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RESEARCH PAPER

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Understanding dispersal limitation through the assessment of diversity patterns across phylogenetic scales below the species level

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Abstract

Aim: We show how macroecological patterns at different phylogenetic scales below the species level may aid the identification of the predominant process controlling biological assemblages (niche versus dispersal). We compare two taxa with different ecological and dispersal requirements (terrestrial molluscs and leaf beetles) in the same geographical setting.

Location: Iberian Peninsula.

Time period: 2010–2015.

Major taxa: Terrestrial molluscs and leaf beetles.

Methods: The *cox1*-5′ fragment was sequenced for 1,592 mollusc specimens in 20 localities. Leaf beetle assemblages had been sequenced previously in 15 of these localities. Species richness, distance decay of similarity, endemism and range size were measured at two levels: molecular variants (i.e., haplotypes) and putative species (i.e., operational taxonomic units). Using a multi-hierarchical macroecology approach, distance-decay patterns were measured at multiple intermediate genealogical levels (nested clades) to assess whether the geometry of the ranges of lineages followed a fractal pattern.

Results: Richness and distance-decay patterns at both molecular variant and species levels were different in leaf beetles and terrestrial molluscs, although both taxa showed a fractal pattern in the distance decay of similarity across genealogical levels. The self-similarity of the distance-decay pattern across phylogenetic scales suggests a predominance of neutral, but limited, dispersal driving macroecological patterns in both taxa. Endemism was similar in both taxa at the level of molecular variants but higher at the species level in terrestrial molluscs, and range size was smaller at both levels in terrestrial molluscs. Taken altogether, our results suggest that dispersal limitation is stronger in terrestrial molluscs.

Main conclusion: The assessment of how diversity patterns change at different phylogenetic scales below the species level allowed us to identify unifying characteristics in otherwise seemingly heterogeneous biological systems. Congruence was observed in diversity patterns of leaf beetles and terrestrial molluscs, suggesting that dispersal is a relevant process in both taxa but acts at a different strength.

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KEYWORDS
beta diversity, dispersal, distance-decay, endemism, multi-hierarchical macroecology, phylogenetic scale, range size, species–genetic diversity correlation

1 | INTRODUCTION

Large-scale spatial patterns are key for inferring the potential drivers of biological diversity (Willig, Kaufman, & Stevens, 2003), which is usually measured at the species level (Diniz-Filho et al., 2008). However, large-scale patterns of genetic diversity are largely unknown (but see Miraldo et al., 2016; Pelletier & Carstens, 2018) even though they are a fundamental facet of biological diversity (Blanchet, Prunier, & Kort, 2017; Diniz-Filho et al., 2008). Concordance in the geographical distribution of molecular variants of different species has been used to infer common historical processes (comparative phylogeography; Arbogast & Kenagy, 2001), but little is known about the broad-scale spatial regularities of genetic variation across higher taxa (i.e., genetic diversity of full communities; but see, e.g., Paz-Vinas, Loot, Stevens, & Blanchet, 2015).

Genetic and species diversity represent two levels in the evolutionary continuum of biodiversity and, as such, better understanding of ecological and evolutionary processes can be gained when they are interpreted together (Diniz-Filho & Bini, 2011). One approach that considers both levels is the measurement of genetic variation with a neutral molecular marker, thus discarding a causal effect of one level on the other (Vellend & Geber, 2005), and assessing whether genetic and species diversity vary in concordance, an outcome expected if similar processes act in parallel at both levels (Kahilainen, Puurtinen, & Kotiaho, 2014; Vellend & Geber, 2005). Given that different molecular variants (i.e., haplotypes) of a neutral marker do not differ in their ecological niches, congruence at species and genetic levels can be interpreted as evidence of dispersal and ecological drift at the species level because migration and drift would be the only processes acting at the genetic level (Vellend, 2016; Vellend et al., 2014). At a macroecological scale, several studies have shown the concordance of alpha- and beta-diversity patterns at the species and genetic levels, mostly in insects (e.g., Múrria, Rugenski, Whiles, Vogler, & Beggs, 2015; Papadopoulou et al., 2011; Sei, Lang, & Berg, 2009). However, little is known about other taxonomic groups with different dispersal and physiological strategies.

The most widely used approach for assessing the congruence between diversity patterns at the genetic and species level is the species–genetic diversity correlation (SGDC; Vellend, 2005; Vellend & Geber, 2005), which measures the relationship between the genetic diversity of a focal species in several sites with the species richness of communities in those sites. To account for the spatial structure of biological assemblages, the SGDC can be extended to beta-diversity measures (β-SGDC; Kahilainen et al., 2014). A further step would be to assess whether these diversity patterns might vary across phylogenetic scales (Graham, Storch, & Machac, 2018). Although phylogenetic scale is usually addressed above the species level, it is possible to conduct this type of assessment at infraspecific levels (Graham et al., 2018). Following this rationale, the β-SGDC approach was extended to distance-decay patterns at multiple intermediate genealogical levels between the molecular variants and the species, thus explicitly accounting for the spatial structure of evolutionary divergence within species (multi-hierarchical macroecology; Baselga, Gómez-Rodríguez, & Vogler, 2015).

Multi-hierarchical macroecology provides a framework for assessing whether the variation in biological assemblages is predominantly driven by dispersal (i.e., neutral) or niche-based processes (Baselga et al., 2013, 2015). It is based on the concept of "fractality" or "symmetry under magnification", which is observed when a small piece of a magnified object looks very much like the whole object (Frame & Urry, 2016). Applied to diversity patterns, fractality would be observed when lineage distribution patterns at the haplotype level are similar to distribution patterns at the species level and other genealogical levels in between (i.e., self-similar pattern across genealogical levels). This type of fractal pattern can be attributed to a predominance of dispersal processes in the system because the geometry of the distributional ranges of lineages at multiple hierarchical levels is self-similar only under neutral evolutionary and ecological dynamics, thus providing a testable unique prediction (Baselga et al., 2013, 2015). This prediction derives from the fact that neutral and niche-based processes may drive the geographical distributions at the species level, but niche-based processes should not control the ranges of mitochondrial DNA haplotypes (Avise, 1994; Slatkin, 1985). At present, the multi-hierarchical macroecology framework has been applied to two different beetle groups (aquatic beetles and leaf beetles) and, in both, assemblage similarity increased regularly from lower to higher genealogical levels, pointing to such a fractal geometry in the spatial distribution of lineages (Baselga et al., 2013, 2015). This result suggests that the distributions of genetic variants, intermediate lineages and species are the result of similar processes of range expansion through time. Hence, range size variation at different genealogical scales is relevant for understanding diversity patterns.

