



Longitudinal gradients in the phylogenetic community structure of European Tenebrionidae (Coleoptera) do not coincide with the major routes of postglacial colonization

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Species specific colonization abilities and biotic and abiotic filters influence the local and regional faunal composition along colonization trajectories. Using a recent compilation of the occurrences of 1373 darkling beetle (Tenebrionidae) species and subspecies in 49 European countries and major islands, we reconstructed the tenebrionid postglacial colonization of middle and northern Europe from southern European glacial refuges and linked species composition to latitudinal and longitudinal gradients in phylogenetic relatedness across Europe. The majority of European islands and mainland countries appeared to be phylogenetically clustered. We did not find significant latitudinal trends in average phylogenetic relatedness of regional faunas along the supposed postglacial colonization routes but detected a strong positive correlation between mean relatedness and longitude of mainland faunas and an opposite negative correlation for island faunas. The strength of phylogenetic relatedness in the regional tenebrionid faunas decreased significantly with latitude and to a lesser degree with longitude. These findings are in accordance with two trajectories of postglacial colonization from centres in Spain and middle Asia that caused a strong longitudinal trend in the phylogenetic relatedness. Subsequent pair-wise analyses of species co-occurrences showed that species of similar distributional ranges tend to be phylogenetically clustered and species of different spatial distribution to be phylogenetically segregated. Both findings are in accordance with the concept of ‘range size heritability’. Our study demonstrates that taxonomic data are sufficiently powerful to infer continental wide patterns in phylogenetic relatedness that can be linked to colonization history and geographic information.

Many important macroecological and evolutionary patterns and processes change along environmental or geographical gradients (Lomolino et al. 2010). Best known in this respect are the latitudinal and elevation gradients in species diversity (Lomolino 2001, Willig et al. 2003) or the decrease in community similarity with spatial or temporal distance (Soininen et al. 2007).

Colonization trajectories are particular gradients where stochastic processes, species specific colonization abilities, and biotic and abiotic filters work together to differentially structure local communities (Leibold et al. 2004, Graham and Fine 2008). Particularly, directional changes in patterns of species co-occurrences and beta-diversity have attracted interest (Meier et al. 2011, Swenson 2011). Recently, several studies reported nested subset patterns of both meta-community organization (reviewed by Ulrich et al. 2009) and genetic diversity (Habel et al. 2013) along these trajectories. A nested pattern refers to an ordered loss of species along an environmental gradient and when applied to colonization trajectories this is in accordance with an

ordered step-wise loss of species or genetic diversity during the spread of small founder populations along the gradient (Reinig 1937, Hewitt 1996, Hampe and Petit 2005).

Differences in functional traits are often linked to phylogenetic history (Webb et al. 2002, Cavender-Bares et al. 2009). Ever since Darwin’s (1859) naturalization hypothesis, ecologists have noticed that phylogenetically closely related species tend to share similar habitat requirements (Burns and Strauss 2011, Violle et al. 2011) and are thus less likely to coexist if local communities are mostly structured by competition (Ricklefs and Latham 1992). The extent of phylogenetic preservation of functional traits has been a matter of discussion (Losos et al. 2003, Cavender-Bares et al. 2004, Schreeg et al. 2010); however, recent works indicate that phylogenetic trait conservatism is generally strong and widespread (Burns and Strauss 2011, Cadotte and Strauss 2011). Thus, we can expect that the spatial distribution of functional traits might translate into respective patterns of phylogenetic relatedness along colonization trajectories. For instance,

Stevens et al. (2010) reported a significant positive phylogenetic signal in the dispersal ability of European butterflies, whereas Cadotte and Strauss (2011) found that leguminous that are good colonizers in Swiss artificial plots of the European Biodepth project (Pfisterer et al. 2004) are often close relatives. Particularly, the latter study reports phylogenetic clumping (i.e. a high number of close relatives in a focal community) with respect to colonization, but no phylogenetic signal in extinction patterns. In general, speciation events along the trajectory (Parent and Crespi 2006) might strengthen the change in phylogenetic signals, because non-random speciation increases phylogenetic relatedness (phylogenetic clustering) at the terminal nodes of the phylogeny. Assuming this pattern to be general, we argue (hereafter, hypothesis 1) that the positive correlation between dispersal ability and phylogenetic signal should result in an increase in average relatedness among species along a colonization trajectory. As a consequence, communities at the front edge of a colonization trajectory should be phylogenetically more structured than communities at the rear edge (the centre of colonization).

In turn, if colonization were a neutral drift of functionally equivalent species, no phylogenetic community structure should emerge (Kembel and Hubbell 2006). In fact, neutrality might come in a strong and a soft version. Under strong neutrality (Hubbell 2001), pure ecological drift operates at all levels along the colonization trajectory. Therefore the centre of colonization already lacks any phylogenetic structure, and we do not expect any gradient along the trajectory (hereafter, hypothesis 2a). In the soft version of neutrality, the species composition at the centre of colonization might well have a distinct functional and phylogenetic structure, whereas the colonization is a pure ecological drift process. This would cause lower average phylogenetic relatedness in the front edge communities with respect to the rear edge (hypothesis 2b).

