

LETTER

Ice age climate, evolutionary constraints and diversity patterns of European dung beetles

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Abstract

Current climate and Pleistocene climatic changes are both known to be associated with geographical patterns of diversity. We assess their associations with the European Scarabaeinae dung beetles, a group with high dispersal ability and well-known adaptations to warm environments. By assessing spatial stationarity in climate variability since the last glacial maximum (LGM), we find that current scarab richness is related to the location of their limits of thermal tolerance during the LGM. These limits mark a strong change in their current species richness–environment relationships. Furthermore, northern scarab assemblages are nested and composed of a phylogenetically clustered subset of large-range sized generalist species, whereas southern ones are diverse and variable in composition. Our results show that species responses to current climate are limited by the evolution of assemblages that occupied relatively climatically stable areas during the Pleistocene, and by post-glacial dispersal in those that were strongly affected by glaciations.

Keywords

Biodiversity gradients, climate variability, community assembly, current climate, Europe, geographically weighted regressions, phylogenetic structure, Pleistocene glaciations, spatial stationarity.

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INTRODUCTION

Contemporary climate is commonly thought to exert a major influence on the geographical patterns of species richness (e.g. Currie 1991). In general, present water availability and ambient energy are strongly correlated with species richness of many groups of organisms (e.g. Hawkins *et al.* 2003; Whittaker *et al.* 2007), suggesting that these factors control the geographical distributions of species. However, current species distributions are also influenced by the interplay of adaptations developed throughout their evolutionary history, the restrictions to dispersal imposed by the geographical and environmental characteristics of continents, and other factors causing the local extinction of populations. The dynamics of speciation and extinction, coupled with historical dispersal events and climatic oscillations, generate region-specific patterns that must be understood to achieve a comprehensive understanding of diversity gradients (Dynesius & Jansson 2000; Hawkins *et al.* 2007b; Ricklefs 2007). The drastic climatic changes occurring during the Pleistocene represent one such historical event that must have profoundly shaped diversity gradients in northern latitudes, where extensive glaciation has left a legacy of impoverished faunas and floras (e.g. Hawkins & Porter 2003;

Montoya *et al.* 2007; Svenning & Skov 2007). Given the limited time for recolonization since the extreme conditions of the last glacial maximum (LGM, 21 000 years ago), the richness and composition of previously glaciated areas may be affected by incomplete post-glacial recolonization due to dispersal limitation (Svenning & Skov 2007).

The geographical imprint of glaciations on current diversity has been evaluated using dichotomous maps that differentiate between glaciated and non-glaciated areas (Currie & Paquin 1987), maps of the age when the ice retreated from each area (Hawkins & Porter 2003; Montoya *et al.* 2007), or surrogates of the overall change in climate, such as climate stability (Araújo *et al.* 2008). However, the variables describing current and past environmental gradients are spatially correlated (Hawkins & Porter 2003; Araújo *et al.* 2008). Thus, to disentangle the potential contributions of past and present climates, it is important to evaluate the geographical concordance between richness gradients and both current conditions and historical changes in climate. If past climate has had a significant effect, then the relationship between species richness and a variable accounting for climatic changes will differ between the areas where the effect of glaciations was strong enough to extirpate large numbers of species and those where local and regional extinctions were not as widespread.

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For example, the relationship between species richness and historical climate change will be non-stationary (i.e. the shape and strength of the relationship are not constant across space), shifting according to the impact of glaciations on local assemblages.

Herein, we attempt to disentangle the contributions of past and contemporary climate on current diversity of Scarabaeinae (Coleoptera: Scarabaeidae) dung beetles in Europe, a species-rich group with a supposed high dispersal capacity inferred from their adaptations to exploit ephemeral habitats and well-developed flying abilities. Scarabaeinae dung beetles, or scarabs for short, are an ideal model invertebrate taxon for biodiversity research due to their high diversity, complex evolutionary history, wide geographical distribution and functional plasticity (Spector 2006). In particular, the importance of their thermal adaptations on their geographical distributions may minimize that of other factors, providing a way of evaluating the relevance of historical climate changes in more detail. Scarabaeinae probably originated during the Mesozoic (Philips *et al.* 2004) under the tropical macroclimates prevailing in Gondwanaland (Hanski & Cambefort 1991; Davis *et al.* 2002; Scholtz *et al.* 2009), and can be considered a warm-adapted group for whom temperature is a well-known constraint (Lobo *et al.* 2002; Menéndez & Gutiérrez 2004; Hawkins *et al.* 2007a). This may well be rooted in their ancestral adaptations towards tropical environments (Davis *et al.* 2002), and is also favoured by their nesting behaviour, consisting of burying their nests in the ground (Hanski & Cambefort 1991), which makes them sensitive to long periods of freezing conditions in the soil. Their high dispersal ability may have also facilitated the continuous mixing of gene pools in consecutive interglacial stages, producing some evolutionary stasis in their thermal requirements (see Coope 2004). Given their evolutionary history and known adaptations, here we hypothesize that the need for warm climates is a phylogenetically conserved trait for European Scarabaeinae, and that the strength of this conservatism has limited their capacity to adapt to the cold temperate conditions that are part of Earth's climate since the beginning of the Pleistocene.