The study of distributional ranges at the species level has always been at the core of large-scale diversity assessments (Gaston, 2003), but little is known below the species level. Based on neutral molecular markers, lineages are expected to spread constantly and isotropically in space until they reach the spatial limits of the species' niche (Figure 1). The assessment of how distributional range patterns change below the species level will reveal how fast distributional ranges grow with time (i.e., lineage age) and, therefore, it will provide insight into the long-term dispersal ability of the taxon. Although species ranges are frequently considered an expression of ecological niche (Sexton, McIntyre, Angert, & Rice, 2009), we can exclude ecological niche as a constraint for distributional ranges of

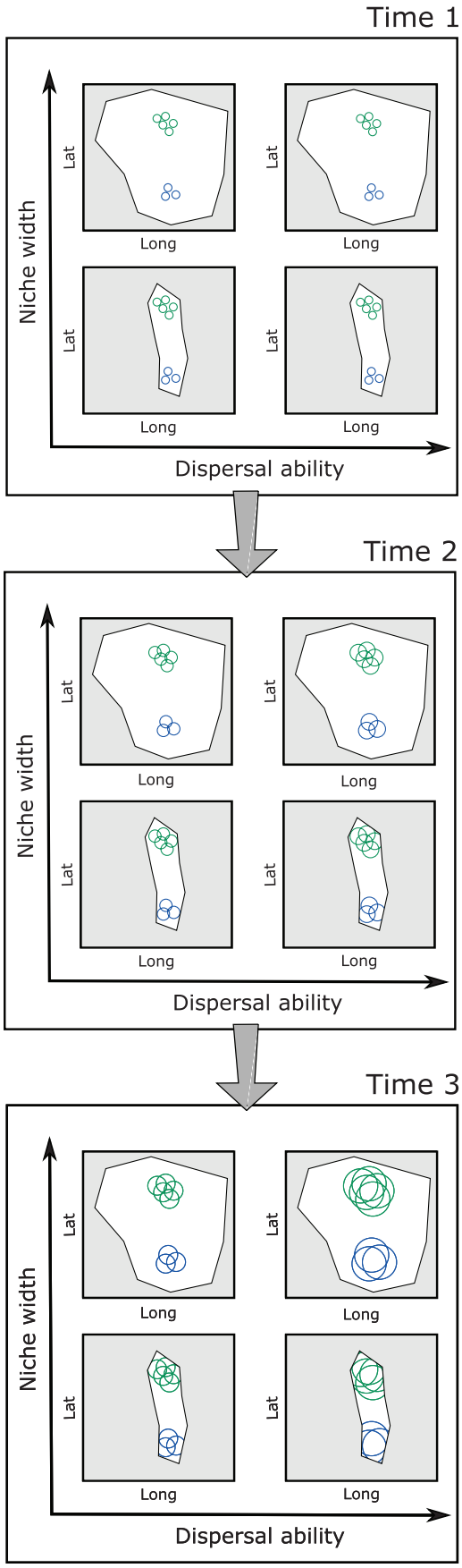

FIGURE 1 Schematic representation of range expansion of neutral genetic variants over time under different scenarios of dispersal ability and niche width. The spatial extent of suitable conditions (projection of potential niche) is represented as a white polygon surrounded by a grey area (unsuitable environmental conditions). The distributional range of genetic variants (haplotypes) is represented as circles. Molecular variants of the same species are the same colour. The size of these circles increases isotropically with time. The distributional range at the species level is the area covered by all the molecular variants of the same species [Colour figure can be viewed at wileyonlinelibrary.com]

molecular variants (and intermediate lineages), because the ecological requirements of two conspecific variants of a neutral marker are assumed to be the same and, thus, spatial ranges of these molecular variants would be mostly dispersal controlled (Avise, 1994; Diniz-Filho & Bini, 2011; Slatkin, 1985).

The aims of this study are threefold. First, we compare macroecological patterns at multiple genealogical levels in two biological groups with different dispersal and ecological requirements. Second, we want to challenge the generality of the fractality in distance-decay patterns that has been reported previously for beetles (aquatic beetles: Baselga et al., 2013; leaf beetles: Baselga et al., 2015). Third, we aim to illustrate how distributional range size at different genealogical levels may help us understand large-scale diversity patterns. To achieve these objectives, we assessed diversity patterns of terrestrial molluscs across the same latitudinal gradient previously studied for leaf beetles in the Iberian Peninsula (Baselga et al., 2015), thus ensuring that any observed differences are attributable to biological rather than geographical deviations.

Terrestrial molluscs offer an interesting case study to apply the multi-hierarchical framework for several reasons. First, compared with leaf beetles, terrestrial molluscs are, in principle, more dispersal limited owing to the lack of flight (Barker, 2001). However, some species are subject to passive dispersal by humans (e.g., Aubry, Labaune, Magnin, Roche, & Kiss, 2006; Barker, 2001) and other animals (Pearce, Mulvihill, & Porter, 2012), effectively leading to large variability in the dispersal abilities among species. Second, their life history and physiological requirements are very different from leaf beetles, particularly with regard to their dependence on high levels of environmental humidity (Barker, 2001). Thus, we hypothesize that climate-related factors might play a more important role in constraining species distributions in terrestrial molluscs than in leaf beetles (see a more detailed literature review in Supporting Information Appendix S1). Therefore, we expect a weak fractal pattern in the distance-decay patterns across genealogical levels in terrestrial molluscs. However, if this hypothesis is not confirmed and terrestrial mollusc assemblages were mostly constrained by dispersal limitation (i.e., fractal pattern in the distance decay of similarity), we would expect higher endemism and smaller range sizes, at least at the deeper phylogenetic scale (species level), in terrestrial molluscs, in accordance with stronger dispersal limitation in the long term.

2 | MATERIAL AND METHODS

2.1 | Molluscs: Field sampling and *cox1*-5′ sequencing

Terrestrial mollusc assemblages were sampled in 20 localities in the Iberian Peninsula in autumn 2015 (Figure 2). Vegetation was dominated by different oak species, within shrubs and meadows. In each locality, specimens were manually collected during two consecutive days and nights when climatic conditions were adequate for mollusc sampling (air temperature 15–20 °C; humidity > 80%). During daylight sampling, potential hiding places (i.e., rocks, logs) were inspected for 3 hr by two people each day. Nocturnal sampling was conducted for 5 hr per night, totalling a sampling effort of 16 hr in each locality. All specimens were drowned in water before being placed in 96% ethanol for preservation and DNA extraction. A preliminary identification of morphospecies was conducted by an expert taxonomist (J.C.), in order to select a maximum of 10 specimens per morphospecies for DNA sequencing.

