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Phylogenetic diversity of regional beetle faunas at high latitudes: patterns, drivers and chance along ecological gradients

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Abstract

Patterns in phylogenetic diversity are poorly known for many taxonomic groups, including hyperdiverse insect taxa. We contrasted patterns in the species richness and phylogenetic diversity of provincial beetle faunas in northern Europe (54°N to 71°N). We found that species richness and phylogenetic diversity varied rather predictably along ecogeographical gradients, with species richness and a proxy measure of phylogenetic diversity, average taxonomic distinctness (AvTD), decreasing from south to north and being strongly positively related to maximum temperature. A proxy measure of variation in phylogenetic diversity, variation in taxonomic distinctness (VarTD), was also strongly related to maximum temperature, but the relationship was negative. This was a novel finding, showing a reversed latitudinal gradient in a facet of biodiversity. In more than half of the provinces, AvTD value was significantly less than expected by chance. Also, more than half of the provinces showed significantly higher VarTD values than expected based on random draws of species. Our results showed that the phylogenetic diversity of beetle faunas is rather strongly associated with climatic gradients at high latitudes. Given that climatic variability and temperature extremes are correlated with phylogenetic diversity, climate change is likely to modify strongly this facet of diversity. Average phylogenetic diversity is likely to increase in the northernmost parts of the study area if climate and vegetation become more suitable for many southern beetle species. Our statistical approach to test chance expectations based on random draws of species from larger-scale species pool is highly flexible in tackling this question when true phylogenies are not available.

Keywords: climatic variability, precipitation variability, species richness, taxonomic distinctness, temperature.

Introduction

Biodiversity of regional biotas is shaped by both historical and currently prevailing factors, resulting in patterns we observe along major ecogeographical gradients (Rosenzweig 1995; Lomolino et al. 2010). Such trends in biodiversity are well known and understood for many conspicuous elements of regional biotas, such as mammals (e.g. Mazel et al. 2014), birds (e.g. Devictor et al. 2010) and trees (e.g. Wang et al. 2009). In contrast, many less-conspicuous organismal groups, such as many insect taxa, remain poorly known (e.g. Leather 2009), as are also the factors that influence their species, functional and phylogenetic diversity patterns at broad spatial scales in the present day (e.g. Diniz-Filho et al. 2010). This lack of knowledge hinders our attempts to predict changes in much of biodiversity to be expected in the future.

Species richness is the simplest and the most commonly used measure of biological diversity in studies at broad spatial scales (e.g. Magurran 2004). However, simply tallying the number of species inhabiting a certain area is not necessarily the best measure of biological diversity (e.g. Vellend et al. 2010). For example, an area hosting a large number of species, which are phylogenetically closely related, should receive a lower conservation priority than an area hosting a smaller number of species, which are phylogenetically distantly related (Posadas et al. 2001; Strecker et al. 2011; Luz Ribeiro et al. 2012; Hidasi-Neto et al. 2015). Phylogenetic diversity can be used as a proxy of ecological differences among species in biological assemblages, but has rarely been considered for many, if not most, organismal groups. Differences in ecological niches among species are also usually expressed as functional diversity (e.g. Mouquet et al. 2012). However, the use of functional diversity in ecological studies is, unfortunately, hampered by severe difficulties in measuring various important functional traits similarly for large numbers of species (e.g. Cadotte et al. 2009).

Phylogenetic diversity, typically defined as average phylogenetic distance between species in an assemblage (e.g. Vellend et al. 2010), has recently gained increasing interest from ecologists and evolutionary biologists (e.g. Devictor et al. 2010), because it can be measured in a standardized way over an immense range of organisms (e.g. Cadotte et al. 2009). Moreover, if average phylogenetic distance between species in an area is also a good proxy for their average ecological differences, then it is related to functional diversity (Srivastava et al. 2012; Winter et al. 2013) and can be used extensively in studies focusing on biodiversity patterns (Cadotte et al. 2009; Ricklefs and Jenkins 2011). For example, if phylogenetic diversity is related predictably to altitudinal or climatic variation in the present day, it may also portray ecological responses of species assemblages to global changes in the future. Understanding those patterns is hence of profound interest if we want to predict future alterations in regional biotas in the face of global climate change.

Global climate change has been under increasing interest among researchers and the public in the last two decades (IPCC 2014). Biological climate change research has mostly focused on predicting changes in biotas based on future climate scenarios (Malcolm et al. 2006; Thomas et al. 2010; Chatrou et al. 2010; Cowie 2013), and most studies have concentrated only on species richness or the distributions of single species in relation to climate change scenarios (Parmesan, 2006; Rödder et al. 2011; Fordham et al. 2013). Instead, relatively few studies have associated potential changes in phylogenetic diversity to their climatic and other ecological drivers (Thuiller et al. 2011; Pio et al. 2014). Furthermore, many small but important players in ecological systems, such as most insect groups, remain poorly studied in this context both globally and in high-latitude regions in particular. High-latitude regions have experienced and are predicted to experience stronger changes in climate compared to many other regions in the future (Anisimov et al. 2007; Lenton et al. 2008; Heino et al. 2009; Cowie 2013), but little is known how the phylogenetic diversity of insect faunas is associated with changes, variations and extremes in climatic conditions

(Andrew et al. 2013). Furthermore, given that both aquatic and terrestrial vegetation is likely to change profoundly in the face of climate change in high latitudes (Heino et al. 2009; Alahuhta et al. 2011), many insects associated with terrestrial, semi-aquatic and aquatic habitats will likely respond to those changes rapidly (Hickling et al. 2006; Thomas et al. 2006). This is because most insects rely on plants either directly as food sources or indirectly as habitat structure provided by vegetation.