Although we lack data on the past distributions of scarabs, the current northern limit of the most cold-tolerant species roughly coincides with the 0 °C isotherm (Fig. 1). As few, if any, species could have survived above the limit defined by the 0 °C isotherm at the LGM, the richness and structure of the assemblages placed north of that limit would be due entirely to the establishment of new assemblages following the change in environmental conditions as the climate warmed. In contrast, the areas south of the 0 °C isotherm at the LGM would be affected by both environmental changes since the LGM and long-term historical and community assembly processes. Assuming that no scarabs occurred north of the 0 °C isotherm during the LGM, we can predict that the relationship between species richness and climate variability since the LGM will change its shape roughly around the past location of this isotherm (Prediction 1).

During the LGM, the distance between the 0 °C isotherm and the ice caps (which reached southern England and northern Germany) was 500 km or more, ensuring that the exclusion of Scarabaeinae during this period was due to climatic constraints rather than to the physical impediment of inhabiting glaciated areas, except perhaps in the montane glaciers in the Pyrenees, Alps, Balkans and Caucasus. The lack of major dispersal barriers north of these mountain ranges and the current abundance of food sources due to widespread cattle and sheep farming may leave climate as the most important filter for the establishment of dung beetle populations after glacial retreat. Therefore, in the north, recent colonizations should strongly influence

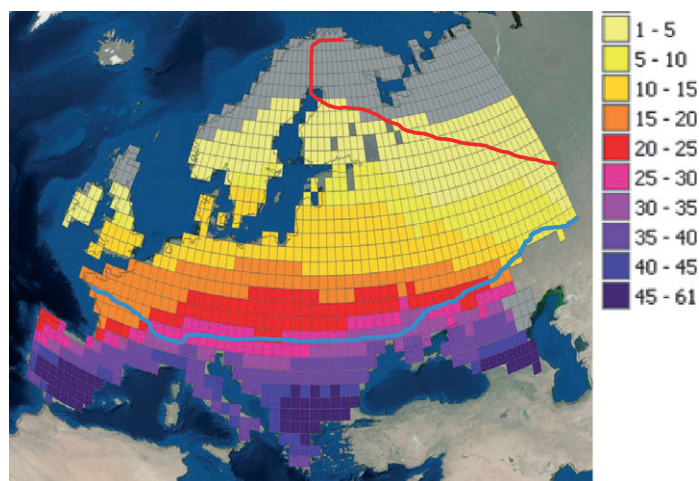


Figure 1 Geographical distribution of Scarabaeinae dung beetle species richness in Europe. The red and blue lines indicate the current and LGM location of the 0 °C isotherm, respectively (see Fig. S1).

the diversity and structure of assemblages, whereas in the south this will be less important because these assemblages originate from more complex interactions of historical and current effects. This, together with a richer species pool in the south due to the existence of glacial refuges, higher speciation and lower extinction rates in the areas less affected by historical climate changes (Dynesius & Jansson 2000), may weaken associations of richness with current climate. Hence, we can predict that the association between current environmental conditions and scarab richness will be stronger in the northern part of the continent (Prediction 2).

Finally, the known physiological limitations of insects in general and Scarabaeinae in particular make it highly probable that temperature has strong influence on the richness and structure of northern assemblages. First, if the need for warm temperatures is a phylogenetically conserved trait within Scarabaeinae, then only a few 'escapee' species would have been able to colonize the north, representing a reduced number of clades that developed adaptations to colder environments throughout the successive glacial–interglacial periods of the Pleistocene. If such phylogenetic niche similarity (*sensu* Swenson 2011) is true, we can predict that current northern assemblages would be composed of phylogenetically clustered subsets of the European pool (Prediction 3). Second, given this phylogenetic signal, we can also predict that climate filtering processes will be comparatively more important in the northern assemblages. Therefore, they will follow an orderly exclusion of species towards the north (i.e. a nested taxonomic pattern) as current temperature decreases (Prediction 4). Third, in the south of Europe, assemblages originate from complex interactions of historical and current species sorting mechanisms, in which evolutionary processes and long-term biotic interactions gain relevance. This will cause a preponderance of the replacement of species among regions (i.e. species turnover) rather than their orderly loss, forming phylogenetically overdispersed assemblages (Prediction 5). We use data on the distribution and phylogeny of European Scarabaeinae to evaluate these five predictions.

