

# ECOGRAPHY

## Research

### Variation among European beetle taxa in patterns of distance decay of similarity suggests a major role of dispersal processes

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The decay of assemblage similarity with spatial distance can be explained by alternative mechanisms: dispersal limitation and species sorting. To understand their relative contributions, we compare the decay in faunal similarity with spatial distance and, independently, with climatic distance, of 21 beetle taxa with varying dispersal abilities and ecological niches, in southern and northern Europe. Similarity in beetle faunas was associated to spatial but not to climatic distances, pointing to the preponderance of dispersal processes rather than niche constraints. In most taxa, southern faunas were more dissimilar than northern ones: smaller initial similarity and steeper distance decay rate. Distance decay patterns in the north were relatively flat and very similar across taxa, suggesting that only good dispersers would have reached those latitudes after the glacial retreat. The difference in distance decay patterns between north and south is correlated with the taxon's slope of the distance decay pattern in the south and with its latitudinal richness difference. That is, in taxa with distance decay patterns similarly flat in the south and the north, the latitudinal richness gradient is weak. This correlation points again to differences in dispersal ability as a major determinant of biogeographic patterns in European beetles. Both dispersal and niche-related characteristics explained north-south slope differences, but dispersal attributes turned out to be more relevant when initial similarity and distance decay strength were considered together. Our results show that, to understand diversity patterns in Europe, closely related biological groups cannot be assumed to be surrogates and regions with different historical biogeography should be analysed separately. Paradoxically, the study of beetle faunas of southern Europe will shed light on the processes controlling the recolonization of northern latitudes.

Keywords: Coleoptera, Beta diversity, latitudinal richness gradient

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#### Introduction

The negative relationship between assemblage similarity and spatial distance (i.e. distance decay of similarity) is a general macroecological pattern (Nekola and White 1999) that has been studied across a wide range of organisms, geographic gradients



and environments (Poulin 2003, Qian and Ricklefs 2007, Soininen et al. 2007). Because of its ubiquity, it has been considered a central property of biological assemblages (Morton et al. 2008) but its causes cannot be easily disentangled because the decay of similarity with spatial distance is predicted by alternative theories invoking completely different mechanisms (Nekola and White 1999, Condit et al. 2002, Tuomisto et al. 2003). Despite some secondary variants, the major candidate mechanisms are dispersal limitation and species sorting (i.e. selection of species by their ecological niches). In the first case, the decay of assemblage similarity with spatial distance would just reflect the decrease in the probability of species reaching distant localities because of their limited dispersal ability. As a consequence, the more distant two assemblages are, the less probable is that species are present in both assemblages, so the lower the similarity between those assemblages. In the second case, the decay of assemblage similarity with spatial distance would be a secondary outcome derived from the spatial autocorrelation of environmental conditions, resulting in closer localities having more similar climates, soils, and other environmental variables. Thus, the environment would select species based on their respective ecological niches, and this would make assemblages more dissimilar when environmental conditions are more different. That is, closer localities would usually have more similar environmental conditions and a negative relationship between assemblage similarity and spatial distance would arise. The relative relevance of both alternatives (dispersal vs niche processes) has been assessed multiple times by measuring how well spatial and environmental distances explain assemblage dissimilarity (Genner et al. 2004, Qian et al. 2005, Baselga and Leprieur 2015). However, empirical tests are rarely conclusive because environmental and spatial distances are inherently correlated (Tuomisto et al. 2003). To move forward, we here propose that comparing distance decay patterns across taxa with varying dispersal abilities and/or different ecological niches can shed light on the processes controlling the decay of assemblage dissimilarity with spatial distance.

Some previous studies have followed a trait-based approach in the analysis of diversity patterns, usually encompassing a wide variety of organisms (Soininen et al. 2007, Fitzpatrick et al. 2013). However, inherent limitations to this approach arise because organism type largely influences the distance decay relationship (Soininen et al. 2007), making it difficult to compare studies directly unless biological characteristics are comparable. Besides, the dependence of the distance decay relationship on the geographic position and extent of the study area (Soininen et al. 2007, Steinbauer et al. 2012) also complicates the trait-based comparative approach. A way forward would be to focus on a biogeographical region and gather distributional data for multiple taxa with varying dispersal abilities and ecological niches, as first introduced by Nekola and White (1999) in their seminal paper and later by De Bie et al. (2012) at a metacommunity scale. However, quantifying dispersal ability and ecological niche for multiple species belonging to multiple biological groups is far from

trivial, because direct measures are rarely available. Alternatively, we can measure morphological characteristics related to dispersal ability (such as the presence of wings or the body size, Roff 1977, Roslin 2000, Ikeda et al. 2012) or ecological niche (such as the main habitat or the trophic position of the species). These traits provide a currency that we can use as a surrogate of dispersal ability and ecological niche, but this will work only if the different taxa share a common currency. For example, body size is tightly related to dispersal ability but the relationship is not linear across the full spectrum of body sizes (Martiny et al. 2006). Beetles offer a good opportunity to conduct such a comparative study, as their enormous diversity includes many different taxa (families, subfamilies, genera) with comparable sizes and physiologies but still with enough variation in dispersal ability and ecological niches.