Most previous studies have modelled climate effects on biotas across a set of many assemblages (i.e. the modelling approach), whereas little is known if an area comprises levels of phylogenetic diversity that differs from chance expectations of random draws of species from a larger species pool (i.e. the assemblage-by-assemblage approach). Such an approach was developed by Clarke and Warwick (1998, 2001a) to examine the effects of anthropogenic disturbance on the taxonomic distinctness of marine faunas. Subsequently, this approach has been used extensively in marine (e.g. Clarke and Warwick 1998), freshwater (e.g. Heino et al. 2007) and terrestrial (e.g. Baños-Picón et al. 2009) ecosystems. However, to the best of our knowledge, this approach has not been used in insect biogeographical and macroecological studies encompassing large geographic areas. This is surprising because testing the levels of taxonomic distinctness in an area against random expectations is similar to testing the pure chance effects on phylogenetic diversity, which may complement findings derived from the commonly-used modelling approaches.

In this study, we focused on beetles which comprise the largest order of life on Earth (Thomas 2008) and are phylogenetically, biologically and ecologically the most diverse insect order at high latitudes in Europe (http://www.faunaeur.org/). We hence collated literature data for the occurrence of species in main beetle families in the biogeographical provinces of the Nordic countries (for a similar approach, see Väisänen et al. 1992). Subsequently, we measured taxonomic distances between all of the 867 beetle species in 11 aquatic, semiaquatic and terrestrial families and calculated phylogenetic diversity measures for each province (Warwick and Clarke 1995;

Clarke and Warwick 2001a). We used taxonomy as a proxy for phylogeny because there are no available phylogenetic reconstructions for all the species included in this study. However, recent studies have demonstrated that taxonomic hierarchies are good proxies of dated phylogenetic reconstructions (Ricotta et al. 2012).

We put forward five main hypotheses about how phylogenetic diversity is expected to vary in relation with ecological and geographical factors. We first hypothesized (H_1) that phylogenetic diversity should decline toward Arctic regions, following a similar decline in species richness (Hawkins et al. 2004; Lomolino et al. 2010; Fattorini and Ulrich 2012a; Fritz and Rahbek 2012). Second (H_2), we hypothesized that phylogenetic diversity should increase with increasing altitudinal range because it is related to variation in climatic and habitat conditions within a province. It is known that more heterogeneous and physically complex environments host more diverse assemblages (Kerr et al. 2001; Rahbek and Graves 2001) and that species richness tends to be higher in areas with pronounced elevation range (Ricklefs et al. 2004; Keil et al. 2008). Third (H_3), phylogenetic diversity should be driven by climatic variability, such as range in annual temperature and variation in precipitation (Currie et al. 2004; Hawkins et al. 2007). Fourth (H_4), phylogenetic diversity should be associated with minimum and maximum temperatures because only certain lineages tend to survive in climatic extremes, although we are not aware of previous findings of such trends. Fifth (H_5), based on random resampling from the larger regional species pool, we hypothesized that phylogenetic diversity in each biogeographic province is not different from that expected by chance. To the best of our knowledge, these questions of phylogenetic diversity patterns have not been tackled using beetles as the model organismal groups.

Materials and methods

Study area, datasets and study organisms

We collated data for beetles from the biogeographic provinces belonging to the Nordic countries: Denmark, Sweden, Norway and Finland (for a similar approach, see Väisänen et al. 1992; Väisänen and Heliövaara 1994). Prior to the analyses, we merged small coastal provinces in Norway and omitted a single small Swedish island province (Gotska Sandö) to provide a better and more accurate representation of species ranges. After these modifications, the number of provinces we analysed decreased from 101 to 79 (Heino and Alahuhta 2015). The insect faunas in the study area are relatively well-known, providing good data for many insect groups that are used infrequently in biogeographical and macroecological studies (Väisänen et al. 1992; Väisänen and Heliövaara 1994). Furthermore, use of more natural biogeographical units may be a good option over the use of grid data (Heino and Alahuhta 2015). We therefore used the 79 provinces as sampling units, where all the species recorded from each province represents a single regional assemblage. Our analyses were hence based on province-by-diversity index and province-by-predictor variables matrices.