DATA AND METHODS

Data on the known distributions of the 106 European Scarabaeinae species were gathered for mainland Europe, including Russia west of

the Ural Mountains, based on monographies and regional catalogues (Appendix S1). We preferred range maps to hypotheses on species distributions based on primary biodiversity data such as Atlas data (see Hortal 2008) due to the incompleteness and unevenness of information on the occurrence of scarabs throughout Europe. Given the lack of precision of range maps, a compromise between data quality and resolution had to be made (Hortal 2008). Thus, we binned these data in a $1^\circ \times 1^\circ$ grid (Fig. 1), which we considered appropriate to minimize omission and commission errors and the mismatch with Atlas data (Appendix S1). Latitudinal variation in the surface area of these grid cells is unlikely to affect our results (see Nogués-Bravo & Araújo 2006). All islands except Great Britain and Ireland and cells with no scarab species were excluded from the analyses (Appendix S1).

For the sake of comparability, we extracted current and past climatic conditions from the same Atmosphere–Ocean General Circulation Model. Data on present and LGM (21 000 kyr) temperature and precipitation were extracted from the ECHAM3 palaeoclimatic model (Braconnot *et al.* 2007), downscaled to $1^\circ \times 1^\circ$ (Appendix S1). Following Araújo *et al.* (2008), we calculated the historical variability in temperature and precipitation as the difference between current and LGM values (hereafter, climatic variability for short; note that these variables were called climate stability by Araújo and colleagues). These measures are in fact temperature and precipitation anomalies from the LGM, and so the smaller the value of climate variability, the more stable the climate has been; hence, negative relationships with richness indicate fewer species in the areas that have changed the most in climate.

We assessed the spatial heterogeneity (i.e. non-stationarity) in the relationship between scarab richness and climate variability using geographically weighted regression (GWR; Fotheringham *et al.* 2002; see also Cassemiro *et al.* 2007; Svenning *et al.* 2009 and references therein). Geographically weighted regression performs a regression for each data point (focal point), wherein all data points within a given bandwidth are weighted according to their geographical distance to the focal point following a predefined function. Herein, we assumed a Gaussian function for decay of the weight with distance; to allow comparability among the results from different grid cells, we used a fixed bandwidth, determined using the Akaike information criterion (AIC)-based optimization algorithm (Burnham & Anderson 2002) included in SAM 4.0 (Rangel *et al.* 2010). Variation in the GWR regression coefficients identified regions with different strengths of the relationship between richness and climate variability. The border between these regions was detected by the change in the slope of the richness–climate variability relationship through piecewise linear regression. If this border is roughly coincident with the 0°C isotherm in the LGM, we interpret this as support for our first prediction and conclude that current diversity patterns are driven by the restrictions imposed by past climate to the distribution of scarabs.

Several factors apart from temperature and annual precipitation are known to affect the diversity of European scarabs at broad scales, namely topography, water-energy balance, seasonal precipitation, soil characteristics and land use (Hortal *et al.* 2001; Lobo & Martín-Piera 2002; Lobo *et al.* 2002). To account for these factors, data on altitudinal range, actual evapotranspiration (AET), potential evapotranspiration (PET), water balance, current spring and summer precipitation, amount of organic matter and pH in the surface horizons of the soil, diversity of land-cover categories and the proportion of agricultural land on each grid cell were obtained from

several sources (Appendix S1). Additional analyses on the relationships between these predictors and scarab richness were measured by ordinary least-squares (OLS) regression models; model comparison and selection was based on the AIC (Burnham & Anderson 2002; Diniz-Filho *et al.* 2008). Stronger richness–environment relationships in the north are consistent with our second prediction.