In Europe, Pleistocene refugia located in southern areas were both centres of speciation and sources of recolonization (Hewitt 1999, Baselga 2008). Both processes had a major impact on the current spatial distribution of species across Europe (Fattorini and Baselga 2012, Fattorini and Ulrich 2012b) and should introduce observable latitudinal and longitudinal gradients in phylogenetic community structure across Europe. While latitude is mainly a surrogate variable for temperature regimes (Hawkins 2001), longitude often correlates with continentality gradients linked to absolute differences in temperature and precipitation (Callisto and Goulart 2005, Thielges et al. 2011). For the European continent, Fiera and Ulrich (2012) reported a marked longitudinal gradient in species composition and range size coherences of springtails, in accordance with a postglacial colonization from a middle Asian refuge. However, longitudinal gradients in community composition and phylogenetic structure have received far less attention than latitudinal ones (Fiera and Ulrich 2012), and with respect to phylogeny there are apparently no studies dealing with large scale longitudinal gradients.

In this study we focus on darkling beetles (Tenebrionidae), a very large family of mainly saprophagous beetles of worldwide distribution (Fattorini 2008). Many of them are flightless and probably weak dispersers. Tenebrionidae

are often thermophilous and in Europe they have their highest diversity in the Mediterranean region, while species richness sharply decreases towards Scandinavia (Fattorini and Ulrich 2012a, b). In Fattorini and Ulrich (2012b), we have reconstructed the tenebrionid postglacial colonization of northern Europe and detected multiple Mediterranean glacial refuges. The major colonization trajectories correlated highly with latitude but not with longitude.

Using an updated version of the faunistic data set of Fattorini and Ulrich (2012b) on the European distribution of 1373 tenebrionid species and subspecies in 49 European countries and major islands, we present here a study of latitudinal and longitudinal gradients in phylogenetic faunal composition across Europe. In previous studies, we detected already explicit gradients in species richness (Fattorini and Ulrich 2012a) and patterns of species co-occurrence (Fattorini and Ulrich 2012b). We hypothesize here that these continental richness and structural gradients translate into differential phylogenetic structures of regional assemblages along the presumed south-to-north route of colonization.

Material and methods

Biological data

We considered the faunal composition of 49 faunistically well known European mainland areas (hereafter simply 'mainlands') and larger islands colonized by a total of 1373 tenebrionid species or subspecies, using an updated version of the European tenebrionid database given in Fattorini and Ulrich (2012a, b). This revised database is contained in Supplementary material Appendix 1, whereas indication of updates is given in Supplementary material Appendix 2. Details of the main sources used to compile country and island lists were already given in Fattorini and Ulrich (2012b).

The current taxonomic division into species and subspecies, as applied to the tenebrionids of Europe, is arguably arbitrary. Recent morphological (Ferrer 2008, 2011, Trichas 2008, Condamine et al. 2011) and molecular (Pons et al. 2004, Soldati and Soldati 2006, Stroschio et al. 2011) analyses showed that populations traditionally classified as subspecies are really 'evolutionarily significant units' (sensu Ryder 1986), usually demanding a species status. Thus, in the present analysis we considered both species and subspecies as terminal taxonomic units and call them, for simplicity, 'species'.

As for most arthropod groups, fine grained tenebrionid distribution data are unavailable for large areas. However, previous work showed that even coarse grained data (whole country species richness and climate variables) are able to identify major environmental correlates of animal species richness (Baselga 2008, Hortal 2008, Keil and Hawkins 2009). In particular, Keil and Hawkins (2009) found that species distribution models returned qualitatively similar results irrespective of whether the environmental variables were based on grid or country models. Therefore models fitted with country inventories are an acceptable tool for describing broad scale diversity patterns when more precise data are lacking.

As for virtually all of the larger arthropod taxa, also for the Tenebrionidae no comprehensive phylogenetic analysis is available. When sufficiently resolved phylogenetic trees are missing, any study of large scale phylogenetic community structure has to be based on taxonomic resolution. This limitation necessarily reduces the power of phylogenetic tests (Vamوسي et al. 2009, Ricotta et al. 2012). Nevertheless, many studies that used either species/genus ratios (Krug et al. 2008) or average node distances (Gittleman and Kot 1990, Ricotta et al. 2012) demonstrated that the use of taxonomic hierarchies and respective node distances in phylogenetic analyses can have a good power to infer the degree of phylogenetic community composition in macroecological research (see also Foote 2011 for a discussion on the use of the distribution of species among genera and higher taxa to infer macroevolutionary dynamics).