For molecular analysis, a piece of foot tissue (*ca*. 5–10 mg) was taken from the collected specimens and soaked in water for 30 min before genomic DNA extraction with DNeasy Blood & Tissue Kit (Qiagen, Düsseldorf, Germany). A 655 bp region from the 5′ end of mitochondrial *cox1* ("barcode region") was amplified with standard LCO/HCO primers (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994). Amplification was performed with Bioline MyTaq and the following cycling: 94 °C for 2 min and 30 s, 40 cycles of 94 °C for 30 s, 47 °C for 45 s and 72 °C for 1 min and 15 s, and final extension of 72 °C for 10 min. The PCR products were sent to StabVida (Portugal) for purification with magnetic beads and sequencing in both directions using ABI 3730xl DNA Analyzer. Sequence chromatograms were assembled and manually edited using Geneious v.5.6. (Biomatters Ltd, Auckland, New Zealand) DNA sequences are available under GenBank accession numbers MF981937–MF983528.

2.2 | Leaf beetles: Available *cox1*-5′ sequences for full species assemblages

As part of a previous study (Baselga et al., 2015), full leaf beetle assemblages have been sampled and sequenced (*cox1*-5′) in 15 of the localities selected for mollusc sampling. A total of 3,997 specimens in 197 morphological species were collected, and 3,529 were successfully sequenced for the barcode region (88.3%), totalling 1,634 different *cox1*-5′ haplotypes (see details in Supporting Information Appendix S2). Putative species richness in each locality (hereafter referred to as 'species richness' for simplicity) ranged from 39 to 80 (mean = 56.6; Figure 2). DNA sequences from Baselga et al. (2015) are available under GenBank accession numbers KF134544–KF134651 and KF652242–KF656666.

2.3 | Identification of lineages below species level (haplotype network)

To identify intermediate lineages and delimit putative species based on molecular variation [operational taxonomic units (OTUs); equivalent to 'species level'], a haplotype network analysis was conducted

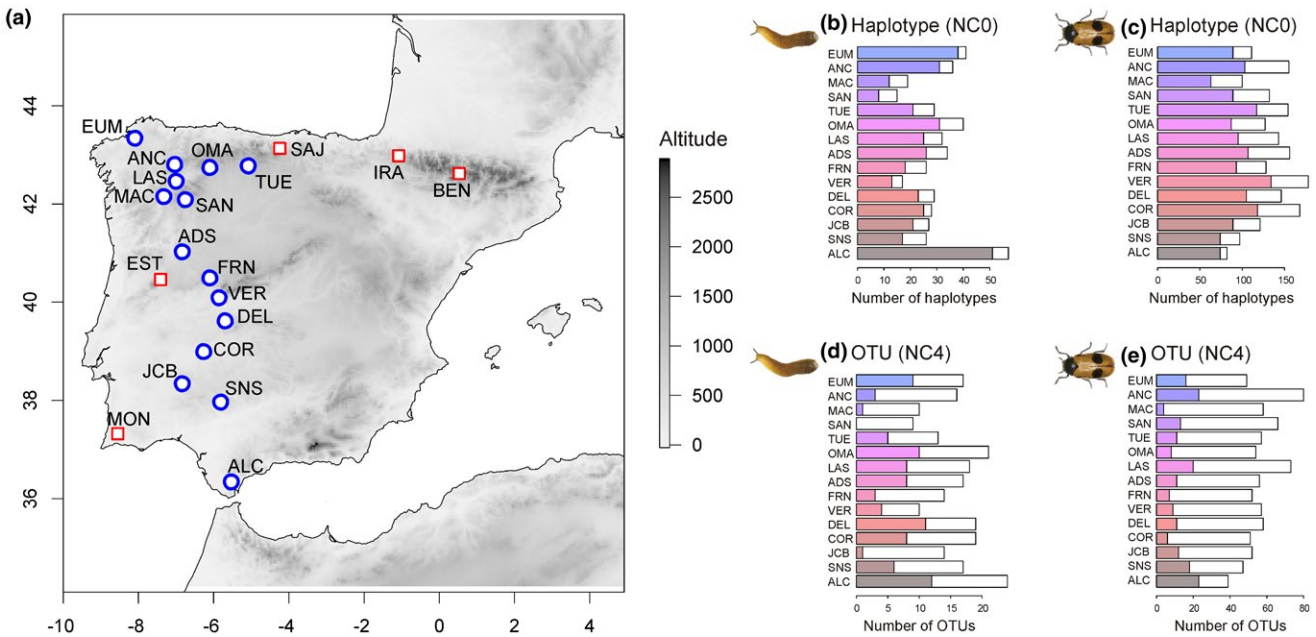

FIGURE 2 Map showing the sampling localities with data for both terrestrial molluscs and leaf beetles (blue circles; *n* = 15) and with data for terrestrial molluscs only (red squares; *n* = 5). Histograms represent the degree of endemism in each locality as the number of local lineages (coloured bars) with respect to the total number of lineages (white bars) at the haplotype (b, c) and species [OTU] level (d, e). Data are presented for both terrestrial molluscs and leaf beetles. Pictures of a terrestrial mollusc and a leaf beetle were downloaded from Wikimedia Commons (under Creative Commons license, authors Günter Wondrak and Udo Schmidt, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

for sequences from terrestrial molluscs. Leaf beetles were not analysed because Baselga et al. (2015) provided this information for the specimens under study. The *cox1*-5′ sequences were aligned with transAlign (Bininda-Emonds, 2005), and identical haplotypes were collapsed into a single sequence with a custom Perl script. Haplotype networks were created using the TCS software (Clement, Posada, & Crandall, 2000) and a nesting algorithm implemented in ANeCA v.1.2 (Panchal, 2007). TCS uses statistical parsimony to estimate haplotype networks of closely related individuals from DNA sequence data, which is defined by the 95% confidence interval for connections between haplotypes to be non-homoplastic in the network analysis (Templeton, Crandall, & Sing, 1992). The nesting algorithm generates *n*-step hierarchical nested clades of increasingly more inclusive groups of haplotypes, following rules for initially connecting all haplotypes (NC0) that can be linked by one mutational step ("1-step networks"; NC1), which then are incorporated into groups requiring a connection of a maximum of two steps ("2-step networks"; NC2), and so on. The procedure implements a stopping rule for the maximum level by which haplotypes are included into a single network based on the probability of encountering homoplastic changes in the connections of two haplotype groups. Thus, this algorithm creates a nested design by hierarchically clustering haplotypes into groups known as "clades", which here will be also referred to as intermediate lineages. The independent networks that are generated can be used as operational species units (OTUs), or putative species, owing to their strong correspondence to Linnaean species (Hart & Sunday, 2007). Haplotype and nested clade assignment (i.e., lineages at different genealogical levels) for each specimen were retrieved with a custom R script ("uncollapse") that restored the information removed when collapsing identical haplotypes. Minor uncertainty in the haplotype identity in 15 sequences owing to partly missing sequence data was resolved by assigning the haplotypes to one of the fully sequenced haplotypes in the same (*n* = 13) or a nearby locality (*n* = 2). For more details on the methodology used, see Baselga et al. (2015).