We constructed a complete phylogeny for all European Scarabaeinae species and used the net relatedness index (NRI; Webb *et al.* 2002) to evaluate whether any assemblage is a phylogenetically structured subset of the whole regional pool. We started with Villalba *et al.*'s (2002) phylogenetic hypothesis, which includes 33 of the total of 106 species, and assigned missing species to the most likely node in the phylogeny as unresolved polytomies, based on additional molecular, morphological and taxonomic information (Appendix S2). To account for the uncertainty in tree topology generated by these polytomies, we created 1000 phylogenetic trees by shuffling the position of the newly added species within the node to which they were assigned, thus creating an array of possible topologies, and calculated NRI values for each of these trees. As NRI approximates the Z distribution, values higher than 1.96 indicate subsets of species that are significantly clustered. Given the phylogenetically conserved response to temperature hypothesized here, it can be assumed that climate filtering had a major role in the assembly of scarab communities hosting clustered subsets of species. We analysed phylogenetic structure at two scales. First, we evaluated whether the species that were able to make it to the north are a clustered subset of all European scarabs. Second, we evaluated whether there are differences in the phylogenetic structure of local communities by calculating NRI in each grid cell (excluding those with five or fewer species to avoid the spurious effects of low sample size). Finding that the overall group of 'escapee' species is phylogenetically structured and/or that assemblages are more clustered in the north than in the south represents evidence for our third prediction.

The spatial replacement and nestedness components of the compositional variation in community composition among all the grid cells within each of the two regions identified by the GWR and piecewise regression analyses were compared using the multiple-site dissimilarity measures β_{SIM} (Baselga *et al.* 2007) and β_{NES} (Baselga 2010b) respectively. These dissimilarity measures are additive fractions of β_{SOR} (Baselga 2010b), an overall measure accounting for all aspects of compositional variation (i.e. non-directional beta diversity *sensu* Anderson *et al.* 2011), and directly linked to true beta diversity (*sensu* Tuomisto 2010), as the Sørensen index is a monotonic transformation of true beta diversity (see Jost 2007). These dissimilarity measures, as derived from multiplicative beta diversity, are known to be independent from gamma diversity (Jost 2007; Baselga 2010a), therefore allowing the direct comparison of the components of compositional variation caused by species replacement and nestedness between different regions (see also Svenning *et al.* 2011). As β_{NES} is a measure of the compositional variation due to nested diversity patterns rather than a true metric of nestedness, we assessed whether its results were consistent with common nestedness measures (Appendix S3). All these analyses allow testing our fourth and fifth predictions.

OLS and GWR analyses were conducted in SAM v4.0 (Diniz-Filho *et al.* 2008; Rangel *et al.* 2010), faunistic dissimilarity analyses in R using the code provided by Baselga (2010b), and phylogenetic structure analyses in PAM v0.9 (*Phylogenetic Analysis in Macroecology*; T.F. Rangel and J.A.F. Diniz-Filho, unpublished). All other analyses were done in STATISTICA.

RESULTS

European scarabs show a marked decrease in richness towards the north (Fig. 1), following a linear relationship with current temperature ($r^2 = 0.72$; Fig. S1a,b). A model including all known large-scale determinants of scarab species richness (except the area of agricultural land, discarded by the AIC criterion) identifies a strong relationship with current environmental gradients ($R^2 = 0.84$; Table S1a). Besides the strong explanatory power of current conditions, climatic variability also has a strong relationship with richness ($R^2 = 0.50$). Almost all this variation is explained solely by temperature variability ($r^2 = 0.50$), with precipitation variability having much less explanatory power ($r^2 = 0.08$). Therefore, we based all subsequent analyses and discussion of climatic variability on temperature variability only.

The slope of the relationship between scarab richness and temperature variability changes drastically from steep in the richest areas to shallow in the poorer areas (Fig. S1d). Geographically weighted regression provides a spatially explicit interpretation of this result; a piecewise linear regression between GWR slopes and richness identifies two regions in Europe [breakpoint = -1.088 ; region 1 (south): $n = 354$, intercept ($\pm 95\%$ CI) = -1.222 ± 0.206 , slope ($\pm 95\%$ CI) = -0.033 ± 0.006 ; region 2 (North): $n = 701$, intercept = -0.247 ± 0.027 , slope = -0.017 ± 0.002 ; $r^2 = 0.84$], separated by a sharp transition along an $E-W$ axis placed north of the Pyrenees-Alps-Balkan-Caucasian mountain axis. This border approximately coincides with the 0°C isotherm at LGM (Fig. 2), supporting Prediction 1. Although in the north, the relationship between temperature variability and richness has GWR regression coefficients close to zero and is relatively stationary, in the south the relationship is steeper, but non-stationary. It could be argued that the smaller range of climate variability in southern Europe (Fig. S1d) could make estimating unbiased regression coefficients difficult. However, it is unlikely that this affected our results because the overall relationship between richness and temperature variability is sharper in the south (Fig. S1d), and the local r^2 values obtained with the GWR are high throughout both northern and southern Europe, except a large area of the Russian plains and the very tips of the Iberian, Italian and Balkan peninsulas (Fig. S2).