In the specific case of tenebrionid beetles, several lines of evidence indicate that the current tenebrionid taxonomy broadly reflects real phylogenetic relationships. Regarding the allocation of tribes into subfamilies and subfamily delimitations, we referred to the cladistic analysis of the major lines proposed by Doyen and Tschinkel (1982) and Doyen (1993) on a cladistic basis. Current information also indicates that the tribes used in tenebrionid taxonomy are monophyletic units. For example, the evolutionary lineages found by Doyen and Tschinkel (1982), Doyen (1993), and Iwan (2001) largely fit traditional tribes. Also, morphological analyses of the mouthparts of Pimeliinae based on comparison of several genera within major tribes revealed that there is minimal variation among genera belonging to the same tribe, whereas between-tribe differences are very strong (Fattorini and Di Giulio unpubl.). Recent phylogenetic analyses also show that traditional species groups within genera based on morphological characters generally correspond to monophyletic lines as reconstructed using fine morphological or molecular data (Chatzimanolis et al. 2003, Pons et al. 2004, Condamine et al. 2011).

Phylogenetic analyses

In this study we transformed memberships of six taxonomic levels (subspecies, species, subgenus, genus, tribe, subfamily) into a distance matrix \mathbf{D}_{phyl} for all 1373 'evolutionarily significant units' (below species). We used the number of steps from lowest joint taxonomic unit to each species as the pair-wise distance, thus *Phaleria* (subgenus *Phaleria*) *bimaculata pontica* and *Phaleria* (subgenus *Phaleria*) *provincialis intermedia* differ by four steps.

We related this matrix to the 1373×49 species \times island-mainland matrix \mathbf{M}_{occ} and to a 3×49 matrix \mathbf{V}_{env} that contained for each island and mainland information on the ln-transformed number of species, the latitude *Lat*, and longitude *Long* of their geographical centroid. To infer the variability of phylogenetic species assembly across Europe we used four different approaches.

1) First, for each of the 49 European countries and islands we calculated the nearest taxon index *NTI*, which is the standardized mean nearest neighbour phylogenetic distance (*MNND*) and focuses on the extent of terminal phylogenetic clustering in the co-occurrences of species (Webb et al. 2002).

2) Second, we performed analogous analyses using another index, the net relatedness index *NRI*, which returns the standardized form of the mean phylogenetic distance (*MPD*) (Webb et al. 2002). Both *NTI* and *NRI* increase with increasing phylogenetic clustering, but focus on different parts of the phylogeny. *NRI* reflects clustering (underdispersion) across the whole phylogeny, whereas *NTI* is most sensitive to clustering at the tips of the phylogeny.

3) As a third, very different approach, we used logistic eigenvector regression *LER* (Diniz-Filho et al. 1998, 2012). *LER* allowed us to infer the part of variance in species occurrences (quantified by the associated χ^2 statistics of goodness-of-fit of the logistic regression) of each mainland or island explained by phylogenetic distances. We used the phylogenetic information contained in the first eigenvector of the phylogenetic distance matrix being the only significant one when compared to a Poisson distribution of eigenvalues.

4) Finally, we used a co-occurrence approach (*CO*) as proposed by Ulrich et al. (2012) because common metrics of phylogenetic community structure do not account for multiple patterns of species co-occurrence within the same species \times sites matrix (Gotelli and Ulrich 2012, Ulrich and Gotelli 2013). The method proposed by Ulrich et al. (2012) links phylogenetic community structure and site specific variables to pair-wise patterns of species co-occurrences in the underlying species \times site matrix. For this, average phylogenetic and environmental distances, ΔP and ΔE respectively, of all species pairs at two focal sites are calculated with respect to three distinct patterns: 1) aggregated (defined by clumped $\{\{1,1\},\{1,1\}\}$ 2×2 species \times sites submatrices), 2) segregated (checkerboard $\{\{1,0\},\{0,1\}\}$ submatrices), and 3) togetherness ($\{\{1,1\},\{0,0\}\}$ submatrices) (cf. Ulrich and Gotelli 2013). Therefore, this co-occurrence method explicitly considers matrix-wide differences in the pattern of species co-occurrences (reviewed by Gotelli and Ulrich 2012). The aggregated and segregated patterns are commonly linked to filtering and reciprocal species exclusion, respectively, whereas the togetherness pattern indicates similar niche requirements (cf. Stone and Roberts 1992, Ulrich et al. 2012). Positive correlations between phylogenetic distance and the distance of the predefined site-specific variables with respect to a clumped or togetherness pattern (and respective negative correlations in the case of segregated co-occurrences) indicate niche conservatism. Low scores of ΔP and ΔE in combination with clumped and togetherness patterns indicate phylogenetic and environmental clumping (Ulrich et al. 2012).

All four methods (*NTI*, *NRI*, *LER*, *CO*) of quantifying phylogenetic community structure rely on a certain null model to which raw scores are compared. *NTI* and *NRI* are in fact the negative standardized effect sizes (*SES*, see below) of *MPD* and *MNND* with respect to the predefined null model distribution. At higher species richness, the probability to include small and distantly related taxa into the community increases and consequently *MPD* and *MNND* decrease. Both metrics are also sensitive to phylogenetic autocorrelation of species abundances or numbers of occurrences (Hardy 2008). To eliminate this bias in statistical inference null or neutral models have to be applied (Gotelli and Ulrich 2012).

