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PAPER

# Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles

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## ABSTRACT

**Aim** A debate exists as to whether present-day diversity gradients are governed by current environmental conditions or by changes in environmental conditions through time. Recent studies have shown that latitudinal richness gradients might be partially caused by incomplete post-glacial recolonization of high-latitude regions; this leads to the prediction that less mobile taxa should have steeper gradients than more mobile taxa. The aim of this study is to test this prediction.

**Location** Europe.

**Methods** We first assessed whether spatial turnover in species composition is a good surrogate for dispersal ability by measuring the proportion of wingless species in 19 European beetle clades and relating this value to spatial turnover ( $\beta_{sim}$ ) of the clade. We then linearly regressed  $\beta_{sim}$  values of 21 taxa against the slope of their respective diversity gradients.

**Results** A strong relationship exists between the proportion of wingless species and  $\beta_{sim}$ , and  $\beta_{sim}$  was found to be a good predictor of latitudinal richness gradients.

**Main conclusions** Results are consistent with the prediction that poor dispersers have steeper richness gradients than good dispersers, supporting the view that current beetle diversity gradients in Europe are affected by post-glacial dispersal lags.

## Keywords

**Beta diversity, Coleoptera, dispersal, diversity gradients, Europe, post-glacial recolonization, richness.**

## INTRODUCTION

A central but unresolved question in macroecology is the relative role played by present-day versus past environments in shaping current species ranges and thus species diversity patterns (Ricklefs, 2004). Present-environment hypotheses propose that current conditions (mostly energy and water) directly control species diversity, with one major hypothesized mechanism being that species richness gradients reflect filtering of species according to their climatic tolerances (Hawkins *et al.*, 2003; Currie *et al.*, 2004). Alternatively, historical hypotheses explain present species distributions and diversity patterns as controlled by the interplay between past environmental conditions and their effects on speciation and extinction rates and the ability of species to colonize suitable environments as they

become available (Ricklefs & Schluter, 1993; Dynesius & Jansson, 2000; Hawkins & Porter, 2003; Ricklefs, 2006).

Arguably, both present-day and historical processes interact in determining current species distributions and diversity patterns. A potentially crucial factor modulating the relative signatures of modern versus historical factors on the distribution of species is their dispersal ability. Higher dispersal ability should yield higher likelihood that populations track climatic conditions as they change, thus maintaining species distributions in a quasi-equilibrium state with climate. In contrast, the more limited the dispersal ability, the lower the likelihood that populations track changing climatic conditions. In such cases, a species will not occupy the whole area that is climatically suitable for it; in other words its distribution will not be in equilibrium with current climate (Ricklefs & Schluter, 1993; Svenning

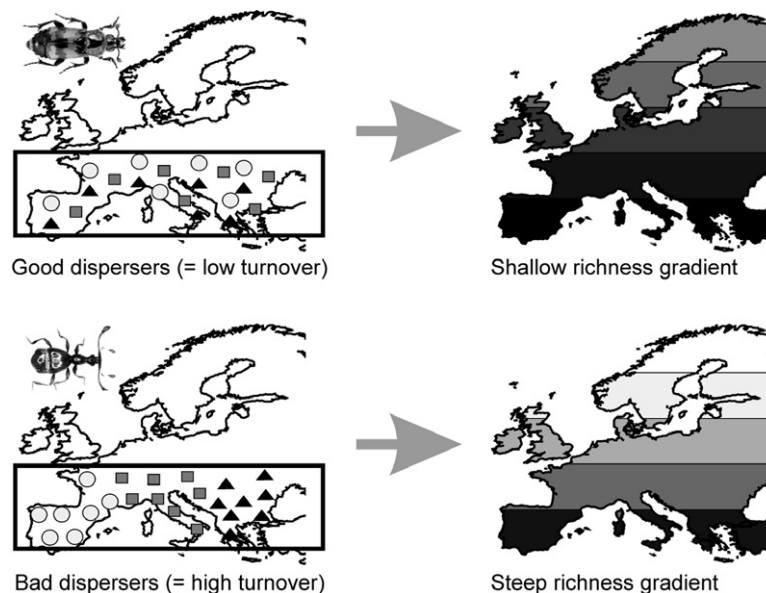
& Skov, 2004; Araújo & Pearson, 2005). Since there might be a lag between a change in climate and a species' response to it, it is often said that lack of equilibrium reflects historical processes such as local extinctions and dispersal limitation from the place of origin (speciation without subsequent expansion to other climatically suitable areas) or from past refugia. It is proposed that when historical factors affect a significant number of species, assemblages will not be in equilibrium with current climate either (Araújo & Pearson, 2005; Baselga & Araújo, 2010).