We analyzed biological data for 867 species in 11 beetle (Coleoptera) families. The families included: Dytiscidae (155 species), Gyrinidae (16 species), Haliplidae (22 species), Hygrobiidae (1 species), Noteridae (2 species), Carabidae (389 species), Hydraenidae (23 species), Spercheidae (1 species), Hydrophilidae (92 species), Cerambycidae (118 species) and Buprestidae (48 species). These beetle families represent much, but certainly not all, of the taxonomic, biological and ecological variation among beetles, including major taxonomic suborders, body size variations and habitat types inhabited by beetles. For example, diving beetles (Dytiscidae) occur in all kinds of freshwater ecosystems, and some species may also be found in brackish waters. Most diving beetle adults and larvae are predaceous, although there are also some detritivorous and herbivorous species (Nilsson and Holmen 1995). Whirlirlig beetles (Gyrinidae) are aquatic insects, which are predaceous both as larvae and adults. Squeak beetles (Hygrobiidae) are a small family of aquatic insects, which feed on various benthic material. Burrowing water beetles (Noteridae) are aquatic as larvae and adults, and most species are predaceous (Holmen 1987). Ground beetles (Carabidae) are a very large family of insects, whose adults are predaceous, omnivorous, granivorous or herbivorous, whereas their larvae are mainly predaceous, occurring in most terrestrial habitat types (Lindroth 1985). Crawling water-beetles (Hydraenidae) are aquatic or semi-aquatic as larvae and adults. They are mostly phytophagous, although some saprophagous and predatory species are also known (Hansen 1987). Filter-feeding water scavenger beetles (Spercheidae) are a small family of aquatic beetles (Hansen 1987). Water scavenger beetles (Hydrophilidae) are mostly aquatic or semiaquatic beetles, which are scavenging, predaceous or herbivorous as adults, and predaceous as larvae (Hansen 1987). Some are coprophagus beetles associated with faeces of various terrestrial animals. Longhorn beetles (Cerambycidae) are terrestrial, living mainly in timber as larvae and being herbivorous as adults, although adult food sources vary considerably (Bílý and Mehl 1989). Also, some longhorn beetle species develop in herbs or leaves of trees. Jewel beetles (Buprestidae) are terrestrial insects. Their larvae bore trough logs, branches, roots and leaves of many plant species. Some species are largely restricted to recently burned forests (Bílý 1982).

Species occurrence data for each province was collated from the literature (Bílý 1982; Lindroth 1985, 1986; Hansen 1987; Holmen 1987; Bílý and Mehl 1989; Nilsson and Holmen 1995). Full provincial species lists can be found in the above references. Although these faunistic data are not very recent, they represented well the distributions of species and served as useful data for our analyses. Newer province data were not easily available in the literature.

Explanatory variables

We had eight predictor variables in our main statistical analyses. Province area was used for controlling sampling effects because larger areas are likely to sample more species, whereas the mid latitude of each province was used to control for latitudinal gradients (Lomolino et al. 2010). The remaining six variables we divided into three variable groups. First, *elevation variables* included mean altitude (meters above sea level) and altitude range (meters), which are strongly related to the range of natural aquatic, semiaquatic and terrestrial habitat types in a province. Elevation variables were obtained from 3D Digital Elevation Model over Europe with 25 m resolution. Second, *temperature variables* included minimum temperature of the coldest month (°C) and maximum temperature of the warmest month (^{o}C). Third, *climatic annual variability variables* included annual temperature range (°C) and coefficient of variation in precipitation. The temperature and precipitation variables were averaged values for each biogeographical province and were derived from WorldClim with 0.93 km × 0.93 km resolution (Hijmans et al. 2005).

Proxy measures of phylogenetic diversity

Owing to lack of true phylogeny comprising all the beetle species in our data, we used taxonomic hierarchies as a proxy for phylogenetic relationships, as has been done in many studies dealing with phylogenetic diversity (for example, see Purvis et al. 2005). Higher taxonomic levels for each species were checked from Fauna Europaea (http://www.faunaeur.org/). Hence, after taxonomic checks, there were seven taxonomic levels above species level in the taxonomic aggregation matrix. For calculating phylogenetic diversity, we used two indices that are based on taxonomic distances between species. We thus calculated average taxonomic distinctness (AvTD; Warwick and Clarke 1995) and variation in taxonomic distinctness (VarTD; Clarke and Warwick 2001a) for the beetle faunas in each province (Fig. 1). We used equal branch lengths and seven supra-species taxonomic levels for the calculation of taxonomic distances between species: genus, tribe, subfamily, family, superfamily, suborder and order. For some species, the taxonomic level “tribe” was not found in the literature and, hence, we substituted missing information by abbreviation of subfamily name (e.g. *Haliplus confinis* < *Haliplus* < Haliplini < Haliplinae < Haliplidae < Caraboidea < Adephaga < Coleoptera). After the calculation of taxonomic distances, which takes into account the taxonomic relatedness of species in the taxonomic hierarchy, we followed Clarke and Warwick’s (1998, 2001a) original approaches to calculate the two indices. AvTD measures the mean taxonomic (or phylogenetic) distance between species in an assemblage (Clarke and Warwick 1998). Hence, a province with high values for AvTD is phylogenetically diverse, and vice versa. Similarly, large VarTD index values indicate a phylogenetically variable province (Clarke and Warwick 2001a). These indices are mathematically unrelated to variation in species richness and are thus suitable measures of phylogenetic diversity in datasets where species richness varies widely. We calculated AvTD and VarTD for each province using PRIMER version 6 (Clarke and Warwick 2001b).

