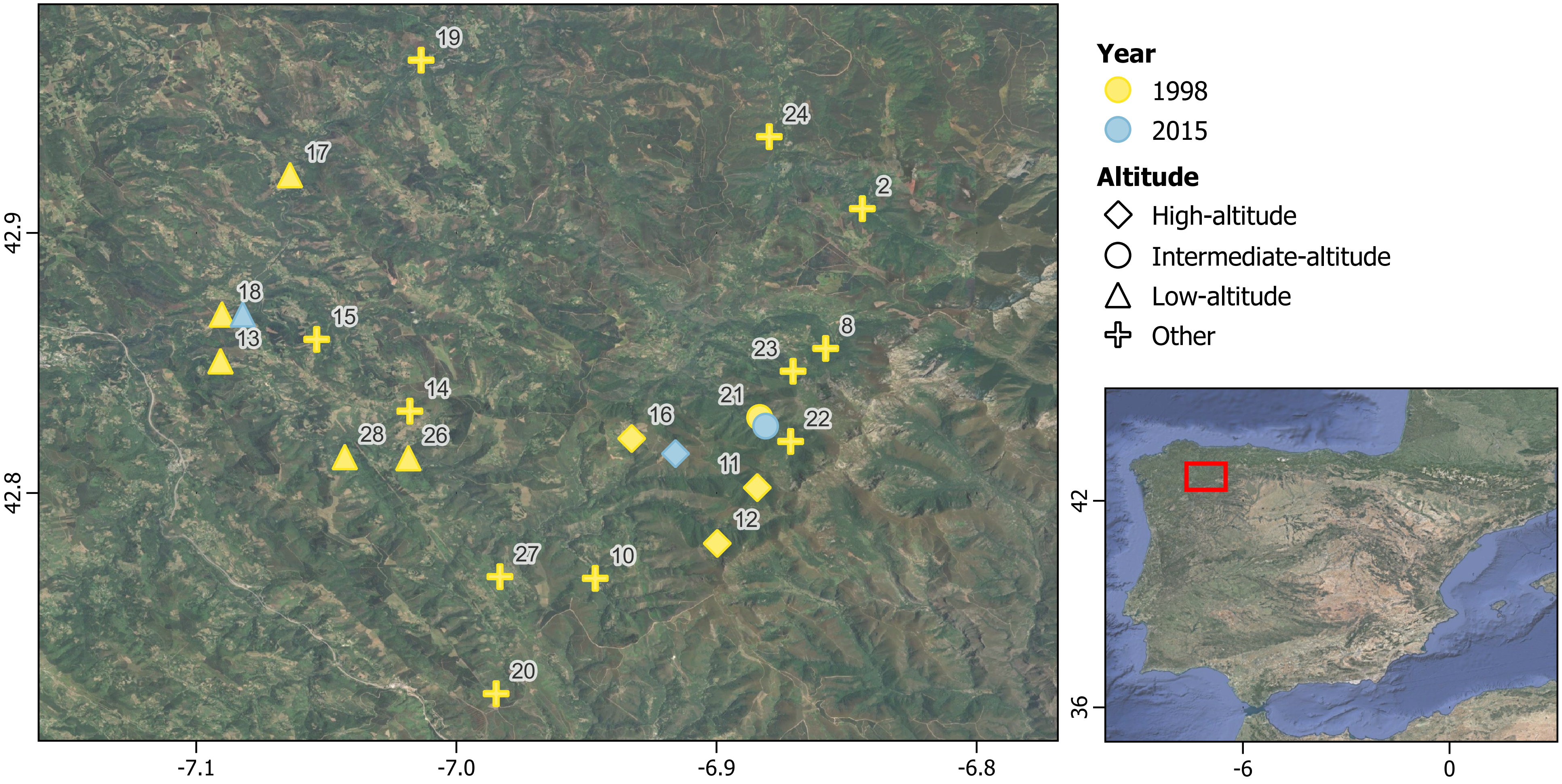
Figure 1. Map of the study area, including the sites intensively sampled in 2010-2015 (blue) and the sites extensively sampled in 1998 and previously reported in Baselga & Novoa (2000). Here, only sites in the NW slope of the range and up to 1300 m are shown. Symbols identify the 1998 sites that were aggregated for the community-level analyses (low, intermediate and high altitude). The remaining sites (marked as “other”) were only used to estimate altitudinal ranges. The Iberian Peninsula map on the bottom-right corner shows the location of the study area as a red rectangle.