The question which null model to use is crucial in any phylogenetic analysis and results heavily depend on proper null model choice (Gotelli and Ulrich 2012, Ulrich and Gotelli 2012). In the present case any randomization of occurrences among the European islands and mainlands has to account for differences in species richness caused by differences in area size. The null model should also account for different range sizes that might be caused by geographical constraints. Endemics should remain endemics even after randomization. Thus a null model must not destroy observed row (incidence) and column (richness) totals of the species \times island–mainland matrix \mathbf{M}_{occ} . Here we use the recently developed proportional–proportional null model *PP* of Ulrich and Gotelli (2012) that resamples the focal presence–absence matrix (containing the whole European species pool) in a four step procedure proportional to observed row (species) and column (mainland or island) totals and proved to give unbiased random matrices with respect to both marginal totals (Ulrich and Gotelli 2012). This model avoids undesired properties of the common fixed – fixed null model (reviewed by Gotelli and Ulrich 2012), but in contrast to more liberal null models (Gotelli and Ulrich 2012) still accounts for unequal probabilities of incidences within matrix cells due to observed differences in incidence frequency among species and species richness among sites. In the present case it accounts for species differences in range size and island–mainland differences in area and therefore species richness. Null expectations, and standard deviations of the *PP* null distributions, were in all cases based on 200 randomizations. All calculations were done with the Fortran software applications Niche (Ulrich et al. 2012), PhylEigen, and PhylDist (Ulrich unpubl.). Because null distributions appeared to be approximately normal, we could use the standardized effect sizes (calculated from the observed score x and the mean μ and standard deviation σ of the null distribution: $SES = (x - \mu) / \sigma$) also to infer statistical significance. At the two sided 95% error levels *SES* scores should range within ± 1.96 . Source code is available from WU upon request.

NRI and *NTI* were not significantly spatially autocorrelated (Moran's *I*: all gaps $p > 0.05$). Therefore we used general linear modelling (Hawkins 2012) to relate both metrics to geographic variables and species richness. In turn, χ^2 and the respective *SES* were spatially strongly autocorrelated and we used a simultaneous autoregression model (SAR) as implemented in SAM (Rangel et al. 2010) with default settings.

Results

NTI and *MNND*, and *NRI* and *MPD*, were highly negatively correlated (note that positive *MPD* and *MNND*, and negative *NRI* and *NTI* scores indicate phylogenetic segregation: $r = -0.85$ and $r = -0.72$, respectively) and pointed qualitatively always in the same direction. Thus we report *MNND* and *MPD* scores in Table 1, and focus below on *NRI* and *NTI* only. In nine of the 49 islands and mainlands (namely, Balearic Islands, Madeira, Austria, Germany, Poland, Slovakia, Czech Republic, Spain, Moldavia) we found a significantly ($p < 0.05$) positive *NTI*

score that indicates phylogenetic clustering of terminal nodes (Table 1). We did not detect islands or mainlands with significant phylogenetic segregation (Table 1). Out of 49 *NRI* scores, 31 scores pointed to a significant degree of phylogenetic clustering ($NRI > 1.96$). Spain, Madeira and the Canary Islands had the highest *NRI* signals (Fig. 1, Table 1).

We did not find clear latitudinal gradients in *NTI* and *NRI* (Table 2). *NTI* decreased with latitude (islands: $r = -0.23$, $p > 0.20$; mainlands: $r = -0.33$, $p = 0.06$), but this was not significant, and probably caused by collinearity of latitude and richness (Table 2). *NTI* and *NRI* increased with increasing richness (Table 2). Model selection using the Akaike information criterion *AIC* confirmed this result. The model with the lowest *AIC* score did not contain latitude (Supplementary material Appendix 3). However we found consistent and highly significant longitudinal gradients in phylogenetic relatedness. Island *NTI* and *NRI* decreased with longitude, whereas mainland *NTI* and *NRI* increased with longitude (Fig. 1), although the latter trend was weak. General linear modelling revealed significant positive quadratic regression terms of longitude, which indicates that islands and mainlands of intermediate longitude were phylogenetically most diverse (Table 2, Fig. 1, Supplementary material Appendix 4A, B). Neither area nor latitude entered the model significantly. Again, *AIC* model selection confirmed the results (Supplementary material Appendix 3).

The phylogenetic eigenvector regression pointed to a significant latitudinal gradient in the strength of the phylogenetic relatedness (χ^2 and the respective *SES* scores), whereas the longitudinal gradient was of minor importance (Fig. 2, Supplementary material Appendix 4C). Particularly for mainlands, the importance of phylogeny in community composition decreased with latitude (Fig. 2A, B) and was in 12 out of 14 northern islands or mainlands (latitude $> 50^\circ$) significantly ($p < 0.001$) lower than expected from the *PP* null model distribution. In southern Europe the phylogenetic component was insignificant in 28 out of 35 islands or mainlands (Fig. 2, *SES* scores $< |2|$). *LER* detected a significant positive phylogenetic pattern in community composition only for Spain. SAR modelling confirmed these results and returned latitude but not species richness and area, nor longitude, as significant predictors of χ^2 and the respective *SES* scores (Table 3, Supplementary material Appendix 3).