The richness–current climate relationship is stronger in the north ($R^2 = 0.84$; Table S1b) than it is in the south ($R^2 = 0.66$; Table S1c), supporting Prediction 2 to some extent. Importantly, the richness–current environment relationships not only change in strength but also in steepness; the slopes of all variables except spring precipitation and soil pH vary from one region to the other (Table 1).

The differences between southern and northern scarab assemblages are also phylogenetically structured. The subgroup of ‘escapee’ species that have established populations in the north are phylogenetically clustered (average NRI = 2.150, $P < 0.05$; 637 of the 1000 replicate phylogenies were significantly clustered), suggesting that the response to temperature is a phylogenetically conserved trait in this group, and that climate filtering is determining their ability to live in the north. This is also evident in the assemblages present in each grid cell; central Europe shows consistently higher NRI values (Fig. S3). Regardless of local variations, average NRI values per cell are much smaller in the south than they are in the north (NRI south = 1.085 ± 0.618 ; NRI = 2.388 ± 1.085 ; $t = 21.497$, $P < 0.001$); 75.53% of the grid cells in this latter region show significantly clustered NRI values for more than 50% of the randomized tree topologies. These results are consistent with Prediction 3.

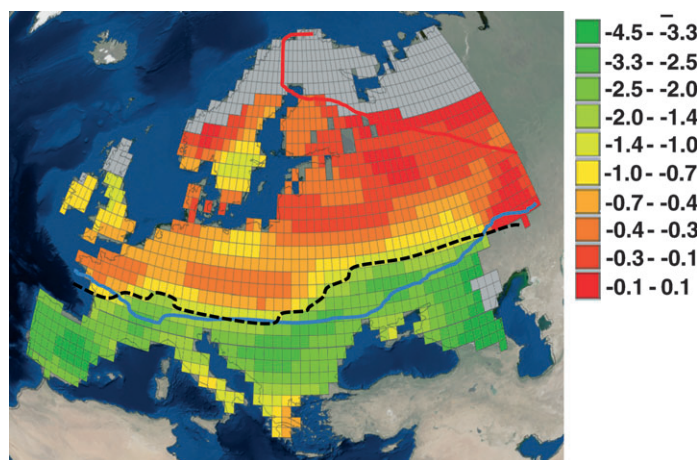


Figure 2 Non-stationarity in the relationship between scarab richness and temperature variability since the last glacial maximum (LGM). The maps show the distribution of the slope of the geographically weighted regression (GWR) model for each grid cell, identifying two distinct regions in Europe, with slopes close to zero in the north and negative slopes in the south (see text). The discontinuous black line indicates the approximate limit between these two regions, as identified by a breakpoint regression between species richness and the slope provided by the GWR model (see text). The continuous red and blue lines indicate the current and the LGM location of the 0°C isotherm, respectively (see Fig. 1 and Fig. S1).

Table 1 Differences between the slopes of the ordinary least-squares regression between scarab species richness and all seven environmental predictors in the north and south regions (mean \pm SD), according to t -tests with degrees of freedom corrected (d.f.*) for the inflation due to spatial autocorrelation in each variable.

	North	South	t -value	d.f.*	P
Current temperature	0.458 \pm 0.343	0.961 \pm 0.355	-9.66	199	< 0.001
Altitudinal range	0.017 \pm 0.173	0.151 \pm 0.101	-13.48	170	< 0.001
Spring precipitation	0.011 \pm 0.123	-0.004 \pm 0.153	1.80	130	0.076
AET	0.114 \pm 0.125	0.091 \pm 0.081	3.09	129	0.002
Soil organic matter	-0.012 \pm 0.083	-0.076 \pm 0.202	7.23	146	< 0.001
Soil pH	0.004 \pm 0.068	-0.004 \pm 0.141	1.22	181	0.2237
Agricultural land use	0.036 \pm 0.063	0.092 \pm 0.070	-13.16	157	< 0.001

AET, Actual Evapotranspiration.