How could such a lack of equilibrium affect diversity gradients? The latitudinal richness gradient is probably the best known and most studied macroecological pattern (Willig *et al.*, 2003), and the existence of a strong correlation between species richness and variables reflecting current climate has lend support to the present-environment hypotheses as the dominant explanations for diversity gradients (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Whittaker *et al.*, 2007). However, since climatic factors are spatially structured, recent work has led to the suggestion that present-day climate–richness relationships need not be the result of causal mechanisms, but could simply be the outcome of other spatially structured processes that covary with climate (Bahn & McGill, 2007; Currie, 2007). Aligned with this proposition, several studies in Europe have shown that historical factors can influence the distribution of species richness at a continental scale. Notably, patterns of species richness in small-range trees, herptiles and mammals are all, at least partially, explained by historical rather than current climate (Svenning & Skov, 2007b; Araújo *et al.*, 2008; Fløjgaard *et al.*, 2011). These studies lend support to the

proposition that modern patterns of species richness, to some extent, are the result of incomplete post-glacial recolonization from southern glacial refugia; an explanation that invokes limited dispersal as a candidate mechanism.

The proposition that species richness in Europe is partially controlled by the historical effect of glaciations and incomplete post-glacial recolonization due to dispersal limitation leads to the prediction that spatial distance to southern refugia should be a strong predictor of species richness. This prediction was tested for European trees by Svenning & Skov (2007a), who found broad support for it, and for Holarctic trees by Montoya *et al.* (2007), who reported a significant, but secondary role for distance-to-refugia predictors compared with 'current climate' predictors. Here, we propose a second prediction directly derived from the dispersal-limitation hypothesis: if the latitudinal richness gradient is caused by incomplete post-glacial recolonization, then the strength of the gradient for a given taxon (the slope of the richness–latitude relationship) should be determined by its dispersal ability. In other words, less vagile taxa should show steeper latitudinal richness gradients than more vagile taxa (Fig. 1).

The aim of this study is to assess this prediction. Beetles represent an excellent biological model as their outstanding diversity allows the comparison of a large number of phylogenetically related groups (each with high numbers of species) with different life strategies, ecological specializations and dispersal abilities, while keeping body size, body structures and physiology relatively constant. While there is evidence that some beetle



**Figure 1** Framework describing the major hypotheses tested in this study. All other things being equal, good dispersers should have wider geographic ranges and, as a result, low spatial turnover in species composition. In contrast, poor dispersers should have small geographic ranges and, as a consequence, high spatial turnover. If the latitudinal richness gradient is at least partially caused by the post-glacial recolonization process in combination with differential dispersal abilities of species, the strength of the gradient (slope of the richness–latitude relationship) should be steeper for less vagile groups because a higher proportion of species would have failed to reach northern regions due to dispersal limitation. Note that we measured turnover only within southern European countries in order to avoid any effect of the post-glacial recolonization process on turnover values. Symbols of the left maps represent different species and shades of the right maps represent species richness, from high (black) to low richness (white).

**Table 1** Beetle taxa included in this study, including their respective taxonomical rank, trophic specialization, total number of species in the studied area (continental Europe), proportion of wingless species, and mean size. ? = not determined.