Previous papers comparing diversity patterns of multiple European beetle taxa have shown that 1) dispersal ability is a good predictor of the slope of the latitudinal richness gradient (Baselga et al. 2012b) and 2) dispersal ability and ecological niche are both related to the variation in total heterogeneity and pairwise dissimilarity patterns among territories (Gómez-Rodríguez et al. 2015). In turn, no previous attempts have been done to systematically assess the variation in the patterns of distance decay of similarity among multiple beetle taxa. Some fragmentary data involving very few taxa (Baselga 2007, 2008, Fattorini and Baselga 2012, Freijeiro and Baselga 2016) suggest that 1) distance decay patterns may vary across beetle taxa, 2) decay patterns are usually steeper in southern than in northern Europe and 3) the degree to which the decay rate differs between northern and southern Europe may not be the same in all beetle groups. In this study we assess the cross-taxon variation in distance decay patterns in European beetles, testing the following hypotheses: 1) the distance decay patterns are steeper in southern than in northern Europe because northern faunas are the result of a post-glacial re-colonization process. In other words, the species that have reached northern latitudes are the good dispersers. 2) The latitudinal difference in species richness is related to the north vs south difference in the distance decay pattern because both differences would be associated to post-glacial recolonization process. 3) The difference between distance decay patterns in northern and southern Europe is associated to the dispersal and ecological characteristics of taxa.

## Material and methods

### Data

Our dataset includes presence/absence tables for 21 beetle supra-specific taxa (large genera, tribes, subfamilies or families; 4648 species in total) in 34 European territories (extent: 11°W, 60°E longitude and 36°–72°N latitude). The bulk of this dataset was already described in Baselga et al. (2012b) and Gómez-Rodríguez et al. (2015), to which we

have currently added two new taxa, Cryptocephalinae and Chrysomelinae (Freijeiro and Baselga 2016). The 21 taxa are representative of the major beetle lineages (superfamilies Caraboidea, Staphylinoidea, Scarabaeoidea, Chrysomeloidea and Curculionoidea) and include a wide spectrum of ecological strategies and dispersal abilities. Presence/absence tables were compiled from Löbl and Smetana (2003, 2004, 2006) and the Fauna Europaea Web Service (Fauna Europaea ver. 1.1, <www.faunaeur.org>). Territories generally correspond to European countries but all islands and the smallest countries (<2000 km<sup>2</sup>, i.e. Andorra, Liechtenstein, San Marino, Monaco and Vatican City) were excluded to avoid extreme differences in area and biogeographical patterns linked to insularity. Additionally, Croatia and Bosnia-Herzegovina were pooled into a single unit because the former surrounds the latter, and European Russia was split in three units [north, central and south] given its extremely large area. Luxembourg and Moldova were excluded from the analyses due to the absence of some taxa, which poses problems for faunal dissimilarity computing and statistical comparison with the other territories. For the same reason two taxa included in a previous paper (Baselga et al. 2012b), Baridinae and Nanophyidae, were not considered in this study (absent in Albania, Slovenia and Macedonia). The final dataset comprises the following taxa: *Amara*, Apionidae, *Carabus*, Cerambycinae, *Chaetocnema*, Chrysomelinae, Cryptocephalinae, Hydraenini, Lamiinae, Lepturinae, Limnebiini, Ochthebiini, *Otiorhynchus*, Phyllobiini, Polydrusini, Pselaphinae, *Pterostichus*, Scarabaeidae, Scolytinae, Silphidae, and *Trechus*.

Taxa were classified according to their main habitat (epiedaphic, edaphic, aquatic and epiphytic) and trophic specialization (coprophagous, zoophagous, xylophagous, phytophagous) following Baselga et al. (2012b). As proxies of dispersal ability, the proportion of apterous species and species mean size were also obtained from Baselga et al. (2012b) or compiled from taxonomic monographs in the case of Cryptocephalinae and Chrysomelinae (Doguet 1994, Petitpierre 2000, Warchalowski 2003, Konstantinov et al. 2011). Details are provided in Gómez-Rodríguez et al. (2015: Table 1). Both ecological classification and dispersal ability proxies are coarse characterizations of taxon's niche and dispersal attributes. These proxies are not expected to capture all the niche and dispersal processes controlling European beetle distributions. However, as argued elsewhere (Baselga et al. 2012b, Gómez-Rodríguez et al. 2015), more detailed information on species niches and dispersal abilities is lacking and the surrogates we use should be able to account for the major macroecological patterns.

## Statistical analyses

For each taxon, two presence/absence tables were built: one for northern Europe (territories with centroids at > 48 degrees, n = 18) and one for southern Europe (territories with centroids at < 48 degrees, n = 16). Each of these presence/absence tables was used to compute the similarity between pairs of territories using the Simpson's similarity index