2.4 | Species–genetic diversity correlation

As a measure of genetic diversity, the nucleotide diversity for each OTU at each locality was computed with the nuc.div() function in the pegas package (Paradis, 2010) in R (R Development Core Team, 2013). Only OTUs with five or more individuals were selected to compute the average genetic diversity at a locality. The correlation between species diversity and genetic diversity (SGDC) was assessed in two different ways, as the univariate linear regression between (a) species richness and average genetic diversity and, independently, between (b) species richness and genetic diversity of the most abundant OTU in the dataset (i.e., focal species), using the 15 localities with data for both terrestrial molluscs and leaf beetles.

To assess whether terrestrial molluscs and leaf beetles differed in their species richness and, independently, in their average genetic diversity, repeated-measures ANOVAs were conducted using sampling locality as a within-subjects factor. Additionally, to assess whether they showed similar spatial patterns, a univariate linear regression was computed between species richness in terrestrial molluscs and in leaf beetles and, independently, between average genetic diversity in terrestrial molluscs and in leaf beetles. Linear regression models were also built to assess the relationship between diversity attributes (species richness and average genetic diversity) and topo-climatic variables: latitude, longitude, mean elevation, annual mean temperature (Bio1 in WorldClim data; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and annual precipitation (Bio12 in WorldClim data; Hijmans et al., 2005). Significant predictors were selected following a forward procedure based on the *F*-statistic.

2.5 | Multi-hierarchical assessment of variation in assemblage composition

The analysis of the variation in assemblage composition follows the multi-hierarchical approach to distance-decay patterns suggested by Baselga et al. (2013, 2015). It consists of two main steps. First, the neutral evolution of sequences is tested to validate the assumption that haplotype distributions are not driven by selective processes. Second, the variation in assemblage composition with spatial distance is measured at different genealogical levels, in order to identify a potential emerging fractal pattern.

These analyses had been conducted for leaf beetles in the Iberian Peninsula by Baselga et al. (2015) and thus are not repeated here.

For the terrestrial molluscs, this approach was implemented, using all localities (*n* = 20), as follows. First, the null hypothesis of neutral evolution of mitochondrial DNA was tested with Tajima's *D* test (Tajima, 1989) in the R package pegas (Paradis, 2010), using the *cox1*-5′ sequences of those OTUs with haplotype variability and more than three sequences of different haplotypes (1,337 sequences of 84 OTUs in total). Tajima's *D* values ranging between –2 and + 2 support the hypothesis of neutral evolution. The proportion of OTUs with neutral evolution was computed, and the Kolmogorov–Smirnov test [command ks.test() in R] was also used to assess whether the values of Tajima's *D* followed a normal distribution. Second, the relationship of assemblage similarity with spatial distance (i.e., distance decay of similarity) was assessed independently at each genealogical level (haplotypes, intermediate lineages and OTUs) using the Simpson index of similarity, that is, $1 - \beta_{sim}$ (Baselga, 2010), in the R package betapart (Baselga & Orme, 2012). A negative exponential function [command decay.model() in betapart] was used to adjust a generalized linear model (GLM) with Simpson similarity as response variable, spatial distance as predictor, log link and Gaussian error, maintaining the spatial distances untransformed (Gómez-Rodríguez & Baselga, 2018). Spatial distance was computed in kilometres as the Euclidean distance between the centroids of localities. An arbitrary small quantity (0.01) was summed to all similarity values to avoid undefined $\log_{10}$-transformed values. Fractal systems (i.e., self-similar systems) can be described only by a scale-free function, such as the power law function (Pinto, Lopes, & Tenreiro Machado, 2014). Thus, the existence of a fractal pattern in the distance-decay curves across genealogical levels was assessed by a log–log Pearson correlation

of genealogical level and, independently: (a) number of lineages, (b) initial similarity, and (c) mean similarity. High correlation values are indicative of fractality in lineage branching (i.e., number of lineages) and/or spatial geometry of lineage distributional ranges (i.e., initial and mean similarity).

Equivalent analyses were conducted to assess the relationships of assemblage similarity and topo-climatic distance at each genealogical level. Topo-climatic distance was computed as the Euclidean distance in a multidimensional space consisting of seven standardized topo-climatic variables (Hijmans et al., 2005): elevation, mean annual temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12), precipitation of the wettest quarter (Bio16) and precipitation of the driest quarter (Bio17). This measure of topo-climatic distance is the one used by Baselga et al. (2015) for leaf beetles. Variance partitioning was conducted to assess the fractions of variance in assemblage dissimilarity that were uniquely and jointly explained by spatial distance and topo-climatic distance at multiple genealogical levels.

2.6 | Endemism and range size at the haplotype level and the OTU level

To assess whether terrestrial molluscs and leaf beetles differed in their effective dispersal ability, their endemism and distributional ranges were compared at both the haplotype and the species level using the 15 localities with data for both terrestrial molluscs and leaf beetles. Endemism was computed for each locality as the proportion of lineages (i.e., haplotypes or OTUs, respectively) that occurred at a single locality. For each lineage, the extent of its distributional range was described by the geographical distance between the two most distant localities where it occurred (range size or extent). Differences in endemism between leaf beetles and terrestrial molluscs were assessed with repeated-measures ANOVA, using sample locality as a within-subjects factor. Differences in the extent of the distributional ranges were assessed with Wilcoxon tests, using taxon as a grouping factor. Additionally, to describe how range size varies with genealogical level, density plots of range size were computed for all hierarchical levels, from haplotype (NC0) to OTU (NC4).