Taxon	Rank	Trophic type	Species number	Apterous species (%)	Mean size (mm)
<i>Amara</i>	Genus	Epidaphic, herbivorous	135	0	7
Apionidae	Family	Epiphytic, herbivorous	287	0	3
Baridinae	Subfamily	Epiphytic, herbivorous	71	8	5
<i>Carabus</i>	Genus	Epidaphic, carnivorous	120	100	25
Cerambycinae	Subfamily	Xylophagous	134	0	15
<i>Chaetocnema</i>	Genus	Epiphytic, herbivorous	33	6	2
Hydraenini	Tribe	Aquatic, herbivorous	158	0	2
Lamiinae	Subfamily	Xylophagous	300	53	14
Lepturinae	Subfamily	Xylophagous	119	0	11
Limnebiini	Tribe	Aquatic, herbivorous	43	0	2
Nanophyidae	Family	Epiphytic, herbivorous	31	0	2
Ochtebiini	Tribe	Aquatic, herbivorous	135	0	2
<i>Otiorhynchus</i>	Genus	Epidaphic, rhizophagous	698	100	9
Phyllobiini	Tribe	Epiphytic, herbivorous	93	?	5
Polydrusini	Tribe	Epiphytic, herbivorous	134	?	4
Pselaphinae	Subfamily	Edaphic, carnivorous	817	32	2
<i>Pterostichus</i>	Genus	Epidaphic, carnivorous	241	100	16
Scarabaeidae	Family	Epidaphic, coprophagous	93	0	14
Scolytinae	Subfamily	Xylophagous	236	0	3
Silphidae	Family	Epidaphic, saprophagous	40	15	17
<i>Trechus</i>	Genus	Edaphic, carnivorous	253	93	5

species have responded to the Pleistocene climatic shifts by fast, large migrations (Coope, 1970), there is also evidence that dispersal of other beetle species has been much more limited. Notably, the existence of a clear-cut limit for the northwards distribution of many cave and edaphic blind beetle species was proposed long ago to reflect the inability of these species to recolonize areas strongly affected by Pleistocene glaciations (Holdhaus, 1954). This limit, recently named the Holdhaus line (Habel *et al.*, 2010), roughly coincides with the 0 °C isotherm for the Last Glacial Maximum (see Araújo *et al.*, 2008, and Hortal *et al.*, 2011, for similar patterns in different taxa). Hence, European beetles offer an obvious study group for a quantitative test of the effect of dispersal ability on richness gradients. Here, we used 21 species-rich, supraspecific taxa of European beetles, encompassing 4078 species, to test whether the slopes of their latitudinal richness gradients are associated with their dispersal ability.

## MATERIALS AND METHODS

### Biological data

Our dataset included 21 beetle taxa (large genera, tribes, subfamilies or families; 4078 species in total). Representative taxa belonging to the most diverse beetle superfamilies (Caraboidea, Staphylinoidea, Scarabaeoidea, Chrysomeloidea and Curculionoidea) were selected, including taxa with different life strategies in terms of microhabitat or trophic specialization (see Table 1 for details). The study area included continental Europe across 11° W–60° E longitude and 36° N–72° N latitude. Thirty-three

inventories of each beetle group were obtained from Löbl & Smetana (2003, 2004, 2006) and the Fauna Europaea Web Service (Fauna Europaea version 1.1, available online at <http://www.faunaeur.org>). In general, these inventories refer to European countries, but some countries were split or pooled based on biogeographical criteria. Thus, European Russia was divided into three territories (Northern, Central and Southern) due to its extremely large area, whereas Bosnia and Croatia were combined. Thereafter, for each beetle taxon, we built a table accounting for presence/absence records of each species in the 33 territories.

### Measuring richness gradients

We estimated the strength of the latitudinal richness gradients for each of the 21 considered taxa as the slope of the relationship between the country's species richness and its mean latitude. Since differences in total number of species among different taxa could bias slope values (as the minimum number of species is always zero, but the maximum number of species in a country depends on the total number of species included in a given taxon), we standardized richness values by dividing species richness of country *i* ( $S_i$ ) by the maximum value existing in any country for each taxon ( $S_{max}$ ). These standardized richness values ( $S_{std} = S_i/S_{max} \times 100$ ) were log-transformed to achieve normality of residuals and linearly regressed against mean country latitude (in Universal Transverse Mercator coordinates; km to equator). Log-transformed country area ( $A$ ) was included in the regression as a covariate to control for area differences among countries [ $\log(S_{std}) \sim Y + \log(A)$ ]. The slope for  $Y$  ( $b_Y$ ) in

this regression may be considered as a measure of the strength of the latitudinal richness gradient for each taxon.