$(1 - \beta_{sim} = a/[a + \min(b,c)])$  in R package 'betapart' (Baselga and Orme 2012), where  $a$  is the number of species present in both territories, and  $b$  and  $c$  the number of species unique to one or another, respectively. The spatial distance between pairs of territories was also computed as the Euclidean distance between territories' centroids. Then, for each taxon and region (i.e. southern or northern Europe) the relationship between faunal pairwise similarity and spatial distance was assessed by fitting negative exponential and power-law functions describing the decay in faunal similarity with spatial distance (Nekola and White 1999, Nekola and McGill 2014). To do this, we used the function 'decay.model' (Supplementary material Appendix 1, to be included in R package 'betapart'), which adjusts a GLM with similarity as response variable, spatial distance as predictor, log link and Gaussian error, maintaining untransformed the spatial distances for the exponential decay model or log-transformed for the power-law model. The goodness of fit of these decay models was computed as  $\text{pseudo-}r^2 = 1 - \text{model deviance}/\text{null deviance}$ , and the significance of the relationship by randomizing spatial distances 1000 times and computing the proportion of times in which the model deviance was smaller than the randomized model deviance. Theory suggests that the negative exponential model should better describe distance decay patterns at large spatial scales (Nekola and McGill 2014), as the one we are studying. We empirically tested this assumption by assessing whether the negative exponential or power-law models best fitted our data for northern and southern Europe, comparing the respective AIC values. As expected, the exponential decay model consistently fitted the data best, with lower AIC values than the power law model in 35 out of 42 cases (21 taxa, two regions) and when it was higher,  $\Delta\text{AIC}$  was > 2 in only two cases. Therefore, we selected the negative exponential model and fitted, for each taxon, two negative exponential decay curves for northern and southern Europe, respectively, each described by two parameters (intercept  $a$  and slope  $b$ ). We will refer to these curves as northern and southern distance decay patterns throughout the paper. To assess whether intercepts and slopes differ between northern and southern distance decay patterns, we bootstrapped the parameters (1000 replicates) using the function 'boot.coefs.decay' (Supplementary material Appendix 1, to be included in R package 'betapart'), and then computed the p values as the proportion of times in which the bootstrapped parameters were larger (or smaller) in one of the regions. The scatter plots of assemblage similarity against spatial distance and the distance decay curves were plotted using the function 'plot.decay' (Supplementary material Appendix 1, to be included in R package 'betapart').

We tested whether variation across taxa in the difference between northern slope and southern slope ( $\Delta b$ ) was associated to the slope value in the south or, alternative, with those in the north, using linear regression models. Similarly, a linear regression model was used to assess whether such difference ( $\Delta b$ ) was related to the magnitude of the latitudinal richness gradient. The magnitude of the latitudinal richness gradient was simply measured as the standardized difference between

total number of species in southern Europe ( $S_s$ ) and the total number of species in northern Europe ( $S_n$ ), as  $(S_s - S_n) / (S_s + S_n)$ .

To assess whether the magnitude of the difference between northern and southern distance decay patterns was associated to the taxon's dispersal ability and/or its ecological niche, we built two models. The first model regressed the difference in slope between northern and southern distance decay patterns ( $\Delta b$ ) against two dispersal-related characteristics (proportion of apterous species and mean body size) and two niche characteristics (trophic position and main habitat). To avoid redundant predictors, for each set (dispersal or niche) we selected the variables with a forward stepwise procedure based on the  $F$  statistic to test whether the addition of variables significantly increased the explained variance. In the second model, the dependent variable was the absolute value of the product between differences in slope and intercepts ( $\text{abs}[\Delta b \times \Delta a]$ , thereafter referred as decay-difference index), in order to integrate the differences in slope and intercept into a single index. The initial predictors of this second model were the same as described above. To evaluate the relevance of dispersal-related and niche-related hypotheses, variance partitioning was used to separate the fractions of variation uniquely and jointly explained by each set of predictors (dispersal vs niche hypothesis). Given that the different taxonomic resolution (genus, tribe, subfamily or family) among cases might bias the results, we assessed whether there were significant differences in slope difference or in distance-decay index (dependent variables) among taxonomic ranks using an ANOVA with an ordered factor (1 = genus, 2 = tribe, 3 = subfamily, and 4 = family).

To assess whether the observed relationships are influenced by climatic gradients via species' niche constraints, we replicated the analyses using climatic differences instead of spatial

distances between countries. We computed climatic distances by extracting the mean values of 5 bioclimatic variables for each country from Worldclim (Hijmans et al. 2005): mean annual temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual precipitation (Bio12) and precipitation of the driest quarter (Bio17). Those variables were submitted to a Multidimensional Scaling (function `metaMDS` in `vegan`, Oksanen et al. 2017) with Euclidean distance and 2 dimensions, in order to summarise the climatic variation across countries into two independent variables (which accounted for 97% of the variation). The climatic distance between countries was computed as the Euclidean distance between the countries' scores in the multidimensional scaling. We then 1) fitted exponential decay models for northern and southern Europe describing how assemblage similarity decreases as a function of climatic distance (climatic decay patterns), 2) assessed whether the variation across taxa in climatic  $\Delta b$  was associated to values in northern and southern Europe, and differences in richness, and 3) analysed whether north-south differences in climatic decay patterns were associated to dispersal and/or niche characteristics of taxa. All these analyses were conducted as exact replicates of the spatial analyses, just using the climatic decay patterns.