Figure 2. Variation across altitudes in species richness in 1998 and 2010-2015 (a) and in temporal dissimilarity, partitioned between its turnover and nestedness-resultant components (b).

Figure 3. Community dissimilarity between sites in the different study periods (1998: above the arrow, in black; 2010-2015: below the arrow, in blue). Community dissimilarity has been partitioned into the turnover (Simpson’s index) and nestedness-resultant components following Baselga (2010)’s framework.

Figure 4. Variation in the proportion of chorotypes across altitudes in 1998 and in 2010-2015.
Iber: Iberian; Med: Mediterranean (i.e., species distributed around the Mediterranean basin); North: Northern (i.e., species distributed in the Eurosiberian region); Wide: Widely Distributed (i.e., species distributed both in the Mediterranean and Eurosiberian regions).

Figure 5. Density plot of the difference in species minimum (a) and maximum altitude (b) between 1998 and 2010/2015 for the different chorotypes. Mean values are represented as a vertical line.
Iber: Iberian; Med: Mediterranean (i.e., species distributed around the Mediterranean basin); North: Northern (i.e., species distributed in the Eurosiberian region); Wide: Widely Distributed (i.e., species distributed both in the Mediterranean and Eurosiberian regions).


19
24
17
2
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22
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28
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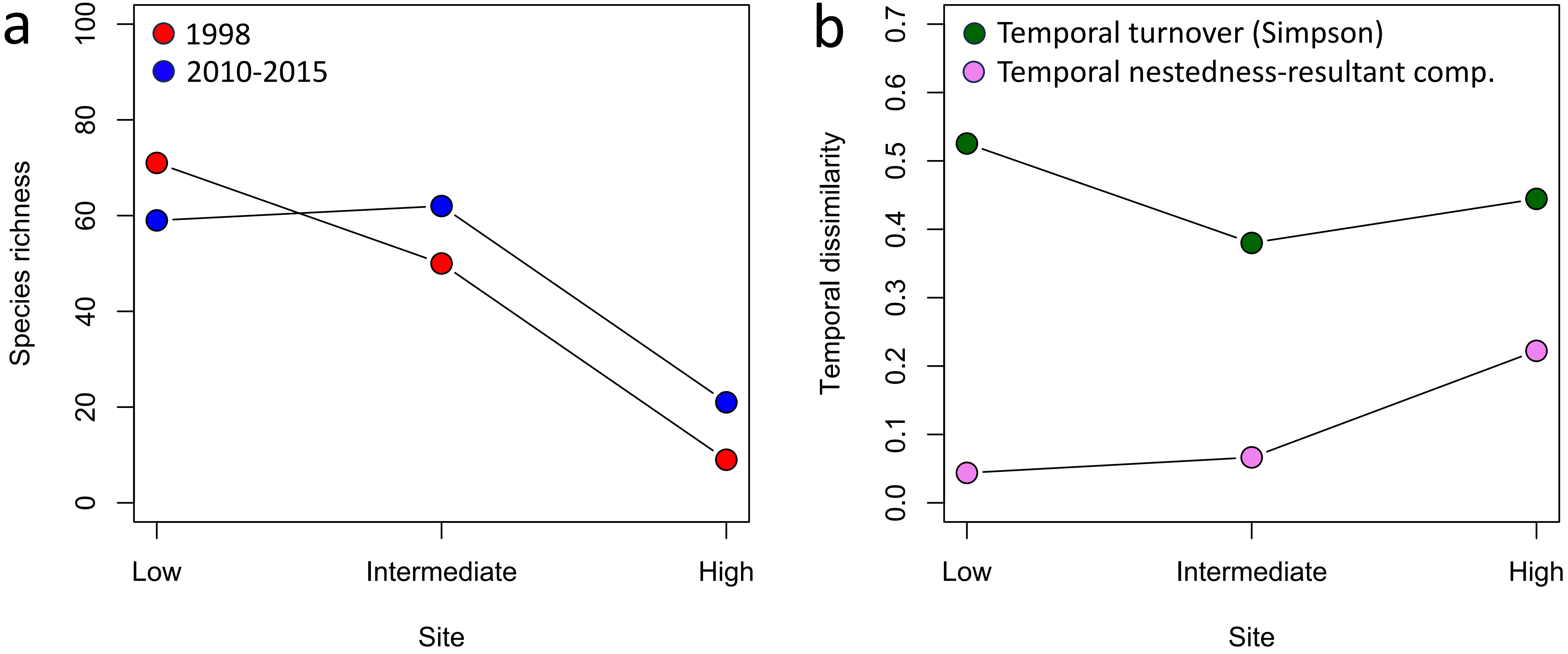
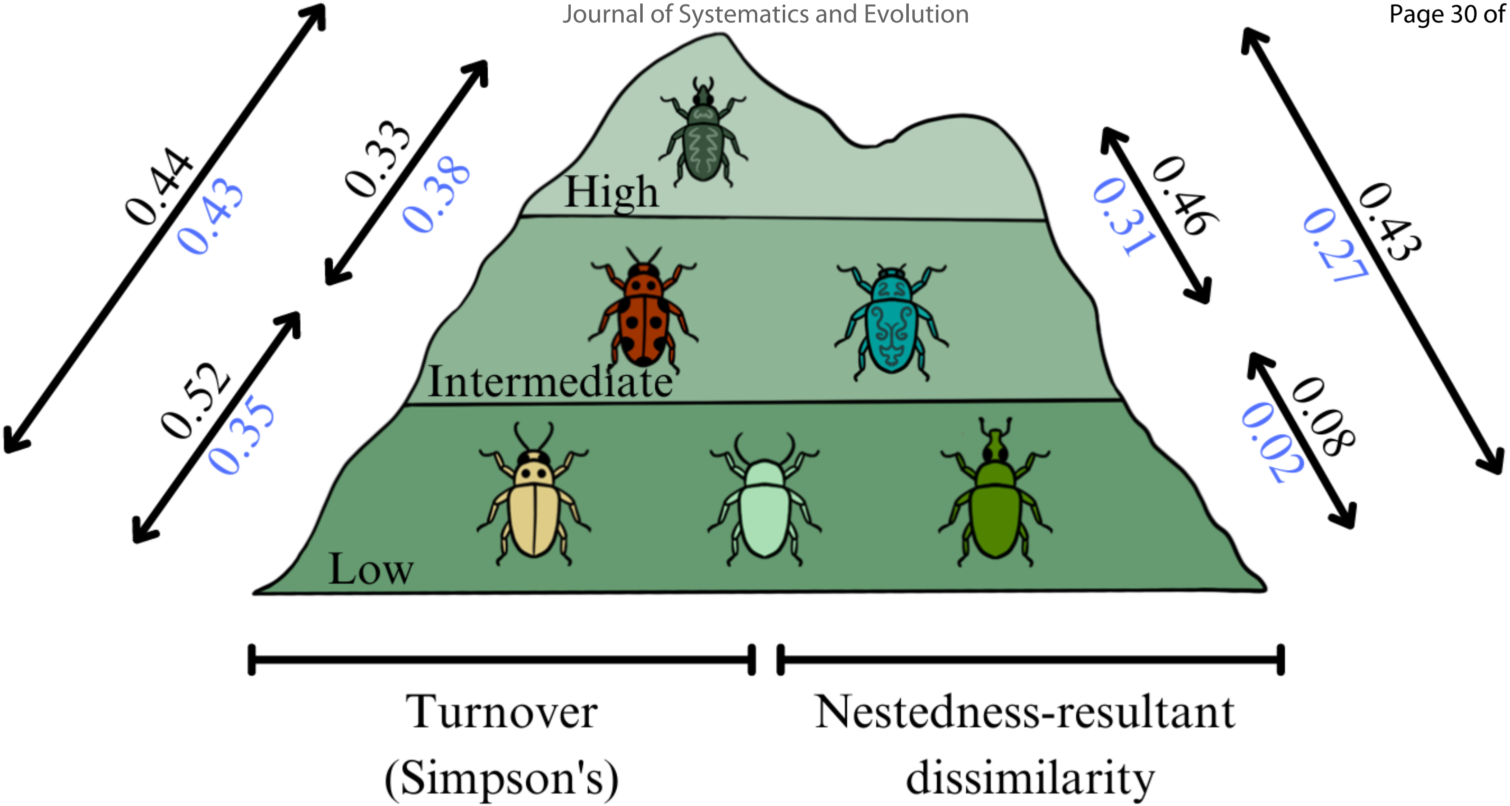
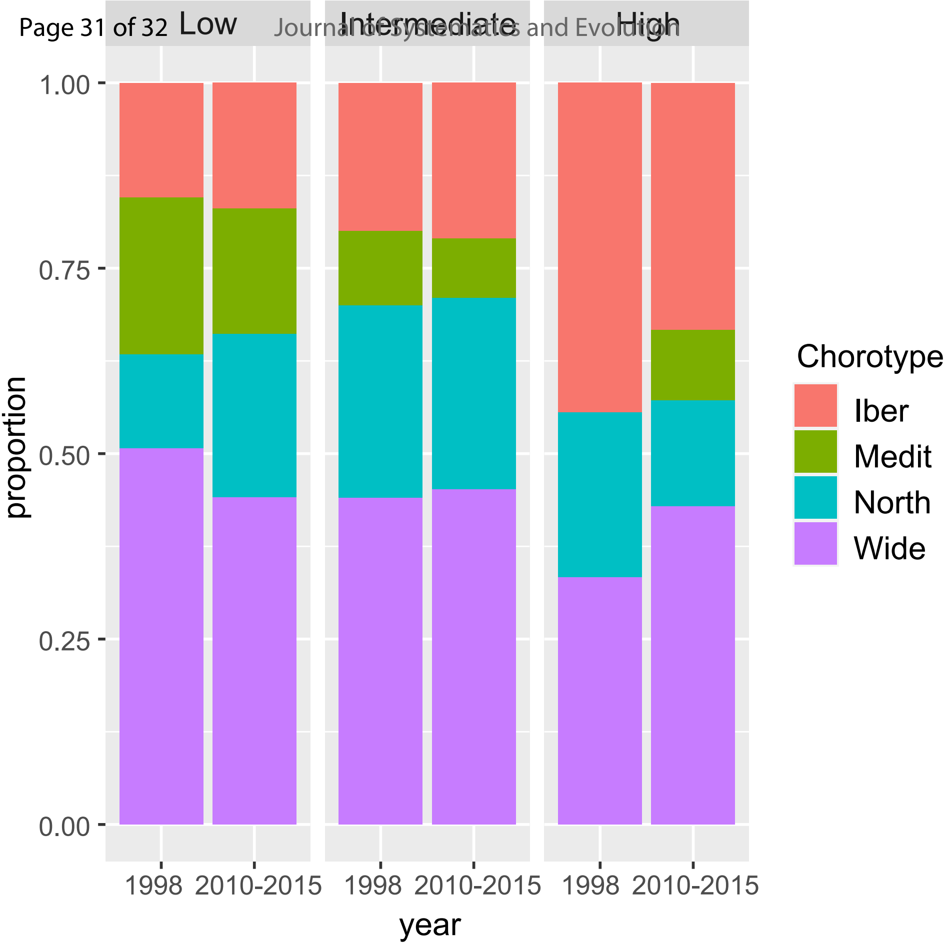
11
12
27
10
20
42.9
42.8
-7.1
-7.0
-6.9
-6.8
Year
1998
2015
Altitude
High-altitude
Intermediate-altitude
Low-altitude
Other
42
36
-6
0


a
b
1998
2010-2015
Species richness
0
20
40
60
80
100
Low
Intermediate
High
Site
Temporal turnover (Simpson)
Temporal nestedness-resultant comp.