Statistical methods for modelling diversity across the provinces

We modelled variation in species richness, AvTD and VarTD using least squares regression and variation partitioning through partial linear regression (Legendre and Legendre, 2012). First, we ran an overall explanatory model for each of the three response variables (i.e. richness, AVTD and VarTD), incorporating six explanatory variables: (1) altitude, (2) altitude range, (3) annual temperature range, (4) coefficient of variation of precipitation, (5) minimum temperature and (6) maximum temperature. Second, for each of the three measure of biodiversity (i.e. the response variable), we ran three models to test separately the effects of altitude (a), climatic variability (b) and temperature extremes (c) as follows:

(a) Diversity ~ latitude + area + altitude + altitude range.

(b) Diversity ~ latitude + area + temperature range + coefficient of variation of precipitation.

(c) Diversity ~ latitude + area + maximum temperature + minimum temperature

In these models, province latitude and province area were used to control for their known effects on biological diversity, whereas the other two predictor variables in each model were used to test our *a priori* hypotheses related to elevation effects (a), climate variability effects (b) and temperature effects (c). Least squares regressions were run using the R package *Rcmdr* (Fox 2014) and variation partitioning using the function "varpart" in the R package *vegan* (Oksanen et al. 2013).

We also ran variation partitioning analyses for each response variable as above (i.e. models a, b and c), but where latitude was substituted by multiple spatial variables obtained from distance-based Moran eigenvector maps (db-MEM; Legendre and Legendre 2012; see Supporting Information, Appendix S1). These additional spatial variables were used because the residuals of the original models, even when including latitude, showed significant spatial autocorrelation, whereas those including the db-MEM variables did not do so. Spatial autocorrelation in model residuals was tested using the function "Moran.I" in the R package *ape* (Paradis et al. 2014). Although spatial autocorrelation in residuals may cause problems in interpreting the results, it is a genuine phenomenon in biogeographical and macroecological studies. Kühn and Dormann (2012) summarized this phenomenon as follows: "If the spatial autocorrelation of an ecological response variable is caused by autocorrelated predictor variables (such as climate, land use, topography, human population densities or virtually any other spatial predictor), we are not alarmed. Of course we do not wish to remove this effect of such predictors." Hence, given that both our response and predictor variables were autocorrelated owing to geographical and climate influences on provincial beetle faunas in our study area (Väisänen et al. 1992; Heino and Alahuhta 2015), we considered spatial autocorrelation as a natural phenomenon that is related to the drivers of diversity. Also, Diniz-Filho et al. (2003) noted that removing spatial patterns in diversity statistically may be problematic if those patterns are generated by broad-scale mechanisms. In our study, space was considered as proxy for temporal trends in species richness and phylogenetic diversity in the face of changing climate.

We also tested for the hypothesis that AvTD or VarTD of a provincial beetle fauna is not different from that expected by chance with respect to the observed number of species in a province (Clarke and Warwick 1998; 2001a). This was done by comparing the observed AvTD or VarTD value with those from 1000 permutations of the data. The permutations selected randomly the same number of species from the regional pool as was observed in a province, calculated expected AvTD or VarTD based on random draws, and compared the observed AvTD or VarTD with a distribution of 1000 randomized index values. This analysis complements the above modelling analyses because it focuses on a single province at a time, whereas modelling analyses focus only on the patterns across all provinces.

Results

Overall models of richness, AvTD and VarTD of beetles showed that maximum temperature was the most influential variable, being significant for all three response variables (Table 1). Altitude range was also significant for AvTD and temperature annual range was significant for VarTD. The explained variation was relatively high for all models, being always more than 60%. While richness and AvTD were negatively related to latitude, VarTD showed an opposite pattern (Supporting Information, Fig. S1). This reversed latitudinal gradient was a particularly novel finding. Residuals of these overall models did not show significant spatial autocorrelation (Moran I, $P > 0.08$). However, those models suffered from multicollinearity, and variance inflation factors were as high as 20 for some variables. Hence, we ran variation partitioning for three subsets of the ecological variables, while controlling for latitude and province area. Variation partitioning showed, first, that models of species richness were slightly better than those for AvTD and VarTD (Table 2), and that the signs of predictor variables were different between species richness or AvTD and VarTD (Table 1). Second, richness and AvTD increased with maximum temperature, whereas VarTD decreased with increasing maximum temperature (Table 1). Third, although the shared effects between the predictor variables were high in altitude, climatic variability and temperature models, pure fractions were significant in some cases (Table 2). For example, temperature annual range was significant for all response variables, and the same was true with regard to maximum temperature. Residuals of these subset models showed significant spatial autocorrelation in all cases (Moran I, $P < 0.05$).

Randomization tests of AvTD and VarTD showed that lower (LS) than expected values of AvTD were generally found in the northern and western provinces, whereas higher (HS) than expected values of VarTD were found in some western provinces (Fig. 2). It was also evident that the number of provinces with non-significant index values (NS) were more common than significantly higher index values for AvTD or lower index values for VarTD. The provinces with non-significant (NS) index values generally occurred in mid-latitudes in the study area.