## Results

The negative exponential model significantly explained the decay in similarity with spatial distance ( $p < 0.001$ ) in most taxa both in southern and northern Europe (Fig. 1), with exception of Scolytinae in the south ( $p = 0.227$ ), and Hydraenini, Limnebiini and Scarabaeinae in the north

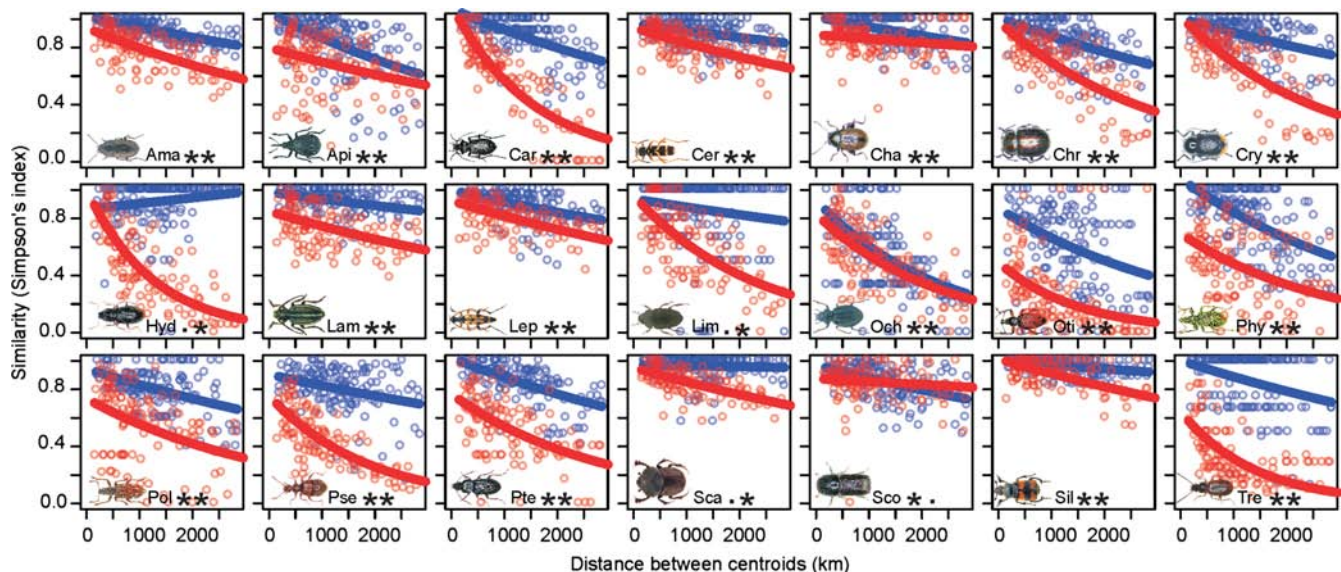


Figure 1. Patterns of decay of similarity with spatial distance in 21 beetle taxa (abbreviations are the first three letters of their names) in northern (blue) and southern Europe (red). Dots represent pairs of European territories and lines are the fitted negative exponential functions. The significance of the relationship (\* for  $p < 0.05$ , • for  $p \geq 0.05$ ) is marked for the north and south of Europe, respectively. Beetle pictures were downloaded from Wikimedia Commons (under Creative Commons licence, author udo Schmidf).

( $p = 0.059$ ,  $p = 0.104$  and  $p = 0.574$ , respectively). The fit of the exponential decay model was better in the south (mean pseudo- $r^2 = 0.36$ ,  $SD = 0.21$ ) than in the north (mean pseudo- $r^2 = 0.19$ ,  $SD = 0.12$ ) of Europe (repeated measures ANOVA  $F_{1,20} = 10.21$ ,  $p = 0.005$ ). The mean slope was significantly steeper in southern than in northern Europe (mean =  $-3.2e-4$ ,  $SD = 2.4e-4$  vs mean =  $-1.1e-4$ ,  $SD = 1.0e-4$ ), respectively, repeated measures ANOVA  $F_{1,20} = 16.39$ ,  $p < 0.001$ ) and mean intercept was significantly lower in southern than in northern Europe 0.87 (mean;  $SD = 0.15$ ) vs 0.98 (mean;  $SD = 0.06$ ), respectively, repeated measures ANOVA  $F_{1,20} = 13.46$ ,  $p = 0.0015$ ). Besides these significant differences in mean parameter values for the full dataset, when the bootstrapped distributions of parameters were compared for each taxon, it turned out that slopes were significantly ( $p < 0.05$ ) steeper in the south in 16 out of 21 taxa, and intercepts were significantly lower in the south in 12 out of 21 taxa (Fig. 2).

Slopes and intercepts of the distance decay curves were very similar across taxa in the north (Fig. 2), resulting in small standard deviations in the data (slope:  $SD = 1.0e-4$ ; intercept:  $SD = 0.06$ ), while the variability in parameter values was higher in the south (slope:  $SD = 2.4e-4$ ; intercept:  $SD = 0.10$ ). As a result, the difference between southern and northern slopes ( $\Delta b$ ) was related to the value of the slope in the south ( $r^2 = 0.82$ ,  $F_{1,19} = 89.04$ ,  $p < 0.001$ ) but not to

the value of the slope in the north ( $r^2 = 0.05$ ,  $F_{1,19} = 0.944$ ,  $p = 0.344$ ). The same is observed for the difference in intercept values ( $\Delta a$  vs south:  $r^2 = 0.85$ ,  $F_{1,19} = 109.5$ ,  $p < 0.001$ ,  $\Delta a$  vs north:  $r^2 = 0.03$ ,  $F_{1,19} = 0.530$ ,  $p = 0.476$ ). The difference in slope was also significantly related to the standardized difference in species richness between northern and southern Europe ( $r^2 = 0.31$ ,  $F_{1,19} = 8.688$ ,  $p = 0.008$ ). The strength of the richness gradient for each taxon is shown in Fig. 3.