### Measuring dispersal ability

Estimating dispersal ability for beetles is far from trivial, as empirical data on migration rates are extremely scarce. For this reason, the use of a surrogate of dispersal ability is required. Recent work has suggested that spatial turnover is a good surrogate of dispersal ability (Steinitz *et al.*, 2006; Qian, 2009). The rationale is that less vagile species would tend to have more restricted distributions; thus, taxa composed of less vagile species should have higher turnover in species composition than more vagile taxa. Of course, the direct predictor of spatial turnover in these cases is range size rather than dispersal, and factors other than dispersal can cause ranges to be small (e.g. Ohlemüller *et al.*, 2008). Therefore, it is important to first test whether spatial turnover correlates with measures of dispersal ability for the taxa being studied. If such correlation exists, the use of spatial turnover as a surrogate for dispersal is justified. We tested this assumption by assessing the relationship between spatial assemblage turnover and two morphological characteristics mechanistically linked with dispersal ability: the proportion of wingless species within a given taxon and mean body size of species within a given taxon. Morphological information was gathered from bibliographic sources and personal communication with several specialists. Data on the presence or absence of wings could be found for the species of 19 out of 21 taxa (see Table 1). The proportion of wingless species was computed for the total number of European species within each taxon, with exception of Pselaphinae, for which we randomly sampled 30 species and computed the proportion of wingless species. Spatial assemblage turnover ( $\beta_{\text{sim}}$ , Simpson-based multiple-site dissimilarity) for southern Europe (minimum latitude  $< 46^\circ$ ) was linearly regressed against the proportion of wingless species and the mean body size.  $\beta_{\text{sim}}$  is a multiple-site measure of spatial turnover in species composition independent of differences in richness among sites (Baselga *et al.*, 2007; Baselga, 2010). Spatial turnover ( $\beta_{\text{sim}}$ ) was measured in this southern subregion of Europe since it is the main glacial refuge in Europe, thereby avoiding any influence of the post-glacial latitudinal recolonization process that we propose to be at least partially associated with the latitudinal richness gradient.

### Assessing the relationship between richness slopes and dispersal ability

Following the framework described in Fig. 1, we tested the hypothesis that the latitudinal richness gradients in European beetles are at least partially controlled by post-glacial migration lag in combination with differential dispersal capacities among the different taxa. The richness–latitude slope values ( $b_Y$ ), our measures of the strength of the latitudinal richness gradient for the beetle taxa, were thus linearly regressed against southern European  $\beta_{\text{sim}}$  values, the selected surrogate measure of dispersal ability.

## RESULTS

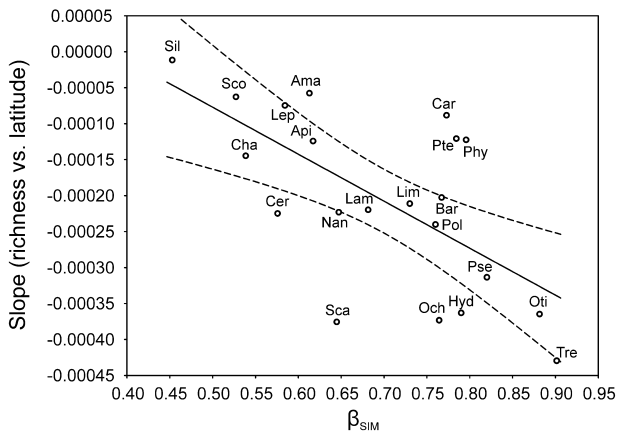
The morphological characteristics of taxa explained much of the variation in  $\beta_{\text{sim}}$  in southern Europe ( $r^2 = 0.62$ ,  $F_{2,16} = 12.84$ ,  $P < 0.001$ ): the higher the proportion of wingless species and the smaller the body size, the higher the spatial turnover in southern Europe. Regarding the richness gradients, the latitudinal slopes ( $b_Y$ ) were significantly different from zero in all but three taxa, but the strength of the latitudinal richness gradient differed markedly among them (Table 2). Some groups showed only a weak relationship (e.g. Silphidae) whereas others had a steep slope (e.g. *Trechus*).