The phylogenetic co-occurrence analysis revealed significant positive correlations between phylogenetic distances and latitudinal, longitudinal and species richness distances for species with a togetherness pattern of co-occurrence ($r > 0.19$, $p < 0.0001$; Table 4) when using parametric test distributions. However, when compared with the *PP* null model that accounts for differences in species richness and range sizes, these correlations appeared to be less than expected by chance. Thus, a larger phylogenetic distance in these species pairs was linked to a smaller latitudinal and longitudinal distance. This tendency was most pronounced for the checkerboard pattern in combination with latitude. Similar low correlations came up for the clumped and checkerboard patterns (Table 4). Only species richness differences were more tightly correlated with phylogenetic distances than expected by chance ($p < 0.0001$).

Table 1. Mainlands/islands included in the present study with centroid latitude and longitude, area, number of tenebrionid species, and the *MPD*, *NRI*, *MNND*, *NTI* and the χ^2 metrics.

Country/island name	Lat	Long	Area (km ²)	Species/ subspecies	<i>MPD</i>	<i>NRI</i>	<i>MNND</i>	<i>NTI</i>	χ^2
Albania	40.7	20.3	28748	74	8.99	1.73	3.68	1.57	1342.7
Austria	47.5	14.9	83871	55	8.80	3.58	3.71	1.97	1107.4
Bosnia and Herzegovina	44.0	17.8	51197	48	8.79	2.00	5.00	1.34	1234.0
Belgium	50.5	4.7	30528	22	9.02	1.80	3.33	2.23	1376.6
Bulgaria	42.7	25.2	110971	98	8.76	2.89	4.74	0.40	1036.1
Belarus	53.4	28.2	207650	35	9.11	0.40	5.36	0.26	1331.8
Switzerland	46.8	8.3	41285	55	9.13	0.25	4.13	1.23	1360.5
Cyprus	35.0	33.1	9250	76	8.96	2.52	3.76	0.44	1298.7
Czech Republic	49.7	15	78866	51	8.74	6.21	3.06	1.42	1333.4
Germany	51.2	10	357021	49	9.09	0.96	3.65	0.72	1363.1
Denmark	56	9.8	43093	26	9.02	1.64	4.59	-1.32	1316.9
Estonia	58.7	27.1	45227	30	9.06	1.23	3.39	1.20	1344.5
Balearic Islands	39.5	2.9	5014	84	8.89	3.06	4.49	-0.72	1353.0
Canary Islands	28.1	-15.2	7270	149	9.17	-0.37	4.61	-1.49	1258.4
Spain	40.3	-3.6	505988	560	8.73	3.77	3.65	2.23	1067.2
Finland	64.0	26.5	338145	26	8.85	2.99	5.00	0.22	964.2
Corsica	42.1	9.1	8680	92	8.83	4.15	3.72	1.12	1344.3
France	46.6	2.8	543965	128	8.67	4.44	4.47	1.41	960.3
United Kingdom	53.9	-2.9	244064	25	8.86	2.46	5.23	0.07	962.6
North Aegean Is.	40.0	25.0	3886	33	9.06	1.07	3.44	0.55	1354.4
Cyclades Is.	37	25.6	2500	69	8.83	3.00	3.76	2.40	1198.6
Dodecanese Is.	39.9	27.2	2663	78	8.92	3.93	2.95	0.78	1334.7
Greece	39.3	22.0	131992	204	8.81	3.83	3.61	1.74	1177.2
Crete	35.2	24.9	8259	75	8.84	1.51	6.60	-0.90	1264.4
Croatia	45.6	16.1	56594	104	9.14	-0.82	3.12	0.66	1356.7
Hungary	47.0	19.3	93054	66	8.71	4.47	5.20	-0.24	1043.9
Ireland	53.3	-8.08	70273	10	8.80	3.15	5.08	0.41	1093.4
Italy	42.4	12.9	301401	170	9.13	0.09	6.88	-1.94	1351.1
Sardinia	40.0	9.1	23813	134	8.89	2.46	4.40	1.21	1352.0
Sicily	37.5	14.2	25426	115	7.98	7.68	3.50	2.83	1343.1
Lithuania	55.3	24.0	65318	24	9.19	-0.48	5.12	-1.43	1284.1
Luxembourg	49.8	5.9	2588	16	8.31	4.46	4.40	2.08	1409.2
Latvia	56.7	24.0	64626	30	8.96	1.41	5.70	-0.35	1118.7
Moldova	47.2	48.4	33709	10	8.89	2.72	5.03	0.11	1353.5
Macedonia	41.5	21.7	25339	35	8.82	2.52	5.33	-0.05	987.6
Malta	35.9	14.5	316	50	8.85	3.24	3.77	1.96	1097.3
The Netherlands	52.2	5.6	41536	20	9.06	1.22	3.09	1.58	1378.2
Norway	65.2	14.5	323963	24	8.97	2.55	3.71	1.01	1278.1
Poland	52.1	19.6	312766	51	9.04	1.68	3.15	1.34	1377.0
Azores	38.3	-27.1	2200	8	9.10	0.58	3.74	-0.14	1299.6
Madeira	32.7	-17.0	789	36	8.80	4.51	3.45	2.49	1125.2
Portugal	39.8	-8.1	91854	134	8.83	3.03	5.03	-0.18	1266.5
Romania	45.8	25	237453	83	8.62	8.20	2.26	2.90	1380.3
Sweden	62.1	16.1	449964	35	8.87	2.58	4.46	0.98	993.6
Slovenia	46.0	14.6	20273	37	8.84	3.48	4.00	1.29	1241.5
Slovakia	48.7	19.3	49049	62	8.61	5.60	3.94	1.08	1328.6
Turkey European part	41.2	27.2	23764	64	9.04	1.51	3.67	1.08	1274.7
Ukraine	49.2	30.8	603886	92	8.87	2.51	5.44	-0.35	1192.7
Yugoslavia (Serbia and Montenegro)	43.9	20.8	102199	38	8.89	2.39	4.37	1.07	1315.7