When we assessed which taxon's characteristics explained the difference in slope between northern and southern Europe ( $\Delta b$ ), we found that only the proportion of apterous species ( $r^2 = 0.20$ ,  $F_{1,19} = 4.717$ ,  $p = 0.043$ ) and habitat ( $r^2 = 0.42$ ,  $F_{3,17} = 4.247$ ,  $p = 0.021$ ) were selected in their respective explanatory sets. The joint model explained more than half of the variance in  $\Delta b$  ( $r^2 = 0.55$ ,  $F_{3,17} = 4.819$ ,  $p = 0.010$ ), implying that only 7% of the variance was jointly explained by both variables, while 13 and 25% was uniquely explained by the proportion of apterous species and habitat, respectively. In the model for the decay-difference index, both the proportion of apterous species and body size were retained in the dispersal set ( $r^2 = 0.61$ ,  $F_{2,18} = 14.13$ ,  $p < 0.001$ ) and only habitat in the ecological niche set ( $r^2 = 0.42$ ,  $F_{3,17} = 4.084$ ,  $p = 0.023$ ). The joint model explained two thirds of the variance in the decay-difference index ( $r^2 = 0.67$ ,  $F_{5,15} = 6.147$ ,  $p = 0.003$ ), implying that 25% of the variance was uniquely explained by the

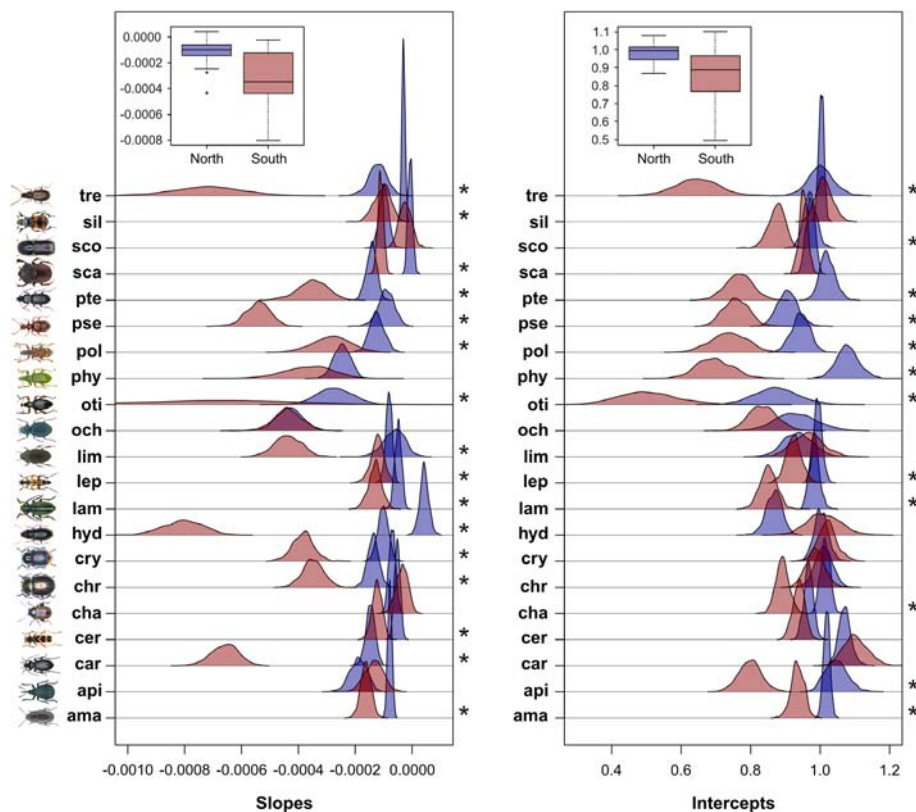


Figure 2. Bootstrapped distributions of the parameters describing the distance decay patterns for 21 European taxa (y-axes) in northern (blue) and southern Europe (red). The inset represents the distribution across taxa of mean parameter values. Significant differences between northern and southern parameters are marked with \* ( $p < 0.05$ ).