Temporal dissimilarity
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Low
Intermediate
High
Site



0.44
0.43
0.33
0.38
0.52
0.35
High
Intermediate
Low
0.46
0.31
0.43
0.27
0.08
0.02
Turnover (Simpson's)
Nestedness-resultant dissimilarity


Low
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proportion
1.00
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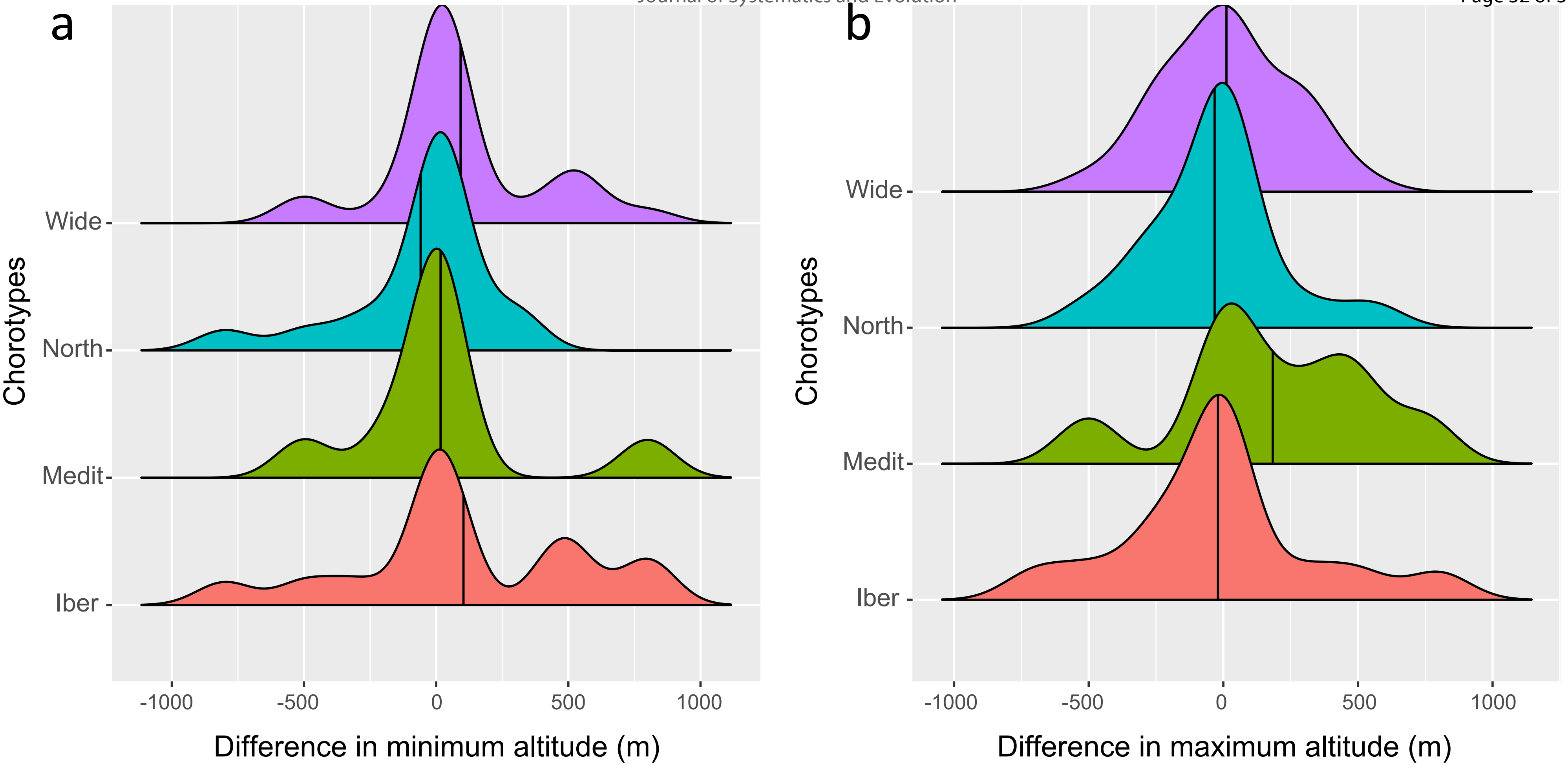
a
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-1000
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1000
Difference in minimum altitude (m)
b
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Medit
Iber
Chorotypes
-1000
-500
0
500
1000
Difference in maximum altitude (m)