Northern and southern Scarabaeinae faunas also show important differences in their richness. Although richness in the south varies from 13 to 61 species per cell (median = 37 species), northern assemblages are much poorer, decreasing gradually towards the north from a maximum of 27 species in the northern foothills of the Pyrenees-Alps-Balkan-Caucasian mountain axis (median = 8 species) (Fig. 1). In fact, the northern fauna is a completely nested subset of the species in the south; only 38 species (36%) inhabit the north, and all of them are present in the south. Most of these species are known to be generalists and widespread (e.g. Hanski & Cambefort 1991). The Mediterranean dung beetle fauna, however, is characterized by high levels of endemism (Lumaret & Lobo 1996), a larger number of trophic specialists (e.g. Lumaret & Kirk 1987; Lobo et al. 2006) and a greater seasonality in the activity of the species (Hanski & Cambefort 1991). These general characteristics also shape the compositional dissimilarity of the faunas within each region. Although true spatial turnover is lower in the north than in the south ($\beta_{\text{SIM}} = 0.74$ and 0.90 respectively; $P < 0.001$), the dissimilarity due to nestedness is higher in the north ($\beta_{\text{NES}} = 0.22$ and 0.10 respectively; $P < 0.001$) (Fig. 3),

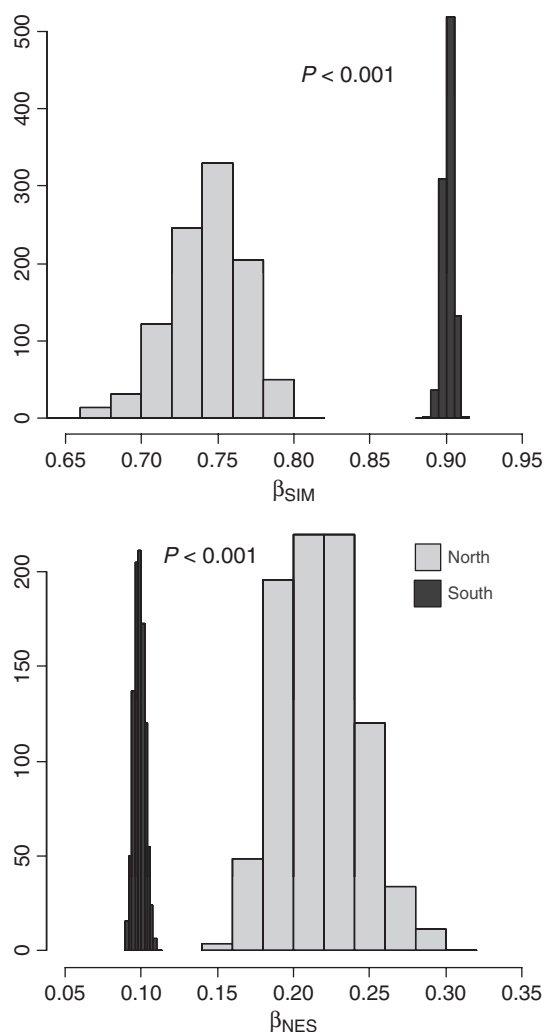


Figure 3 Compositional dissimilarity in the north and south areas identified through a breakpoint regression on geographically weighted regression (GWR)-derived richness–temperature variability slopes (see text and Fig. 2). The upper graph shows the distribution of spatial turnover values (β_{SIM}) and the lower one shows it for values of dissimilarity due to nestedness (β_{NES}). Results correspond to the calculations of each multiple-site dissimilarity measure based on 100 cells randomly selected in each area, repeated 1000 times (see Baselga 2010b for further details). The probability (P) of having obtained the opposite result (i.e. higher turnover or lower nestedness in the north) was computed empirically comparing statistics' distributions.

supporting Predictions 4 and 5. These results are consistent with those obtained with true metrics of nestedness (Appendix S3).

DISCUSSION

Despite the strong correlation between scarab species richness and current temperature, our analyses identify two distinct regions hosting structurally different assemblages, with differing responses to current climate. Other studies have also reported different diversity–environment relationships between northern and southern assemblages in northern temperate regions, often showing consistently similar changes across different groups (Whittaker *et al.* 2007). For example, the changes in the slope of the relationships between scarab richness and both AET and altitudinal range are similar to those found for

European plants (Svenning *et al.* 2009); in both groups the relationship with AET is shallower in the south than in the north and the opposite holds true for altitudinal range. This may indicate that some general mechanisms may be operating at the assemblage level, such as a dominating influence of energy input on diversity in the harsh conditions present in the north (see Hawkins *et al.* 2003; Whittaker *et al.* 2007), or a greater facilitation of coexistence by increasing altitudinal range in the south due to the presence of a more diversified species pool (see Svenning *et al.* 2009 and references therein).