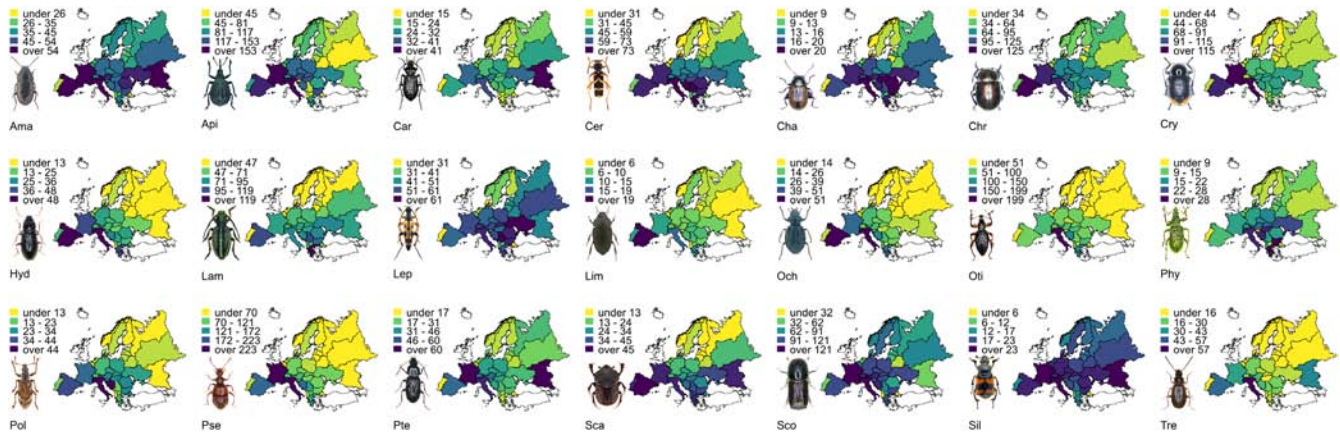


Figure 3. Maps representing the species richness for each taxon in each European territory.

dispersal-related variables, 36% of the variance was jointly explained by both sets, and 6% of the variance was uniquely explained by the taxon's main habitat. The taxonomic rank (i.e. genus, tribe, subfamily and family) does not drive these results as we have not observed Polydrusini differences in the slope difference (ANOVA  $F_{3,17} = 1.1$ ,  $p = 0.366$ ) or in the distance-decay index (ANOVA  $F_{3,17} = 1.7$ ,  $p = 0.212$ ) among taxonomic ranks.

When we analysed climatic decay patterns instead (Fig. 4), it turned out that similarity was significantly related to climatic distance in very few cases: Cerambycinae, Laminae, Lepturinae and Scarabaeidae in northern Europe (mean pseudo- $r^2 = 0.02$ ,  $SD = 0.02$ ), and Polydrusini in southern Europe (mean pseudo- $r^2 = 0.009$ ,  $SD = 0.01$ ). The mean climatic slope was not steeper in southern than in northern Europe. In fact, it was negative in northern Europe and

positive in southern Europe (i.e. similarity increased with climatic distance), a difference that was significant (repeated measures ANOVA  $F_{1,20} = 11.16$ ,  $p = 0.003$ ). The mean climatic intercept was significantly lower in southern than in northern Europe (repeated measures ANOVA  $F_{1,20} = 44.17$ ,  $p < 0.001$ ). The bootstrapped distributions shown that slopes were significantly different ( $p < 0.05$ ) between south and north in only 5 out of 21 taxa (and in all cases slope was steeper in the north), and intercepts were significantly lower in the south in 19 out of 21 taxa (Fig. 5). Differences in climatic slopes were both related to northern ( $\Delta b$  vs north  $b$ :  $r^2 = 0.32$ ,  $F_{1,19} = 9.092$ ,  $p = 0.007$ ) and southern ( $\Delta b$  vs south  $b$ :  $r^2 = 0.25$ ,  $F_{1,19} = 6.191$ ,  $p = 0.022$ ) slope values, and not related to the standardized difference in species richness between northern and southern Europe ( $r^2 = 0.10$ ,  $F_{1,19} = 2.207$ ,  $p = 0.153$ ). Neither the difference in climatic