Discussion

We found that beetle species richness showed a strong latitudinal trend and was strongly related to variation in maximum temperature across the provinces. However, quite unexpectedly, mean taxonomic distinctness (AvTD) was rather weakly related to latitude and temperature variables, and variation in taxonomic distinctness (VarTD) was even negatively related to species richness and AvTD. The reversed latitudinal gradient for VarTD was a particularly novel finding, as it showed a pattern opposite to those found for many other facets of biodiversity. Below, we will consider these main findings in the light of our *a priori* hypotheses and their implications for biological climate change research.

Our first hypothesis (H_1) stated that biological diversity should decrease with increasing latitude. We found partial support for this hypothesis because species richness was strongly negatively related to latitude. Also, AvTD was negatively related to latitude, although this relationship was not particularly strong. These patterns suggest that species richness, and to a lesser extent AvTD, obey the general law of decreasing biological diversity with increasing latitude in general (Hawkins et al. 2003; Hawkins and Diniz-Filho 2004) and in high-latitude regions in particular (Väisänen et al. 1992; Heino 2001). Phylogenetic variability, or rather its proxy measure VarTD, was instead strongly positively related to latitude. However, latitude is at best a proxy for (1) true historical and (2) environmental drivers of biological diversity that should be always considered along with latitudinal gradients. First, the region encompassing the Nordic countries was almost completely covered by ice during Pleistocene glaciations, which effectively erased pre-Pleistocene faunas. Virtually all beetle species currently present in the Nordic countries have colonized this region after deglaciation beginning about 12 000 years ago (e.g. Hewitt 1999). It is well known the persistence, in southern Europe, of small refugia, usually referred to as nunataks, even within, or adjacent to, ice sheets, for example along the Alps (see Schneeweissand Schönswetter 2011 for a critical review). Small, 'cryptic' refugia existed also in the North during glacials (Stewart et al. 2010). However,these Nordic cryptic refugia allowed the persistence of a very limited number of species and their role in determining current distributional patterns is debated (Tzedakis et al. 2013; Rull 2014). Moreover, while southern European regions acted as long-term refugia, which were inhabited throughout full glacial/interglacial cycles, refugial areas in Nordic regions were inhabited only during the contraction phases (Stewart et al. 2010).

Thus, we can assume that Nordic regions were mostly recolonized by species that survived Pleistocene glaciations in southern and central Europe. These species are mainly subsets of the southern biotas, although some species with present-day distribution not including southern and central Europe are also present. Obviously, within the various taxonomic groups which survived in Pleistocene glaciations in more southerly regions, only the most mobile and cold-adapted species have been able to colonize our study area after deglaciation. This likely led to the formation of biotas composed of a small number of species belonging to the most disparate lineages (e.g. Fattorini and Ulrich 2012b). Second, one cannot rule out the effects of climatic factors on the present-day distributions of beetles in our study area, and it may indeed be difficult to disentangle co-varying historical and climatic effects on beetle faunas at high latitudes (e.g. Heino and Alahuhta 2015).

Our second hypothesis (H_2) was related to effects of altitude and altitudinal range on beetle diversity, because those variables are known to be proxies for environmental diversity in an area (Ricklefs et al. 2004; Keil et al. 2008). It was hence surprising that altitudinal variation was not significantly related to species richness or VarTD, although it did explain significant variation in AvTD when other predictor variables were controlled for. This absence of a significant relationship between species richness and altitude range may stem from the geographical variation in altitude range itself. The provinces with larger altitude range are located in the western and northern provinces, which may not be climatically suitable for many beetle species (i.e. too maritime or too cold climates, respectively). Moreover, in most organisms, and especially insects, species richness is known to decrease with increasing altitude (Stevens 1992; Hodkinson 2005) both as a consequence of various abiotic and biotic factors (especially decreasing temperatures) (Kaspari et al. 2000), and as a possible reflection of a variation in range size of the species, the so-called Rapoport’s rule, which is in turn a reflection of variation in species tolerance (Stevens 1992; Sanders 2002). Thus, if from on hand, increasing elevation means more habitat types, on the other hand, over a certain elevational threshold, the environment becomes too harsh (too low temperature, lack of liquid water, lack of trees, etc.) for most species. The species that can be found at higher elevations tend to be – especially for thermophilic insects – mainly a subset of the most tolerant species found at lower elevations, with the addition of only few specialized species restricted to high altitude biotopes (Fattorini 2014)

However, we also found that AvTD increased slightly with altitude range, suggesting that, on average, phylogenetically and thus ecologically different species may sometimes be found in the same region (but probably at different altitudes) when altitude range increases. This is an expected finding because vegetation, physical environment and temperature vary strongly in provinces with a high altitude variation (i.e. there may be deciduous forest, coniferous forest and alpine landscapes in provinces with high altitude range). It is well known that altitude affects not only the species richness, but also the species composition of insect communities (Hodkinson 2005). Of course, larger altitudinal ranges allow more opportunities for species replacement along the elevational gradients, which in turn allow the co-presence, in the same region, of species associated with different biotopes at different elevations.