When patterns of species co-occurrences were related to phylogeny, latitude, longitude, and richness (Table 5), clumped and togetherness co-occurrences were significantly (both $SES < -3.0$) linked to phylogenetic clustering. Consequently, the checkerboard pattern of co-occurrence was significantly linked to phylogenetic segregation ($SES > 10.0$). Clumped species pairs were significantly less segregated in latitude and longitude than expected by chance (Table 5). Checkerboard pairs were less distant in latitude but more distant in longitude, whereas for togetherness pairs the opposite pattern appeared.

Discussion

Initiated by the pioneering work of Elton (1946) on species/genus ratios and boosted by the recent molecular techniques (Swenson 2011), there is now a growing number of studies that assessed the phylogenetic structure of communities from local to regional spatial scales and from ecological to evolutionary temporal scales (Emerson and Gillespie 2008, Graham and Fine 2008, Cavender-Bares et al. 2009). However, our study is the first to analyse continent wide patterns of phylogenetic community structure of

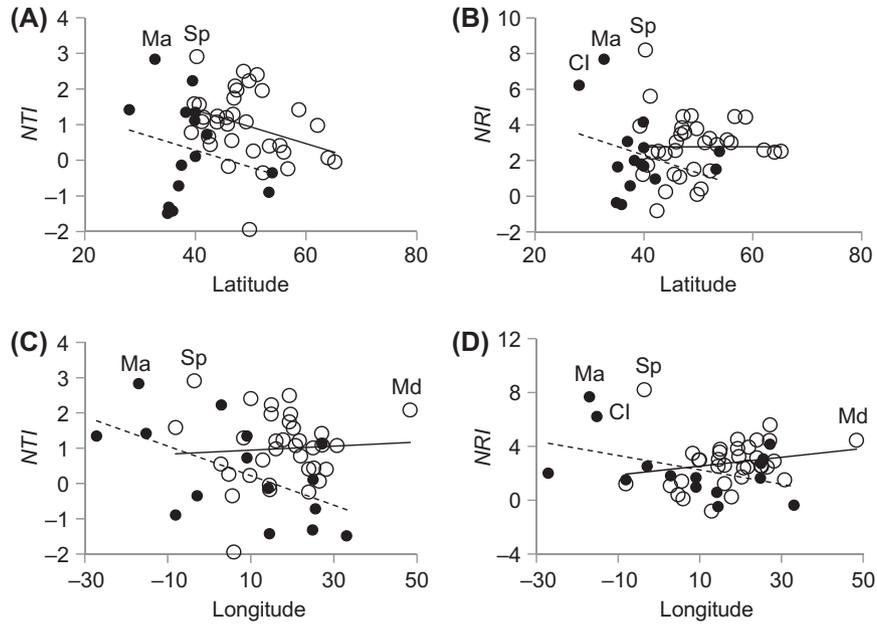


Figure 1. The dependence of the nearest taxon index (*NTI*), and the net relatedness index (*NRI*) on latitude (A, B) and longitude (C, D) for islands (black dots, broken regression line) and mainlands (open dots, continuous regression line). (A) Islands: $r = -0.23$, $p > 0.20$; mainlands: $r = -0.33$, $p = 0.06$. (B) Islands: $r = -0.30$, $p = 0.27$; mainlands: $r = 0.01$, $p > 0.50$. (C) Islands: $r = -0.56$, $p = 0.02$; mainlands: $r = 0.06$, $p > 0.50$. (D) Islands: $r = -0.44$, $p = 0.09$; mainlands: $r = 0.20$, $p > 0.20$ (without Spanish mainland: $r = 0.50$, $p < 0.01$). SP: Spanish mainland, Ma: Madeira, CI: Canary Islands, Md: Moldavia.

a large arthropod family. Comparable in scale and diversity are only the studies of Machac et al. (2011) and Hoiss et al. (2012), who found increasing phylogenetic clustering of ant and bee communities along elevation gradients in North America and Europe, respectively. The latter authors linked the trend towards phylogenetic clustering in European bee communities with increasing environmental filtering at higher altitudes. Wang et al. (2012) interpreted their finding of increasing phylogenetic clustering of bacterial communities along an elevational gradient in a similar way. With regard to vertebrates, Cooper et al. (2008) reported widespread phylogenetic segregation in various mammal assemblages and related their finding to competition between close relatives where traits are conserved and habitat filtering where distant relatives share convergent traits. Graham et al. (2009) reported increasing phylogenetic segregation of Ecuadorian hummingbirds towards lowland communities, whereas Cardillo and co-workers (Cardillo et al. 2008,

Cardillo 2011) found indication of both clumping and segregation among global island and terrestrial African mammal communities depending on environmental variables, particularly habitat diversity.