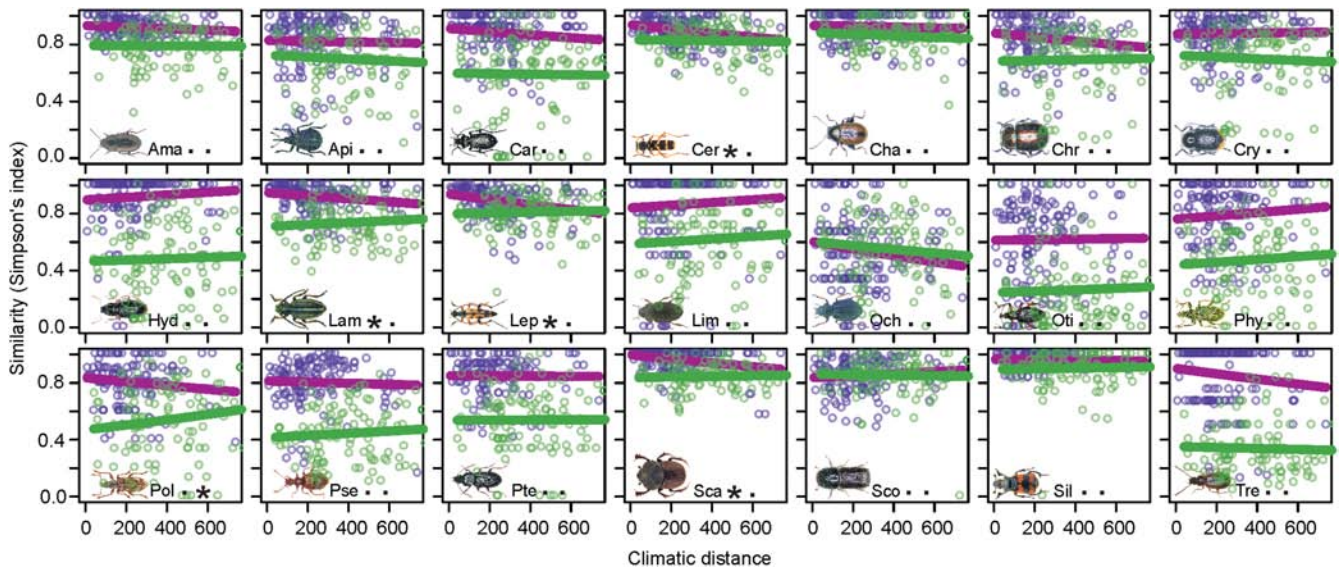


Figure 4. Patterns of decay of similarity with climatic distance in 21 beetle taxa (abbreviations are the first three letters of their names) in northern (purple) and southern Europe (green). Dots represent pairs of European territories and lines are the fitted negative exponential functions. The significance of the relationship (\*for  $p < 0.05$ , for  $p \geq 0.05$ ) is marked for the north and south of Europe, respectively.

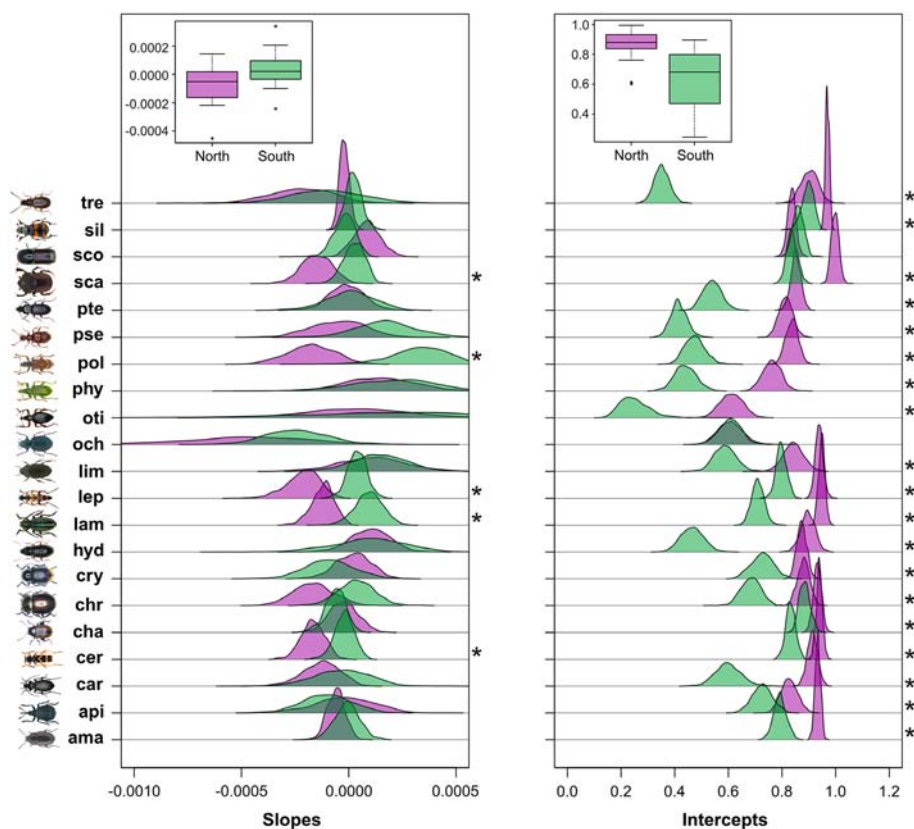


Figure 5. Bootstrapped distributions of the parameters describing the pattern of decay of similarity with climatic distance for 21 European taxa (y-axes) in northern (purple) and southern Europe (green). The inset represents the distribution across taxa of mean parameter values. Significant differences between northern and southern parameters are marked with \*( $p < 0.05$ ).

slope between northern and southern Europe ( $\Delta b$ ) nor the climatic decay-difference index were significantly related to any of the dispersal or niche attributes tested.

## Discussion

Similarity in beetle faunas among European countries was associated to spatial but not climatic distances, pointing to the preponderance of dispersal processes rather than niche constraints in driving beetle diversity patterns in Europe. The decay of similarity with spatial distance was markedly different in the south and north of Europe. Beetle faunas were more dissimilar in the south, with lower similarity at the closest territories (or initial similarity, described by the intercept of the decay pattern) and a higher rate at which assemblage similarity decreases with distance (described by the slope of the decay pattern). Flatter distance decay curves in the north are in agreement with previous studies showing a general decrease in species turnover with latitude (Qian and Ricklefs 2007, Baselga et al. 2012a, Qian and Ricklefs 2012, Castro-Insua et al. 2016, but see Soininen et al. 2007). When the cross-taxon variation of distance decay patterns was assessed, we found that distance decay patterns were relatively similar across taxa in northern Europe, while large differences were observed in the south. A lack of concordance

in distance decay patterns may seem surprising given that most studies on European beetles report similar latitudinal diversity correlations with climatic gradients (Baselga 2008, Schuldt and Assmann 2009, 2011a, b, Fattorini and Baselga 2012, Freijeiro and Baselga 2016). However, broadly coincident patterns may have completely different strengths, with some beetle groups showing strong latitudinal diversity gradients while others would differ little between north and south. Our results show that, in the goal of understanding diversity patterns in Europe, closely related biological groups cannot be assumed to be surrogates, regions with different historical biogeography should be analysed separately and further aspects of diversity, such as the spatial turnover in species (beta diversity), be considered.