Our third (H_3) and fourth (H_4) hypotheses predicted that climatic variability and temperature extremes, respectively, should be associated with variation in biological diversity. We found strong support for these two hypotheses. For example, maximum temperature explained much significant variation in species richness, AvTD and VarTD even when latitude and province area were controlled for (Table 2). However, while species richness and AvTD increased with maximum temperature, VarTD showed a negative relationship with this predictor variable (Table 1). This finding may be explained by the conceptual differences between AvTD and VarTD. Although both are measures of phylogenetic diversity, AvTD is an averaged index, whereas VarTD is a measure of unevenness of the phylogenetic tree where one or a few species distantly related to other species in an assemblage have strong influence on the index values (Clarke and Warwick 2001a). Tolimieri and Anderson (2010) state this difference between the two indices: “Specifically, two taxonomic hierarchies can produce the same AvTD with different VarTD. For example, a species list containing several different orders each with one genus and species, but also with some genera having many species, would give a high VarTD compared to a list (of equivalent AvTD) in which most species were from different families but within the same order." In other words, it seems that temperature extremes "prune" the phylogenetic tree at more basal nodes, resulting in differences between patterns in AvTD and VarTD in our study area.

Our fifth hypothesis (H_5) stated that AvTD or VarTD values should not be different from random draws of species in the larger regional species pool. This null hypothesis could be easily refuted because both AvTD and VarTD values differed from random expectations for about half of the provinces. For AvTD, lower than expected index values were observed in western and northern provinces, whereas significantly higher values were observed in a couple of central provinces. This finding suggests that provinces in maritime or cold climates have phylogenetically poorer beetle faunas than expected by chance, as was also suggested by the modelling approach. In contrast, VarTD showed almost the opposite picture that higher than expected index values were found in northerly provinces, whereas a few lower than expected index values were found in central provinces. This suggest that phylogenetic diversity decreases towards northerly provinces, but some species phylogenetically distantly related to most other species do well in the same northerly provinces. To summarize, it is hence possible that the "pruning" of phylogenetic tree in the northernmost provinces is again responsible for different patterns in AvTD and VarTD based on the assemblage-by-assemblage randomization approach. Such pruning can also be considered to result from historical factors. Following the deglaciation, only a few beetle clades that survived in more southerly areas in Europe were able to reach the northernmost provinces in our study area.

Given that phylogenetic diversity was strongly related to climatic variability or temperature extremes, current trend of increasing temperatures and extreme climatic events are likely to modify the insect faunas at high latitudes (Danks 1992; Hickling et al. 2006; Betzholtz et al. 2012; Devictor et al. 2012). Our "space as proxy for temporal trends" modelling approach strongly suggests that, along with changes in species richness, phylogenetic diversity is also likely to change in the face of climate change. Although we could not provide direct tests of such changes expected with climate change scenarios, we can tentatively suggest that phylogenetic diversity is likely to change, with higher average phylogenetic diversity (AvTD) in the northernmost provinces with climate warming. However, variation in phylogenetic diversity (VarTD) is likely to decrease in northerly provinces owing to invasion of more southern species that are closely related to each other. Although we focused only beetles, we believe that they, being phylogenetically, biologically and ecologically a very variable group, provide an excellent model group to examining climate change effects on phylogenetic diversity and its ecological implications. These ecological implications are that changes in climate will have not only direct effects on ectothermic animals, but also have indirect effects through changes in vegetation and other habitat characteristics in terrestrial and aquatic ecosystems (Parmesan 2006; Heino et al. 2009). Our findings also suggest that using both the traditional modelling and the assemblage-by-assemblage randomization approaches provides complementary information about potential trends in biological diversity in the face of climate change.

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Electronic Supplemental Material

Appendix S1. Alternative spatial modelling and variation partitioning.

Table S1. Alternative variation partitioning tables.

Figure S1. Correlations between species richness, AvTD, VarTD and latitude.

Table 1. Overall multiple regression models for species richness, average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD). The models included the six environmental variables. Bold font indicates significant variables at $\alpha = 0.05$.

a) Richness	Estimate	SE	t	*P*	Model stats
(Intercept)	-151.900	130.100	-1.167	0.247	
Altitude range	0.001	0.042	0.023	0.982	
Altitude mean	0.088	0.104	0.847	0.400	
Temperature Annual Range	3.424	6.573	0.521	0.604	
Precipitation Seasonality	-3.948	2.226	-1.774	0.080	
Maximum temperature	33.800	9.229	3.662	**<0.001**	$F_{6,72} = 41.100$
Minimum temperature	12.360	6.677	1.852	0.068	Adj. $R^2 = 0.755$

b) AvTD	Estimate	SE	t	*P*	Model stats
(Intercept)	51.655	2.072	24.930	<0.001	
Altitude range	0.002	0.001	2.425	**0.018**	
Altitude mean	0.001	0.002	0.843	0.402	
Temperature Annual Range	-0.165	0.105	-1.576	0.119	
Precipitation Seasonality	-0.038	0.035	-1.061	0.292	
Maximum temperature	1.059	0.147	7.208	**<0.001**	$F_{6,72} = 22.140$
Minimum temperature	-0.130	0.106	-1.221	0.226	Adj. $R^2 = 0.619$