3 | RESULTS

A total of 1,792 terrestrial mollusc specimens were collected in the 20 study localities. The *cox1*-5′ sequences were obtained successfully for 1,592 specimens (88.8%), yielding 547 different *cox1*-5′ haplotypes of 17 different families. Haplotype network construction provided evidence for five levels of nested clades (NC0–NC5), although the NC5 level was recovered for a negligible proportion of cases, and results were very similar to NC4 (number of NC4 networks = 190; number of NC5 networks = 187). Therefore, NC4 networks are hereinafter used as OTUs. Species richness (i.e., number of OTUs) ranged from nine (SAN locality) to 29 (EST locality), with an average number of 17.0 ± 5.1. In the reduced dataset (15 localities for which leaf beetle assemblages had also been sequenced), 1,321 specimens were collected, yielding 1,192 *cox1*-5′ sequences and 391 unique haplotypes (Supporting Information Appendix S2).

3.1 | Species–genetic diversity correlation

There was not a significant relationship between species richness and average genetic diversity (terrestrial molluscs: $r^2 = 0.02$; $F_{1,13} = 0.333$, $p = .57$; leaf beetles: $r^2 = 0.005$; $F_{1,13} = 0.061$; $p = .81$; Supporting Information Appendix S3) or between species richness and genetic diversity of the focal species [terrestrial molluscs (*Limax flavus*): $r^2 = 0.10$; $F_{1,13} = 1.52$, $p = .24$; leaf beetles (*Longitarsus cerinthes*): $r^2 = 0.07$; $F_{1,13} = 0.07$; $p = .79$]. The stepwise procedure showed that species richness was inversely related to elevation ($r^2 = 0.33$; $F_{1,13} = 6.4$, $p = .025$) in terrestrial molluscs, whereas it was inversely related to latitude ($r^2 = 0.39$; $F_{1,13} = 8.5$, $p = .012$) in leaf beetles (Supporting Information Appendix S3). None of the variables was selected as a predictor in the models of average genetic diversity (for details on the stepwise procedure, see Supporting Information Appendix S4).

Leaf beetles showed higher local richness (repeated-measures ANOVA $F_{1,14} = 164.1$, $p < .001$) and higher local average genetic diversity (repeated-measures ANOVA $F_{1,14} = 96.7$, $p < .001$) than terrestrial molluscs (Supporting Information Appendix S5), and there was no significant relationship between diversity patterns of both taxa (species richness: $r^2 = 0.12$; $F_{1,13} = 1.8$, $p = .20$; average genetic diversity: $r^2 = 0.04$; $F_{1,13} = 0.602$, $p = .45$; Supporting Information Appendix S6).

3.2 | Multi-hierarchical assessment of variation in assemblage composition

Tajima's *D* tests for the 84 mollusc OTUs with haplotype variability and more than three *cox1*-5′ sequences revealed that the null hypothesis of neutral evolution was not rejected ($-2 < D < 2$, $p > .05$) in 53 OTUs (63%; see details in Supporting Information Appendix S7). When neutrality was rejected, Tajima's *D* was significantly lower than expected ($D < -2$, $p < .05$) in 30 OTUs (36%), suggesting either purifying selection or population size expansion in these putative species, and only higher than expected ($D > 2$, $p < .05$) in one OTU (1%), suggesting either balancing selection or a reduction in population size in this single case. The distribution of Tajima's *D* values was not significantly different from a normal distribution (Kolmogorov–Smirnov $D = 0.14286$, *p*-value = .35; Supporting Information Appendix S8) in the full dataset.

Mollusc assemblage similarity decreased exponentially with spatial distance at all genealogical levels (Figure 3), from haplotype to OTU (NC4). The slopes of the exponential decay curves were very similar at all levels, whereas assemblage similarity increased uniformly from level to level (Figure 3; Table 1). Genealogical level showed a log–log correlation with the number of lineages ($r^2 = 0.99$, $F_{1,3} = 213.8$, $p < .001$), initial similarity (i.e., intercept; $r^2 = 0.99$, $F_{1,3} = 575.3$, $p < .001$) and mean similarity of assemblage composition