As predicted, we found that  $\beta_{\text{sim}}$  in southern Europe is a good predictor of the strength of the latitudinal species richness gradient (Fig. 2). A linear regression between the slope values ( $b_Y$ ) of the species richness–latitude relationships and  $\beta_{\text{sim}}$  within southern Europe explained a large portion of the variation in  $b_Y$  ( $r^2 = 0.41$ ,  $F_{1,19} = 13.47$ ,  $P = 0.002$ ). Considering deviations from this general relationship, there were neither groups presenting high  $\beta_{\text{sim}}$  and shallow richness gradients (upper right corner in Fig. 2) nor taxa with low  $\beta_{\text{sim}}$  and steep richness slopes (lower left corner). However, at intermediate  $\beta_{\text{sim}}$  values we found both types of deviations: taxa with shallower richness gradients than expected from their spatial turnover (e.g. *Carabus*) and taxa with steeper richness gradients than expected (e.g. Scarabaeidae).

**Table 2** Summary statistics for the regressions of log-transformed standardized richness against mean country latitude ( $Y$ ) and log-transformed country area ( $A$ ). The slope values for latitude ( $b_Y$ ) and area ( $b_A$ ) and their respective  $P$ -values are shown. (\*)  $P < 0.1$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

	Multiple				
	$R^2$	$F_{2,30}$	$P$	$b_Y$	$b_A$
<i>Amara</i>	0.49	14.43	$< 0.001$	$-0.6 \times 10^{-4**}$	0.15**
Apionidae	0.09	1.54	0.230	$-1.2 \times 10^{-4} (*)$	0.11
Baridinae	0.39	9.54	0.001	$-2.0 \times 10^{-4**}$	0.72**
<i>Carabus</i>	0.31	6.62	0.004	$-0.9 \times 10^{-4**}$	0.22**
Cerambycinae	0.72	39.38	$< 0.001$	$-2.3 \times 10^{-4**}$	0.29**
<i>Chaetocnema</i>	0.43	11.18	$< 0.001$	$-1.4 \times 10^{-4**}$	0.17**
Hydraenini	0.35	7.91	0.002	$-3.6 \times 10^{-4**}$	0.14
Lamiinae	0.67	30.40	$< 0.001$	$-2.2 \times 10^{-4**}$	0.23**
Lepturinae	0.30	6.56	0.004	$-0.8 \times 10^{-4**}$	0.13**
Limnebiini	0.22	4.34	0.022	$-2.1 \times 10^{-4**}$	0.20
Nanophyidae	0.16	2.91	0.070	$-2.2 \times 10^{-4**}$	0.16
Ochtebiini	0.62	24.07	$< 0.001$	$-3.7 \times 10^{-4**}$	0.32**
<i>Otiorhynchus</i>	0.39	9.70	0.001	$-3.6 \times 10^{-4**}$	0.08
Phyllobiini	0.19	3.58	0.040	$-1.2 \times 10^{-4**}$	0.05
Polydrusini	0.45	12.33	$< 0.001$	$-2.4 \times 10^{-4**}$	0.20*
Pselaphinae	0.57	19.92	$< 0.001$	$-3.1 \times 10^{-4**}$	0.26**
<i>Pterostichus</i>	0.22	4.15	0.026	$-1.2 \times 10^{-4**}$	0.21*
Scarabaeidae	0.88	106.93	$< 0.001$	$-3.8 \times 10^{-4**}$	0.24**
Scolytinae	0.12	1.95	0.160	$-0.6 \times 10^{-4}$	0.18(*)
Silphidae	0.14	2.52	0.097	$-0.1 \times 10^{-4}$	0.07*
<i>Trechus</i>	0.68	31.43	$< 0.001$	$-4.3 \times 10^{-4**}$	0.42**