c) VarTD	Estimate	SE	t	*P*	Model stats
(Intercept)	436.048	16.592	26.281	<0.001	
Altitude range	-0.008	0.005	-1.550	0.125	
Altitude mean	0.015	0.013	1.112	0.270	
Temperature Annual Range	2.084	0.838	2.486	**0.015**	
Precipitation Seasonality	-0.210	0.284	-0.739	0.462	
Maximum temperature	-6.584	1.177	-5.595	**<0.001**	$F_{6,72} = 38.050$
Minimum temperature	0.640	0.851	0.752	0.455	Adj. $R^2 = 0.740$

Table 2. Variation partitioning tables based on partial linear regression. Three models (i.e. geography, climatic variability and temperature) are shown for each response variable (i.e. richness, AvTD and VarTD). Bold font indicates significant pure fraction at α = 0.05. Abbreviations: average taxonomic distinctness (AvTD), variation in taxonomic distinctness (VarTD), temperature annual range (TemAnnRange), coefficient of variation of precipitation (PrecSeaCV), minimum temperature (MinTem) and maximum temperature (MaxTem).

Geography				Climatic variability				Temperature			
	Richness	AvTD	VarTD		Richness	AvTD	VarTD		Richness	AvTD	VarTD
Variables	Adj. R^2	Adj. R^2	Adj. R^2	Variables	Adj. R^2	Adj. R^2	Adj. R^2	Variables	Adj. R^2	Adj. R^2	Adj. R^2
X1 = Latitude	0.626	0.194	0.494	X1 = Latitude	0.626	0.194	0.494	X1 = Latitude	0.626	0.194	0.494
X2 = Area	0.310	0.065	0.412	X2 = Area	0.310	0.065	0.412	X2 = Area	0.310	0.065	0.412
X3 = Altitude mean	0.387	0.084	0.414	X3 = TemAnnRange	0.092	-0.012	0.108	X3 = MinTem	0.392	0.045	0.380
X4 = Altitude range	0.413	0.132	0.414	X4 = PrecSeaCV	0.276	0.024	0.192	X4 = MaxTem	0.528	0.421	0.512
X1+X2	0.650	0.214	0.499	X1+X2	0.650	0.214	0.499	X1+X2	0.650	0.214	0.499
X1+X3	0.728	0.201	0.640	X1+X3	0.704	0.380	0.518	X1+X3	0.646	0.308	0.487
X1+X4	0.730	0.223	0.628	X1+X4	0.623	0.198	0.487	X1+X4	0.772	0.434	0.670
X2+X3	0.479	0.096	0.567	X2+X3	0.301	0.104	0.406	X2+X3	0.400	0.055	0.444
X2+X4	0.491	0.133	0.557	X2+X4	0.383	0.056	0.423	X2+X4	0.593	0.414	0.641
X3+X4	0.406	0.152	0.416	X3+X4	0.269	0.054	0.185	X3+X4	0.750	0.421	0.728
X1+X2+X3	0.784	0.233	0.636	X1+X2+X3	0.725	0.396	0.526	X1+X2+X3	0.664	0.317	0.493
X1+X2+X4	0.788	0.262	0.624	X1+X2+X4	0.647	0.219	0.493	X1+X2+X4	0.809	0.471	0.672
X1+X3+X4	0.729	0.242	0.636	X1+X3+X4	0.736	0.378	0.520	X1+X3+X4	0.772	0.439	0.728
X2+X3+X4	0.486	0.153	0.562	X2+X3+X4	0.411	0.137	0.432	X2+X3+X4	0.769	0.430	0.724
All	0.788	0.281	0.632	All	0.756	0.394	0.529	All	0.814	0.470	0.726
Pure fractions				**Pure fractions**				**Pure fractions**			
X1 | X2+X3+X4	**0.302**	**0.127**	**0.070**	X1 | X2+X3+X4	**0.345**	**0.257**	**0.097**	X1 | X2+X3+X4	**0.045**	**0.039**	0.001
X2 | X1+X3+X4	**0.059**	**0.039**	-0.004	X2 | X1+X3+X4	**0.020**	0.016	0.009	X2 | X1+X3+X4	**0.043**	**0.031**	-0.002
X3 | X1+X2+X4	0.000	0.018	0.007	X3 | X1+X2+X4	**0.109**	**0.175**	**0.037**	X3 | X1+X2+X4	0.006	-0.002	**0.053**
X4 | X1+X2+X3	0.003	**0.047**	-0.005	X4 | X1+X2+X3	**0.031**	-0.002	0.003	X4 | X1+X2+X3	**0.150**	**0.153**	**0.232**
Joint fractions				**Joint fractions**				**Joint fractions**			
X1∩X2	0.020	-0.038	0.150	X1∩X2	0.122	0.067	0.238	X1∩X2	-0.024	-0.021	-0.001
X2∩X3	-0.001	0.001	0.000	X2∩X3	0.004	0.005	-0.003	X2∩X3	-0.006	0.007	0.005
X1∩X3	-0.005	0.002	-0.003	X1∩X3	-0.082	-0.095	-0.028	X1∩X3	0.170	0.019	0.030
X1∩X4	0.003	0.010	0.000	X1∩X4	0.078	0.035	0.023	X1∩X4	0.219	0.223	0.048
X2∩X4	-0.003	-0.006	0.000	X2∩X4	0.001	0.001	-0.001	X2∩X4	-0.024	-0.022	0.009
X3∩X4	0.135	0.002	0.130	X3∩X4	-0.034	0.007	-0.010	X3∩X4	0.009	0.105	-0.060
X1∩X2∩X3	0.015	0.017	0.007	X1∩X2∩X3	0.067	0.033	0.052	X1∩X2∩X3	0.013	0.023	0.059
X1∩X3∩X4	0.000	-0.001	-0.002	X1∩X3∩X4	-0.038	-0.056	-0.013	X1∩X3∩X4	0.053	-0.023	0.127
X2∩X3∩X4	-0.031	-0.014	0.010	X2∩X3∩X4	-0.001	-0.002	0.001	X2∩X3∩X4	0.012	0.005	-0.005