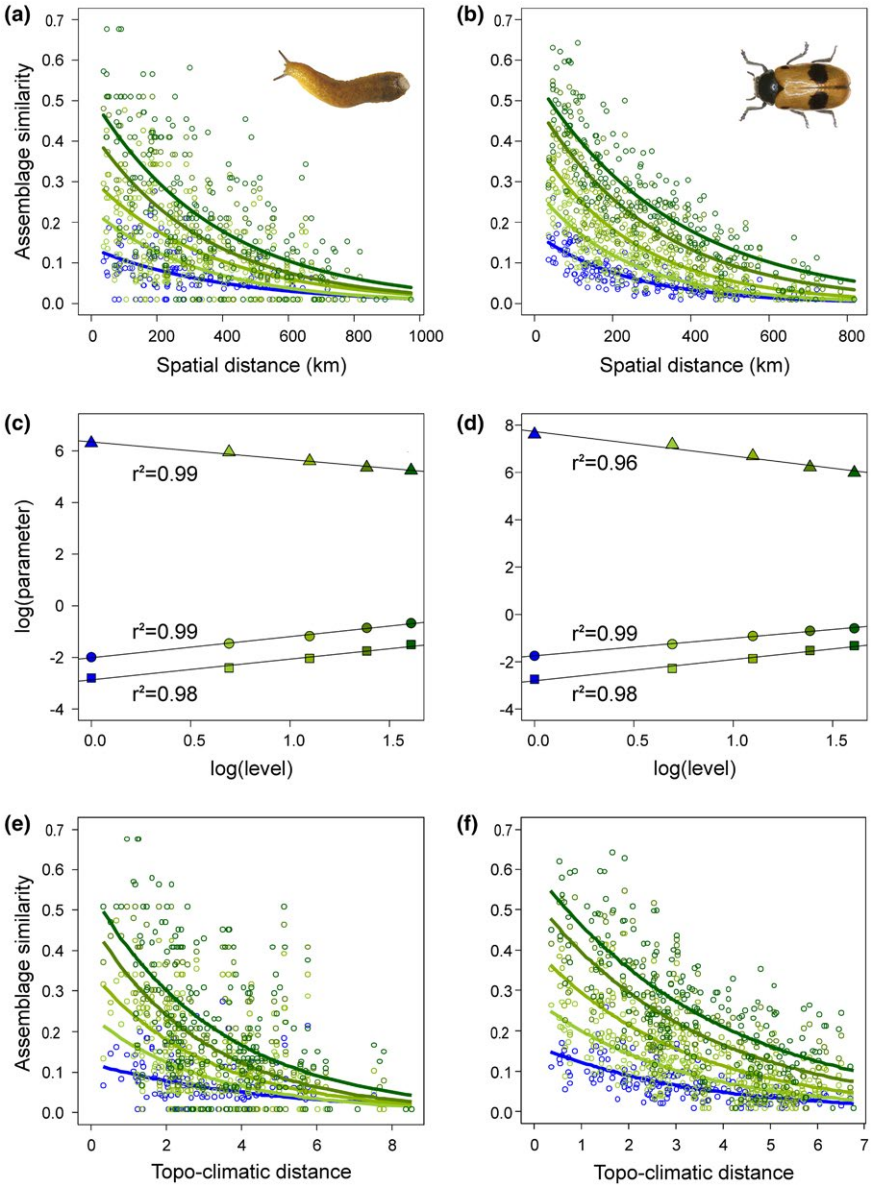

FIGURE 3 Distance decay of assemblage similarity at multiple genealogical levels [haplotype (NC0) and nested clade levels NC1–NC4] in terrestrial molluscs (a) and leaf beetles (b). The relationships between nested clade level and number of lineages (triangles), intercepts (circles) and mean similarity (squares) in terrestrial molluscs (c) and leaf beetles (d) are also shown. The relationship between assemblage similarity and topo-climatic distance at multiple genealogical levels is also shown for terrestrial molluscs (e) and leaf beetles (f). Pictures of a terrestrial mollusc and a leaf beetle were downloaded from Wikimedia Commons (under Creative Commons license, authors Günter Wondrak and Udo Schmidt, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

(r^2 = 0.98, $F_{1,3}$ = 140.5, p = .001). The log–log linear correlations suggest that the patterns of assemblage variation across genealogical levels can be described by a fractal geometry. These log–log relationships were very similar to the ones observed by Baselga et al. (2015) for leaf beetles (see also Figure 3c,d).

The distance-decay relationship showed less scatter and was steeper in leaf beetles (0.74 < r^2 < 0.76; −0.0035 < b < −0.0043; Baselga et al., 2015: table 1) than in terrestrial molluscs (0.25 < r^2 < 0.42; −0.0025 < b < −0.0030) at all genealogical levels from haplotype to NC4 (Table 1; Figure 3; Supporting Information Appendices S9 and S10). Although initial similarity at the haplotype level was similar in terrestrial molluscs and leaf beetles (a = 0.14 in terrestrial molluscs; a = 0.15 in leaf beetles), the initial similarity at the NC4 level (and intermediate levels) was higher in leaf beetles (a = 0.51 at NC4 in terrestrial molluscs; a = 0.62 at NC4 in leaf beetles; Table 1; Baselga et al., 2015: table 1).

Assemblage similarity also decreased with topo-climatic distance at all genealogical levels, from haplotype to OTU (Table 1). However, the fit of exponential decay curves was lower than in the case of spatial distance, with r^2 values ranging from 0.10 (haplotype level) to 0.31 (NC3 level). Importantly, all the variation in assemblage similarity explained by topo-climatic distance was nested in the variation explained by spatial distance (Table 2); that is, the contribution of topo-climatic distance independent of spatial distance was negligible (≤ 1% explained variation at all levels), whereas the contribution

TABLE 1 Relationship between biotic similarity and spatial distance and, independently, topo-climatic distance at multiple genealogical levels (haplotype and nested clade levels NC1–NC4) in terrestrial molluscs

		Spatial distance				Topo-climatic distance			
	Level	*a*	*b*	Pseudo-r^2	*p*	*a*	*b*	Pseudo-r^2	*p*
Haplotype	1	0.14	−0.0025	0.253	<.001	0.12	−0.2203	0.100	.001
NC1	2	0.23	−0.0030	0.354	.002	0.24	−0.3237	0.194	.001
NC2	3	0.31	−0.0027	0.359	.003	0.35	−0.3288	0.245	.001
NC3	4	0.43	−0.0029	0.456	.004	0.47	−0.3349	0.306	.001
NC4	5	0.51	−0.0026	0.419	.005	0.55	−0.2967	0.270	.001

Note. Number of localities = 20. The analysis is based on pairwise Simpson similarity in assemblage composition. *n* is the number of lineages at each genealogical level. Parameters correspond to the model $y = a \times e^{-bx}$, where *y* is similarity and *x* is spatial (or topo-climatic) distance. Coefficients of determination (pseudo-r^2) and *p*-values obtained by Mantel tests are shown.

TABLE 2 Variance partitioning of the distance-decay relationship at multiple genealogical levels (haplotype and nested clade levels NC1–NC4) in terrestrial molluscs

	Total variance	Spatial (unique)	Topo-climatic (unique)	Joint
Haplotype	0.260	0.160	0.007	0.093
NC1	0.354	0.160	0.000	0.194
NC2	0.364	0.119	0.005	0.240
NC3	0.466	0.160	0.010	0.296
NC4	0.430	0.160	0.011	0.259

Note. Similarity in assemblage composition is explained as a function of spatial and topo-climatic distance (total variance). The variance uniquely explained by each predictor (spatial or topo-climatic distance) and the variance jointly explained by both predictors are also shown.

of spatial distance independent of topo-climatic distance was always relevant (≥ 12% explained variation at all levels). Lower r^2 values in topo-climatic distance-decay relationships were also observed in the leaf beetles (Baselga et al., 2015; see details of the scatter of data in Supporting Information Appendix S9 for leaf beetles and in Supporting Information Appendix S10 for terrestrial molluscs).

3.3 | Endemism and range size at the haplotype level and the OTU level

At the haplotype level, endemism was not significantly different between terrestrial molluscs and leaf beetles, with a similar proportion of haplotypes being present in only one locality ("local haplotypes": terrestrial molluscs = 92.1%; leaf beetles = 87.9%; Supporting Information Appendix S2) and a lack of significant differences in the proportion of local haplotypes per locality (repeated-measures ANOVA $F_{1,14} = 2.5$, $p = .139$; Figure 2b,c; Supporting Information Appendix S11). However, the proportion OTUs present in a single locality was significantly higher in terrestrial molluscs ("local OTUs": terrestrial molluscs = 71.2%; leaf beetles = 54.7%), yielding significant differences in the proportion of local OTUs per locality (repeated-measures ANOVA $F_{1,14} = 5.0$, $p = .043$; Figure 2d,e; Supporting Information Appendix S11). The size of the distributional ranges was significantly smaller in terrestrial molluscs, at both the haplotype (Wilcoxon $W = 332{,}760$, $p = .0195$) and the species level (Wilcoxon $W = 25{,}488$, $p = .002555$). Range expansion between the haplotype and the species level was also smaller in terrestrial molluscs [mean range size (haplotype) = 17.0 km; mean range size (OTU) = 88.6 km] than in leaf beetles [mean range size (haplotype) = 25.0 km; mean range size (OTU) = 131.2 km]. Density plots in Figure 4 show the tendency to larger range sizes at deeper phylogenetic levels in leaf beetles compared with terrestrial molluscs (Figure 4a,b). Notwithstanding, the largest ranges were observed in terrestrial molluscs, with a few outlier OTUs occupying most localities. This resulted in a bimodal distribution in the range size of terrestrial molluscs, as can be seen in the density plots per locality (Figure 4e).