Our logistic phylogenetic eigenvector regression, which quantifies the part of species occurrences explained by phylogeny in relation to other ecological factors, particularly environmental variables, pointed to a significant negative latitudinal and a less pronounced longitudinal gradient in the relationship between phylogeny and regional species occurrences and community composition (Fig. 2). The importance of phylogeny in comparison to other factors decreases with latitude, contrary to our hypothesis 1. In nearly all mainlands north of 50° this importance was even less than expected from the 95% confidence limits of the *PP* null model. In the southern European countries the phylogenetic influence on community structure was similar to the null model expectation but exceeded this only

Table 2. General linear model results to test the influence of ln-transformed richness of species (ln S), ln-transformed area, latitudinal and longitudinal gradients (quadratic model), and the mainland/island distinction (MI) on the nearest taxon index (*NTI*) and the net relatedness index (*NRI*) of 49 European islands and mainland countries. *NTI*: $r^2 = 0.39$, $p < 0.01$; *NRI*: $r^2 = 0.29$, $p < 0.05$.

<i>NTI</i>						<i>NRI</i>					
Variable	Parameter	SS	DF	F	p	Variable	Parameter	SS	DF	F	p
Constant	-10.473	3.04	1	3.22	0.080	Constant	0.203	0.00	1	0.00	0.985
ln S	0.928	5.61	1	5.96	0.019	ln S	1.540	15.46	1	5.09	0.030
ln area	-0.099	0.34	1	0.36	0.552	ln area	-0.437	6.56	1	2.16	0.149
Latitude	0.327	2.17	1	2.30	0.137	Latitude	-0.099	0.20	1	0.07	0.800
Latitude ²	-0.003	2.04	1	2.16	0.149	Latitude ²	0.002	1.34	1	0.44	0.510
Longitude	-0.066	11.75	1	12.48	0.001	Longitude	-0.094	23.72	1	7.81	0.008
Longitude ²	0.002	8.67	1	9.21	0.004	Longitude ²	0.004	27.27	1	8.98	0.005
MI	-0.434	3.46	1	3.67	0.062	MI	-0.618	7.02	1	2.31	0.136
Error		38.63	41			Error		124.59	41		

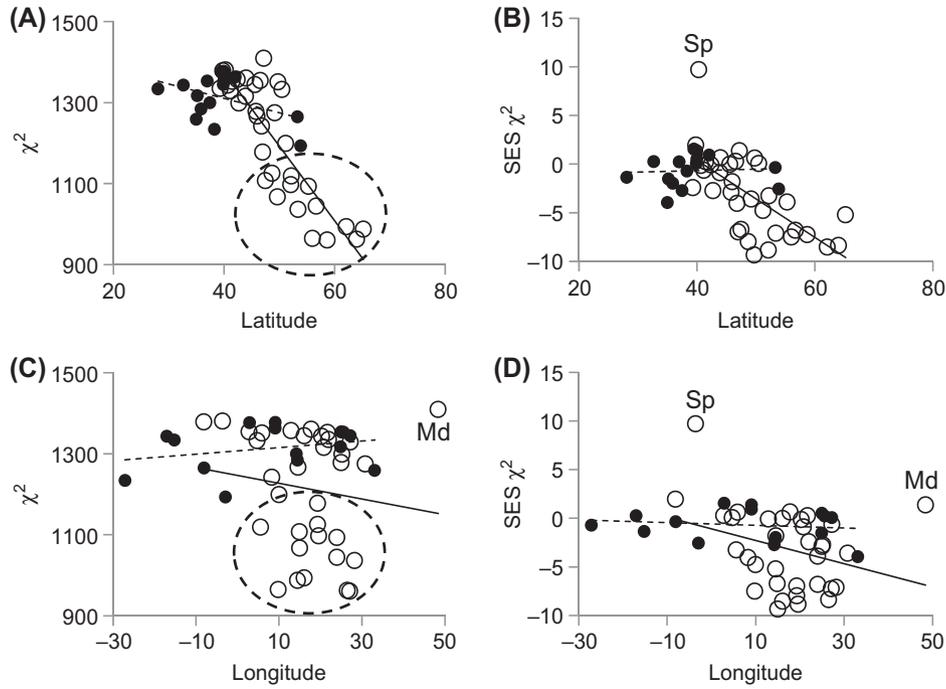


Figure 2. Results of logistic phylogenetic eigenvector regression (*LER*). χ^2 values (A, C) and the respective standardized effect sizes (*SES*) scores (B, D) obtained from the null distribution of the *PP* null model in dependence on latitude (A, B) and longitude (C, D) are given. Islands: black dots, broken regression line; mainlands: open dots, continuous regression line. (A) Islands: $r = -0.43$, $p = 0.10$; mainlands: $r = -0.86$, $p < 0.0001$. (B) Islands: $r = 0.06$, $p > 0.50$; mainlands: $r = -0.66$, $p = 0.0001$. (C) Islands: $r = 0.27$, $p = 0.33$; mainlands: $r = -0.14$, $p > 0.20$. (D) Islands: $r = -0.16$, $p > 0.50$; mainlands: $r = -0.31$, $p = 0.08$. The ovals mark the group of Scandinavia, middle and north-eastern European countries. Sp: Spain, Md: Moldavia.