The small variability observed across taxa in their northern distance decay patterns (i.e. flat decays in all cases) suggests that these beetle assemblages are composed of species with similar characteristics (good dispersers), irrespective to the taxon to which they belong. This inference is based on the fact that the steepness of the distance decay curve can be interpreted in terms of dispersal ability (Qian 2009, Wetzel et al. 2012, Saito et al. 2015) and this would be particularly true in systems in which similarity between faunas is not related to climatic distance, like ours. In turn, the marked heterogeneity in southern decay patterns (flat vs steep decays) implies that assemblages of different taxa are composed of

species with different characteristics (good vs weak dispersers). Moreover, as some particular taxa show marked differences between their northern and southern distance decay patterns, we can infer that the characteristics of the species that live in the north are different to the ones in the south of Europe. In other words, in those taxa, the northern fauna would be dominated by good dispersers while the southern fauna would be mostly composed of weak dispersers. This would be in agreement with the well documented imprint of Pleistocene glaciations in the biota of the European continent, where species living at high latitudes have recolonized those territories from glacial refugia in the south (Hewitt 1999, 2004, 2011, Svenning and Skov 2007, Svenning et al. 2015). Notably, we have observed that the north vs south difference in distance decay patterns is almost exclusively explained by the distance decay pattern in the south and, more importantly, it is related to the latitudinal richness gradient. Thus, when the distance decay in the south of Europe is flat (as in the north), the latitudinal richness gradient is weak, but when the distance decay is steep (contrary to the north), the richness gradient is strong.

Taking altogether, our results are thus consistent with the view that the European beetle fauna still shows the effects of an incomplete re-colonization process after the Pleistocene glaciations due to dispersal limitation (Baselga 2008, Schuldt and Assmann 2009, 2011b, Schuldt et al. 2009, Hortal et al. 2011, Baselga et al. 2012b, Fattorini and Baselga 2012). During the glaciations, beetle assemblages were obliterated in northern Europe, so present faunas are the result of post-glacial re-colonization (Hewitt 1999). Because only species with high dispersal ability would be able to reach the north of Europe (Svenning and Skov 2007, Baselga et al. 2012b), the proportion of poor vs good dispersers in each taxon would determine both 1) the strength of the latitudinal richness gradient (i.e. taxa with high proportion of good dispersers would tend to show a shallow latitudinal gradient) and 2) the magnitude of the difference between northern and southern decay patterns (i.e. taxa with high proportion of good dispersers would tend to show similar flat decay patterns in both regions). We do not neglect the effect of niche filtering in the recolonization process. In fact, we have found that both dispersal- and niche-related characteristics were significantly related to differences in decay patterns between northern and southern Europe, as previously shown to be related to the variation in beta diversity patterns (Gómez-Rodríguez et al. 2015). However, dispersal-related characteristics were more relevant, explaining most of the variation, when the information provided by slopes and intercepts was integrated. It should be noted that integrating variation in slopes and intercepts is crucial (Soininen et al. 2007, Morlon et al. 2008), because the latter can constrain the former: similarity is constrained between 0 and 1, so if close assemblages are very dissimilar (i.e. intercept close to 0), then the slope cannot be large (as similarity cannot be  $<0$ ). In any case, the effect of niche processes is not driving the relationship between difference in decay patterns and richness gradients, as climatic

distances were not significant predictors of faunal similarity, climatic slopes were steeper in the north than in the south, and cross-taxon variation in differences between northern and southern climatic decay patterns were not related to any of the taxon's attributes we tested. If any, the effect of niche processes would be counteracting the patterns we are reporting (i.e. unexplained variance) or acting at different geographical scales (for example, structuring meta-communities at the landscape level).

To conclude, our results lead to a seemingly counter-intuitive generalization: the more difficult the colonization of a region (e.g. because it is farthest from the colonization source), the shallower the distance decay-pattern in that region. The rationale behind is that only good dispersers can arrive to that region and, because they are good dispersers, they are potentially able to occupy large areas, making distant assemblages to be similar. An analogous result was found when distance decay patterns in continental and insular assemblages were compared (König et al. 2017), as the distance decay pattern is steeper in continents than in islands, and steeper in continental than in oceanic islands. In our view, these results imply a pervasive effect of dispersal limitation on distance decay patterns. This is further supported here: if dispersal limitation is a relevant driver of richness gradients, then the steepness of the latitudinal richness gradient should be related to the difference between decay patterns in northern and southern Europe, because both differences arise by the fact that different proportions of species are able to reach northern Europe in each taxon depending on their dispersal abilities. We found evidence that both patterns are correlated, which is only predicted by dispersal processes controlling species distributions. Moreover, our results imply that, despite the existence of broad correlations between latitudinal richness gradients of different beetle groups, striking differences arise in distance decay patterns of southern Europe and these differences are related to the strength of the latitudinal richness gradients. Therefore, paradoxically, it is studying the beetle faunas of southern Europe how we will be able to understand the processes controlling the recolonization of northern latitudes. Understanding those processes would be key to predict the effects of future climate change on biodiversity.

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Supplementary material (Appendix ECOG-03693 at < [www.ecography.org/appendix/ecog-03693](http://www.ecography.org/appendix/ecog-03693) >). Appendix 1.