4 | DISCUSSION

The integrative assessment of genetic- and species-level variation reveals concordance in the diversity patterns of terrestrial molluscs and leaf beetles in the Iberian Peninsula. This pattern of concordance would be overlooked in standard diversity analyses at only one of the levels; that is, species richness, distance decay of assemblage similarity (beta diversity) or local average genetic diversity. Local species richness and average genetic diversity were not only lower in terrestrial molluscs, but they were also not correlated with those of leaf beetles. Likewise, the slopes of the distance-decay curves were different, with terrestrial molluscs showing a slower decrease in assemblage similarity with spatial distance. However, a multi-hierarchical approach (Baselga et al., 2013, 2015) provided evidence that, in both groups, distance-decay patterns across phylogenetic scales were fractal (i.e.,

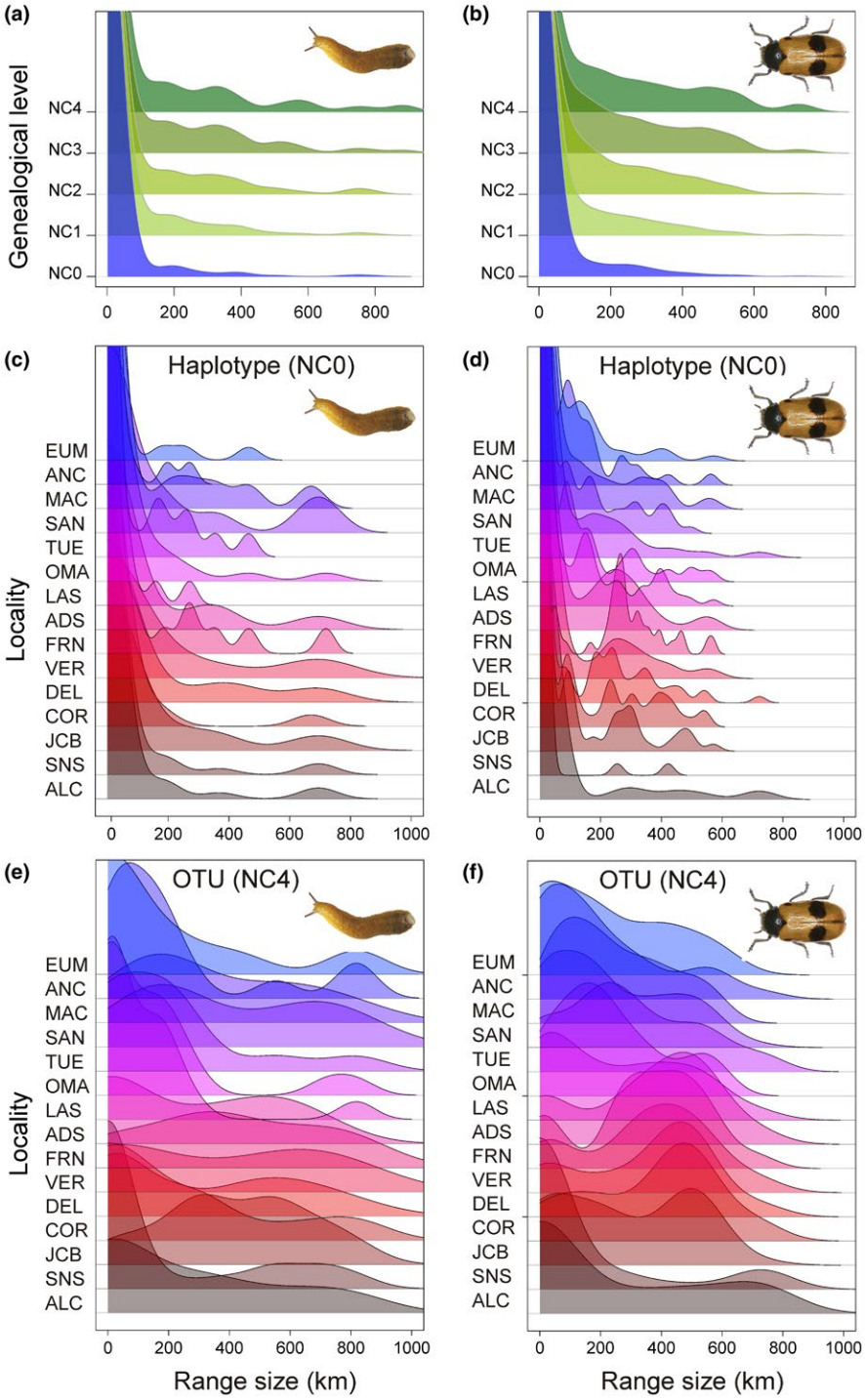

FIGURE 4 Density plots of range size in terrestrial molluscs (a) and leaf beetles (b) at multiple genealogical levels (haplotype [NC0] and nested clade levels NC1–NC4). Density plots of range size distribution in each locality are also shown for the haplotype (c, d) and species [OTU] (e, f) level, for both terrestrial molluscs (c, e) and leaf beetles (d, f). Localities are ordered following a latitudinal gradient. Pictures of a terrestrial mollusc and a leaf beetle were downloaded from Wikimedia Commons (under Creative Commons license, authors Günter Wondrak and Udo Schmidt, respectively) [Colour figure can be viewed at wileyonlinelibrary.com]

similar slopes and regular increase of intercepts, from haplotype to species level). This result shows that assemblage similarity at any given spatial distance regularly decreases from the species to the haplotype level, but the rate at which assemblages become dissimilar with spatial distance does not change with phylogenetic scale. Fractality in beta-diversity patterns has been attributed to a preponderance of dispersal processes (Baselga et al., 2013, 2015) and, thus, contradicts our initial hypothesis of terrestrial mollusc assemblages being controlled mostly by niche factors. In fact, the analysis of range size and endemism at both the haplotype and species levels suggests that dispersal limitation is stronger in terrestrial molluscs. First, range size is smaller in terrestrial molluscs

than in leaf beetles at both the haplotype and species levels. Second, and more remarkably, terrestrial molluscs show higher endemism at the species level, but not at the haplotype level, a result in accordance with range expansion in the long term being more restricted in this taxon. Taken altogether, here we show that some of the differences observed in the diversity patterns of Iberian terrestrial molluscs and leaf beetles could be interpreted not as the result of different macroecological processes, but as the consequence of the same process (dispersal) taking place with different strength in each taxon.