**Figure 2** Relationship between the slope of the richness–latitude regression ( $b_\gamma$ ) and overall spatial turnover in species composition among the southern European countries ( $\beta_{sim}$ ). The fitted linear function ( $r^2 = 0.41$ ,  $F_{1,19} = 13.47$ ,  $P = 0.002$ ) and its 95% confidence interval limits are shown. Text labels correspond to the first three letters of taxa listed in Table 1.

## DISCUSSION

Our analysis supports the view that spatial turnover in species composition can be considered a good surrogate of dispersal ability, as  $\beta_{sim}$  was strongly correlated with species-trait characteristics (flightless condition and body size) that are mechanistically linked to dispersal ability. Based on the evidence that spatial turnover in beetle species composition generally provides a good surrogate for dispersal ability (see also Steinitz *et al.*, 2006; Qian, 2009), we related  $\beta_{sim}$  values with the slopes of latitudinal richness gradients for each one of the 21 beetle clades studied. Consistent with the prediction that the differential post-glacial migration lag – controlled by the variable dispersal ability of different species – is a key mechanism underlying latitudinal richness gradients for beetles in Europe, we found that beetle taxa with different dispersal abilities (as measured with  $\beta_{sim}$ ) exhibit latitudinal richness gradients of correspondingly differing strengths. Taken together, these findings support the view that historical contingencies may cause current species distributions to depart from equilibrium with present climate at continental scales (cf. Svenning & Skov, 2004; Araújo & Pearson, 2005), thereby affecting current species richness gradients (e.g. Ricklefs, 2006).

More specifically, groups with a large proportion of volant species, i.e. with high dispersal ability, such as carrion beetles (Silphidae) and bark beetles (Scolytinae), had the shallowest latitudinal richness gradients. In contrast, taxa such as the large genera *Trechus* and *Otiorhynchus* with a high proportion of wingless species and many range-restricted species presented the steepest richness gradients. The relationship between dispersal ability (as measured  $\beta_{sim}$ ) and the strength of the richness gradient was supported not only by extremes in the dispersal gradient, but also by taxa with intermediate dispersal abilities, such as the Lamiinae or Limnebiini. However, a few groups,

particularly the ground beetle genus *Carabus*, did not follow the general pattern, rather presenting shallow latitudinal richness gradients despite having low dispersal ability. In contrast, the dung beetles (Scarabaeidae) show a richness gradient steeper than expected from their high dispersal ability.

Departures from the main pattern might reflect methodological limitations of our study, in terms of estimating dispersal ability, or the relevance of non-measured factors as determinants of the strength of the latitudinal richness gradient. One potential limitation of our methods is the indirect representation of dispersal ability, i.e. by  $\beta_{sim}$ . Even though we found evidence for a strong relationship between the proportion of wingless species and  $\beta_{sim}$ , other traits (e.g. ecological specialization) might cause species with a restricted range to cluster in specific regions, i.e. affecting  $\beta_{sim}$  (e.g. Gaston *et al.*, 2001; Ohlemüller *et al.*, 2008). However, several studies have shown that spatial turnover values are associated with dispersal ability at very different scales. For example, in small regions (extent < 250 km), Steinitz *et al.* (2006) showed that the distance decay of similarity in species composition is steeper in poorly dispersed groups compared with highly vagile groups (i.e. shallower distance decay for birds than for snails; and within snails, steeper distance decay for big than for small snails, as predicted by the latter being better passive dispersers). At continental scales, Qian (2009) demonstrated that pteridophytes, with their highly dispersive propagules (minute spores), have lower values of spatial species turnover than seed plants, which mostly have less well-dispersed propagules. Likewise, our finding that  $\beta_{sim}$  strongly increases with the proportion of wingless species in a given beetle group provides mechanistic support for the assumption that  $\beta_{sim}$  is a good surrogate of dispersal ability.