What our results clearly indicate is that latitudinal differences in diversity–environment relationships correlate with the climatic history of the region, which interacts with the idiosyncratic characteristics of each particular group. As far as we know, this is the first time the relationship between diversity and historical climate changes has been used to identify the border between the northern and southern assemblages of north temperate continental areas. In our case, changes in the characteristics of scarab assemblages and the strength and steepness of the diversity–environment relationships roughly coincide with the location of the 0 °C isotherm at LGM, consistent with an effect of the past configuration of climate on current diversity. The two areas delimited by this isoline support taxonomically different assemblages; only representatives from a few clades have managed to make it to the north, which is composed of a phylogenetically clustered subset of the southern fauna. Most of these ‘escapee’ species are Onthophagini (28 of 38), nearly half of the 67 European species of this species-rich tribe (Fig. S4). Some representatives of most of the other Scarabaeinae tribes present in Europe are widespread in the north, reaching as far north as the low countries (*Sisyphus schaefferi*, Sisyphini), southern Great Britain (*Euoniticellus fulvus*, Oniticellini), the Russian steppes (*Gymnopleurus geoffroyi*, Gymnopleurini) or southern Finland (*Copris lunaris*, Coprini). In contrast, the Scarabaeini barely reach the central French plains (*Scarabaeus laticollis*), and no species of Onitini have colonized the north (Fig. S4). The impact of this phylogenetically clustered selection of escapee species to live in the north is particularly evident in central European assemblages (Fig. S3).

The particular adaptations of each clade are known to affect diversity patterns both between regions (Ricklefs 2007) and within each region (Hawkins *et al.* 2005, 2007b). Given the probable Gondwanan tropical origin of scarabs we can hypothesize that most, if not all, of the species currently inhabiting northern Europe correspond to relatively recent diversifications, as several clades have evolved adaptations to cold temperate environments. Current knowledge of the evolutionary relationships within Scarabaeinae is limited in its coverage of European species and lacks a proper dating of diversification events (Appendix S2; Villalba *et al.* 2002; Monaghan *et al.* 2007). In spite of these limitations, our analyses were able to detect a significant clustering of northern assemblages, indicating that thermal tolerance may be a phylogenetically conserved trait. Only a few scarab tribes have been able to escape from such limitation and colonize northern Europe, a pattern that seems related to their global success; although Onthophagini, Coprini and Gymnopleurini occur worldwide, most Scarabaeini and all Onitini are restricted to the old world (Monaghan *et al.* 2007). In particular, the highly successful Onthophagini hold a derived phylogenetic position within Scarabaeinae (Villalba *et al.* 2002; Monaghan *et al.* 2007); many of their species from the Oriental and Palearctic regions are considered an Afro–Eurasian lineage that radiated during the Eocene–Oligocene in parallel with the expansion of large herbivores and grassland landscapes (Davis *et al.* 2002; Scholtz *et al.* 2009). In contrast, the

subfamilies restricted to the south (Onitini and Scarabeini; Fig. S4) are ancient clades, where no extant species have developed adaptations to cold temperate environments.

The ecological and evolutionary processes generating the regional pool of European scarabs and the assembly of communities over time have led to important differences in the structure of northern and southern assemblages. The extremely harsh climatic conditions at the LGM impeded the survival of Scarabaeinae species in the north. Thus, the current composition of northern assemblages is the result of post-glacial recolonization by a limited number of generalist species with relatively recent adaptations to cold environments. We argue that in northern Europe the latitudinal gradient in scarab richness is predominantly driven by the northward decrease in current temperature due to the strong phylogenetic conservatism of their need for warm climates (phylogenetic niche similarity *sensu* Swenson 2011). In contrast to other groups, many dung beetles have particularly high colonization abilities (up to tens or hundreds of km per year), and the majority of species inhabiting northern Europe are generalist coprophages (Hanski & Cambefort 1991), and able to feed on the nutrient-rich dung from domestic cattle and sheep herds that are abundant almost everywhere in this region. Thus, it seems unlikely that the current diversity pattern in the north is predominantly shaped by limited post-glacial dispersal, as found for other groups with more limited dispersal abilities (e.g. Svenning & Skov 2007). Rather, the ancestral adaptation of Scarabaeinae to tropical environments imposes a strong constraint on their ability to tolerate freezing conditions. These evolutionary constraints would have prevented most species from colonizing the north, and would still strongly limit the ability of surviving at progressively colder temperatures of those that did colonize such area. In contrast to other groups (Svenning *et al.* 2011), scarab assemblages show significant amounts of nested species loss in the north due to the ordered exclusion of species that are not able to live in progressively colder environments. Given the colonization ability and trophic generalism of these species, they may have been able to colonize all climatically suitable areas, and so the current northern borders of their distribution ranges would be determined by their physiological limitations. This evolutionarily constrained loss generates a tight relationship between richness and temperature (Table S1), and a weaker relationship with climate variability.