In general terms, whereas most studies have focused on how diversity patterns change with phylogenetic scale above the species level (Graham et al., 2018), here we show that diversity patterns below the species level might allow the identification of properties that unify biological systems that would otherwise seem heterogeneous. Moreover, complementing the analysis of distance-decay patterns, as initially proposed in the multi-hierarchical approach (Baselga et al., 2013, 2015), with the analysis of endemism and range size aids the interpretation of the fractal pattern by providing insight about the strength of dispersal processes.

The analysis of the parameters defining the distance-decay curve can also provide information about the strength of the processes driving the variation in assemblage composition (Gómez-Rodríguez & Baselga, 2018). Thus, leaf beetles would have less dispersal ability than terrestrial molluscs, given the steeper distance-decay curves for the leaf beetles at all genealogical levels. This result contradicts the classical view of low active dispersal of terrestrial molluscs (Cameron, 2013) and the results discussed above, but could be explained by the bias introduced by a few mollusc species with very large distributional ranges (such as *Limacus flavus*, *Helix aspersa*, *Lehmannia marginata* or *Deroceras reticulatum*). The high apparent dispersal ability of these species causes a bimodal range size distribution in the data and is probably associated with passive migration by human activities, as has been reported for other terrestrial molluscs (e.g., Aubry et al., 2006). In fact, when these species are removed from the distance-decay analyses, the slope value increases [e.g., slope at species level (NC4) = −0.0078; for details, see Supporting Information Appendix S12], a result in accordance with the lower dispersal ability of most terrestrial molluscs. Besides, distance-decay curves are defined by two parameters (intercept and slope) that should be interpreted together (Gómez-Rodríguez & Baselga, 2018; Morlon et al., 2008). Thus, although small slopes in the distance-decay curve of terrestrial molluscs would suggest a notable proportion of species with high dispersal ability, the lower intercept (i.e., initial similarity) would still suggest that most species are poorly mobile because, at short distances, strong dispersal limitation is more evident.

Another apparently contradictory result of the present study is that distance-decay results suggest the relevance of dispersal processes (i.e., fractality and stronger relationship with spatial distance than with climatic distance), but we do not find the analogous SGDC. In general, a strong positive SGDC is expected when genetic diversity is measured with a neutral molecular marker and when non-selective factors, such as the size and isolation of sampling units, exert a particularly strong influence on diversity patterns (Kahilainen et al., 2014; Vellend et al., 2014). However, previous studies have also shown that any SGDC, including non-significant results, can be compatible with systems dominated by processes such as dispersal and drift (Laroche, Jarne, Lamy, David, & Massol, 2015). In addition, we should not discard methodological limitations inherent to our data, such as the sample size (i.e., 20 localities), which might affect the strength of correlations, or the fact that our sampling localities are not discrete habitat patches (Vellend et al., 2014). Another potential methodological bias might be introduced with the choice of the focal species (Lamy, Laroche, David, Massol, & Jarne, 2017), although we have also found the same lack of positive correlation when measuring genetic diversity in multiple species (as done by Taberlet et al., 2012). In general, it is assumed that the processes affecting the most abundant species might not be representative of the full community and that differences in dispersal ability or ecological responses among species are also likely to affect the SGDC measures (Lamy et al., 2017; Vellend et al., 2014). Thus, a lack of SGDC does not imply that dispersal processes are not important in an ecological system.

Although our results are consistent with dispersal being an important diversity driver in both Iberian molluscs and leaf beetles, species assemblages are the result of multiple processes (i.e., evolutionary dynamics and niche constraints, among others) that hierarchically filter coexisting species in a local community from the regional pool of species (Ricklefs, 2004). We reckon that niche processes are likely to be relevant in the system too, although we have found that the relationship between assemblage similarity and topo-climatic distance was completely derived from its covariation with spatial distance. However, climatic niches do not represent all the environmental dimensions relevant to these species (e.g., local environmental heterogeneity and competition, among others) and, in fact, the larger unexplained variance in the distance-decay curves of terrestrial molluscs suggests the influence of non-spatial processes. Moreover, species richness was correlated with elevation in terrestrial molluscs and with latitude in leaf beetles, and these variables could be associated with ecological limits of the species, although they can be also attributed to historical processes independent of niche filtering (e.g., recolonization of northern regions from southern glacial refugia, in the case of leaf beetles, and valleys acting as glacial refugia, in the case of terrestrial molluscs). A strong effect of multiple glacial refugia and slow recolonization has been proposed to explain the strong geographical structure of genetic diversity in terrestrial molluscs (Dépraz, Cordellier, Hausser, & Pfenninger, 2008; Quinteiro, Rodríguez-Castro, Castillejo, Iglesias-Piñeiro, & Rey-Méndez, 2005), and the Iberian Peninsula is thought to have harboured multiple refugia at very small scales (Gómez & Lunt, 2007).

To conclude, the integrative assessment of multiple macroecological patterns at different phylogenetic scales can shed light on the identity and strength of processes driving diversity patterns. In our biological system, the assessment of how diversity patterns change at different phylogenetic scales below the species level allows the unification of seemingly heterogeneous diversity patterns as the result of a single process acting at different speeds (literally dispersal velocity).

For this reason, new studies across multiple systems and types of organisms are needed to assess the cross-taxon variation (or regularities) in diversity, range size and other macroecological patterns below species level. Such analyses are currently demanding in terms of time and cost, although Next-Generation Sequencing (NGS) approaches, such as mito-metagenomics, offer great promise for diversity assessments, even below species level (Gómez-Rodríguez, Crampton-Platt, Timmermans, Baselga, & Vogler, 2015; Gómez-Rodríguez, Timmermans, Crampton-Platt, & Vogler, 2017). The final goal would be the integration of phylogenetic and macroecological information into a single analysis to assess the spatio-temporal (ecological and evolutionary) continuum behind present biodiversity patterns.

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DATA ACCESIBILITY

Beetle DNA sequences in Baselga et al. (2015) are available under GenBank accession numbers KF134544–KF134651 and KF652242–KF656666. DNA sequences of terrestrial molluscs provided in this study are available under GenBank accession numbers MF981937–MF983528.

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