Another potential source of error is the coarse and unequal grain size of our study units. This said, it has been shown for many groups in Europe that variation in grain size has little effect in the explanatory models for species richness (Nogués-Bravo & Araújo, 2006; Keil & Hawkins, 2009). Regarding area effects, previous papers have shown that country data can provide useful templates for assessing patterns of variation in richness in Europe (Baselga, 2008; Schuldt & Assmann, 2009; Schuldt *et al.*, 2009). Even for complex models accounting for several environmental predictors, the parameters estimated by models using unequal sampling units (countries) or grids of comparable sample size are strikingly similar (Keil & Hawkins, 2009), although grid-based models tend to explain greater proportions of variation. All this evidence could be context dependent, due to the idiosyncratic configuration of European countries, but for the purpose of our study a regression of country richness against mean country latitude, controlling for variation in area, is likely to provide reasonable estimates of the strength of the latitudinal richness gradients in Europe.

Given these considerations, taxon deviations from the general relationship between richness–latitude slopes and spatial-species turnover might instead reflect the influence of other factors on the latitudinal richness gradients. An obvious candidate is physiological and life-history differences among groups, as different taxa may have different evolutionary origins, different adapta-

tions and different potential for adaptive evolution so the climatic gradients may affect them in different ways. For example, the wingless ground beetle genus *Carabus* shows a much shallower latitudinal richness gradient than expected for their observed spatial species turnover, reflecting that high numbers of *Carabus* species are living in northern Europe despite their limited dispersal ability. This discrepancy might be explained by the fact that *Carabus* is a Holarctic taxon with many species adapted to cold climates. Many *Carabus* species could have had northern glacial refugia (Lindroth, 1970; Assmann, 2004) due to their high tolerance to cold conditions, and thus current northern assemblages from this genus might not be the product of post-glacial recolonization from southern Europe alone. If *Carabus* species had northern glacial refugia and/or higher adaptive capacity, even poor dispersal ability would not necessarily yield a steep latitudinal richness gradient. A similar result has been found with boreal plants, for which the occurrence of cold-adapted species is only weakly related to accessibility from the major southern glacial refugia (Svenning *et al.*, 2008). In contrast, among studied beetle groups, the Scarabaeidae showed a steeper than expected richness gradient given their dispersal ability. This deviation may reflect physiological constraints related to the strong limiting role played by temperature for this group: under cold conditions, most of the species are not capable of maintaining the body heat necessary to fly and colonize the ephemeral and patchy resources, such as dung pats, that they depend on (Verdú & Lobo, 2008). This physiological limitation seems to be a phylogenetically conserved trait, and only a few Scarabaeidae clades have managed to colonize higher latitudes (Hortal *et al.*, 2011). A similar deviation from the general tendency was observed for the Ochtebiini and Hydraenini. Most species of these groups usually live in running permanent waters, a habitat association that has been theoretically and empirically linked to low dispersal ability, causing higher rates of speciation (Ribera & Vogler, 2000) and difficulty in recolonizing northern Europe after glaciations, thereby leading to steep richness gradients (Ribera *et al.*, 2003; Abellán *et al.*, 2011). Thus, the downward deviation of Ochtebiini and Hydraenini might probably reflect that post-glacial recolonization for these running water beetles is even more difficult than for terrestrial beetles with similar long-term migration abilities as reflected by  $\beta_{\text{sim}}$  in the non-glaciated area. However, the lack of taxa that combine high vagility with a very steep latitudinal richness gradient suggests that a steep latitudinal richness gradient only arises in poorly dispersed taxa, i.e. in groups with species that are able to colonize large areas, many of these species also have the climatic tolerances needed for colonizing northern cold climates.