In contrast, dung beetle assemblages persisted through the glaciations in the south. Hence, their current composition is the product of a number of ecological and evolutionary processes acting over a larger period of time. Due to this, the number of specialists and species with restricted distributions is much larger in the south than in the north, related with the more complex evolutionary history of the Mediterranean dung beetles (Lumaret & Lobo 1996) combined with longer times for diversification and community assembly. Thus, the correlation between richness and current environment is weaker in the south, and the biotic dissimilarity among scarab dung beetle assemblages is more strongly driven by true replacement of some species than others, forming phylogenetically overdispersed communities.

Our results suggest that the multiple processes driving diversity patterns can be reconciled, supporting Wiens & Donoghue (2004) argument that it is possible to reconcile the hypotheses for the origin of biodiversity gradients based on either current climate (Currie 1991), regional evolutionary constraints (Ricklefs 2007) or the past effects of climate and other factors (Araújo *et al.* 2008) acting at multiple temporal scales (see also Swenson 2011). In the specific case of European scarabs, we show how ice age legacy can shape biodiversity

gradients by limiting the faunas inhabiting some areas to a reduced number of species and clades. In northern Europe, the relationship between past climate changes and species richness is stronger because glaciation disrupted the assemblages existing in the previous interglacial stage (Rodríguez 2006). Hence, current assemblages would be composed of a few generalist species with high dispersal ability that have developed adaptations to live under cold temperate conditions, and richness patterns would be mainly driven by climatic filtering (see Webb *et al.* 2002). In the Mediterranean and Caucasian Europe, however, past climate changes would have had a weaker effect, being local assemblages not as heavily disrupted during the last glaciation as they were in the north. This, together with the longer time to evolve adaptations to warm temperate conditions (Wiens & Donoghue 2004) would result in more complex richness patterns and community assembly processes than in the north, following also other factors not structured in geographical gradients (e.g. biotic interactions). Interestingly, although the historical effects acting at both evolutionary and ecological timescales have resulted in large differences in the composition and structure of scarab assemblages between north and south, their geographical configuration as two latitudinal bands leads to the confounding pattern that their combination at the European extent results in a sharp geographical covariation with large-scale environmental gradients. Such heterogeneity will only be apparent when the stationarity of the effects of current and past environmental conditions is explicitly studied.

European diversity patterns are particularly complex due to its particular history and geomorphological and geographical structure (Whittaker *et al.* 2007). Thus, it could be argued that the results found here are specific to Scarabaeinae dung beetles, being the result of certain particularities such as their high dispersal ability, the general availability of their food sources and their physiological limitations to survive in cold environments. However, similar transitions between northern and southern European assemblages have been also described for other groups. Narrow-ranged species of reptiles, amphibians, longhorn and ground beetles and trees are restricted to the south of Europe, whereas most species inhabiting the north are widespread (Montoya *et al.* 2007; Svenning & Skov 2007; Araújo *et al.* 2008; Baselga 2008; Schuldt & Assmann 2009). Thus, we predict that, once the particularities arising from differences in environmental responses, dispersal ability and other traits are taken into account, the effects of climatic variability found here will hold on for a large number of groups. We can nevertheless conclude that some of the commonly observed strong correlations between current climate and diversity gradients may in fact be of historical origin, for they are ultimately determined by the interplay of recent dispersal processes and the evolutionary history of the regional faunas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data origin.

Appendix S2 Scarabaeinae phylogeny used in the analyses.

Appendix S3 Additional nestedness analyses.

Figure S1 Geographical distribution in Europe of current mean annual temperature and temperature variability since the LGM.

Figure S2 Geographical distribution of the coefficient of determination (r^2) of the species richness–temperature variability GWR model for each grid cell.

Figure S3 Geographical distribution of the values of the Net Relatedness Index (NRI) for each grid cell.

Figure S4 Species richness of the seven Scarabaeinae tribes with European representatives.

Table S1 Results of the OLS models for all Europe and the southern and northern areas identified in this work.

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