X1∩X3∩X4	0.040	0.009	0.020	X1∩X3∩X4	-0.003	-0.049	-0.005	X1∩X3∩X4	-0.095	-0.132	0.008
X1∩X2∩3∩X4	0.250	0.067	0.252	X1∩X2∩3∩X4	0.136	0.001	0.129	X1∩X2∩3∩X4	0.244	0.067	0.222
Residuals	0.212	0.719	0.368	Residuals	0.244	0.606	0.471	Residuals	0.186	0.530	0.274

Fig. 1. Examples of two taxonomic trees each with seven species. These two trees result in exactly the same average taxonomic distinctness (AvTD) index value, but very different variation in taxonomic distinctness (VarTD) value. Figure (a) depicts a highly even taxonomic tree, whereas figure (b) shows a very uneven taxonomic tree due to one species distantly related to the other species. Modified from Clarke and Warwick (2001a).

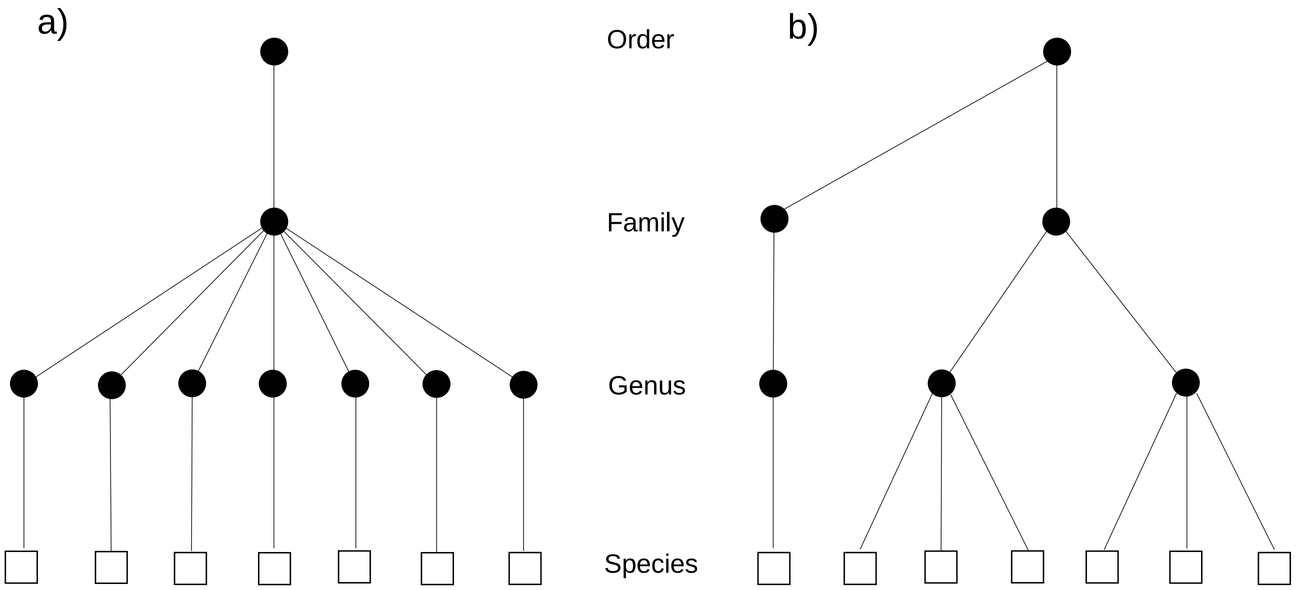

Fig 2. Maps of variation in average taxonomic distinctness (AvTD), variation in taxonomic distinctnes (VarTD), significance of AvTD and significance of VarTD. Abbreviations: NS = non-significant, HS = higher than expected and significant index value, LS = lower than expected and significant index value.