The relationship between dispersal ability and ecological specialization (Dynesius & Jansson, 2000) introduces further complexity in the interpretation of current results. It could be argued that the failure of some taxa to colonize northern European regions could arise from an extreme ecological specialization rather than from their reduced dispersal ability. However, it should be noted that, even for highly specialized species, high dispersal ability would allow populations to track changing climates. Therefore, a causal relationship between ecological spe-

cialization and the strength of latitudinal richness could only be hypothesized by assuming a univocal link between dispersal ability and ecological specialization (Jocque *et al.*, 2010). This hypothesis proposes the existence of a trade-off between dispersal ability and ecological specialization, which would be controlled by climate (i.e. unstable climates would select for generalist species). Under this assumption, ecological specialization and dispersal ability would be like 'two sides of the same coin', and latitudinal richness gradients would be caused by different speciation rates across latitudes (being higher in stable climates) arising by different climates selecting for different parts of dispersal-ecological specialization trade-off. Further investigation is needed to assess this hypothesis, but given the lack of accurate ecological data for European beetles we could not explore this further here.

In sum, despite some deviations from the general tendency, for a wide range of European beetle taxa, dispersal ability was a good predictor of the strength of the latitudinal richness gradients, accounting for almost half of the variation in richness slopes. It is thus reasonable to conclude that dispersal ability has an important role in determining diversity patterns in European beetles. The causal mechanism of this control seems to be that dispersal ability modulates the degree of equilibrium between realized species distributions and potential ones. Examples of beetle species that have suffered marked range shifts during the Quaternary are not rare (see Coope, 2004, and references therein), some having been able to track northwards during short, rapid climate warming episodes (Coope & Angus, 1975). However, virtually all Quaternary fossil records for beetles belong to northern localities rather than southern glacial refugia (Abellán *et al.*, 2011), so known fossils unavoidably belong to species that have dispersal abilities high enough to track climate changes and recolonize northern regions (Ricklefs & Schluter, 1993). Whether southerly distributed species have suffered a comparable range shift remains unknown due to the lack of Quaternary fossil studies. In fact, our results suggest that the large number of range-restricted species in southern Europe among some taxa, such as *Trechus* and *Otiorrhynchus* (as evidenced by their steep richness gradient), corresponds to beetle species with a limited dispersal ability and limited ability to track climate oscillations. Since climatic conditions are temporally dynamic, the signal of historical climatic changes such as glaciations, that have dramatically constrained species distributions in the past, can still be recovered in current species distributions due to dispersal limitation: the lower the dispersal ability, the more pronounced the signal of historical events on species distributions. At the assemblage level, we found that the lower the dispersal ability, the more pronounced the signal of Pleistocene glaciations in northern assemblages, i.e. the steeper the richness gradient.

Our results are relevant for biological conservation studies, because they demonstrate the existence of strong lags in dispersal after climate changes of great magnitude, such as glacial-interglacial oscillations, have occurred. These dispersal lags imply that current species occupancy of suitable climate space is incomplete, thus limiting the ability of phenomemo-

logical niche models to characterize the climatic envelopes where species can live and survive (e.g. Araújo & Pearson, 2005; Baselga & Araújo, 2010; Varela *et al.*, 2010). Even if the potential distributional areas of the species could be well characterized with existing occurrence data (or fossils, e.g. Nogués-Bravo *et al.*, 2008), our results show that the ability to track suitable climates in the future is, for many species of beetles, compromised by dispersal limitation. Hence, when attempting to predict the consequences of climate changes on biodiversity (e.g. Skov & Svenning, 2004; Thomas *et al.*, 2004; Thuiller *et al.*, 2011), it would be important to explore scenarios with contrasting hypotheses about dispersal.

## ACKNOWLEDGEMENTS

A.B. is funded by the Spanish Ministry of Science and Innovation (grant CGL2009-10111), J.C.S. by the Danish Council for Independent Research – Natural Sciences (grant 272-07-0242), P.A. by the Swiss National Science Foundation (PPOOP3\_128375) and M.B.A. by EC FP6 ECOCHANGE project (036866-GOCE) and by the Spanish Ministry of Science and Innovation (grant CGL2008-01198-E/BOS).

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## BIOSKETCH

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Editor: Robert Dunn