in Spain. Thus a major result of our study is a decreasing impact of phylogenetic history on regional tenebrionid community structure along a supposed northern postglacial colonization from multiple southern European refuges (Fattorini and Ulrich 2012a, b). Comparable results were obtained by Cardillo et al. (2008), who reported on average

< 20% of 595 island mammal communities to have a significant phylogenetic structure.

Our *LER* results also imply a low impact of speciation during colonization. Speciation along the trajectory should detectably increase the regional phylogenetic structure with respect to the rear-end (Kamilar et al. 2009). In Tenebrionidae, the opposite took place. Southern Europe underwent extensive cladogenesis in a number of genera probably during the Pleistocene (Chatzimanolis et al. 2003, Papadopoulou et al. 2009, Condamine et al. 2011). As a consequence, the mean phylogenetic clustering in southern Europe appeared to be generally higher than expected from our null model indicating a co-occurrence of phylogenetically related taxonomic units. In line with

Table 3. Simultaneous autoregressive model results to test the influence of ln-transformed richness of species (ln S), ln-transformed area, latitudinal and longitudinal gradients (quadratic model), and the mainland/island distinction (*M/I*) on the raw χ^2 score of the logistic phylogenetic eigenvector regression (*LER*) and the respective standardized effect sizes (*SES*) scores (proportional-proportional *PP* null model) of 49 European islands and mainland countries. Raw χ^2 score: $r^2 = 0.66$, $p < 0.001$. *SES*: $r^2 = 0.40$, $p < 0.01$.

Variable	SAR coefficient	Standard error	T	p
χ^2				
Constant	868.911	407.438	2.133	0.039
ln S	-5.398	28.19	-0.192	0.849
ln area	7.634	11.444	0.667	0.508
Latitude	27.393	16.235	1.687	0.099
Latitude ²	-0.431	0.157	-2.748	0.009
Longitude	-0.15	1.686	-0.089	0.93
Longitude ²	0.013	0.058	0.227	0.821
<i>SES</i> χ^2				
Constant	-24.718	15.28	-1.618	0.113
ln S	1.23	1.059	1.162	0.252
ln area	-0.293	0.434	-0.676	0.503
Latitude	1.036	0.593	1.747	0.088
Latitude ²	-0.012	0.006	-2.13	0.039
Longitude	-0.11	0.059	-1.874	0.068
Longitude ²	0.002	0.002	1.237	0.223

Table 4. Raw Pearson coefficients of correlation between ΔP (phylogenetic distance) and ΔE (latitudinal, longitudinal and richness distances) and the respective standardized effect sizes (*SES*) scores (proportional-proportional *PP* null model) for all species pairs that co-occurred in a clumped, checkerboard, and togetherness manner. Significant correlations and *SES* scores in bold type.

Metric/variable	Latitude	Longitude	Species richness
Pearson coefficient of correlation			
Clumped	-0.020	-0.010	-0.001
Togetherness	0.195	0.214	0.289
Checkerboard	<0.001	<0.001	<0.001
<i>SES</i> score of correlation coefficient			
Clumped	-1.86	-1.77	-1.20
Togetherness	-1.72	-0.91	-0.59
Checkerboard	-4.61	0.17	4.36

Table 5. Standardized effect sizes (*SES*; proportional-proportional *PP* null model) of the phylogenetic distances and the latitudinal, longitudinal and richness distances in species pairs that co-occurred in a clumped, checkerboard and togetherness manner. Significant *SES* scores in bold type.

Metric/ variable	Taxonomy Phyl. distance	Variables		
		Latitude	Longitude	Species
Clumped	-7.17	-3.36	-7.17	-5.86
Togetherness	-3.34	16.71	-3.34	0.42
Checkerboard	10.25	-6.04	10.25	1.61

this argument, we found the proportion of endemics to decrease sharply towards higher latitudes with most countries north of the Alps lacking endemic species (Fig. 3A). A well investigated case is that of the Aegean archipelago with its many island endemics that originated in the Pleistocene after connecting land-bridges were flooded by rising sea levels of the Mediterranean (Fattorini 2006, Papadopoulou et al. 2009). In our study the Aegean archipelago was phylogenetically significantly clustered ($NRI = 2.72$). Particularly impressive is the cladogenesis of the tribe Asidiini (with the genera *Asida* and *Alphasida*) in the western Mediterranean, notably on the Iberian Peninsula. Species within the genera *Asida* and *Alphasida* are very close to each other, but morphologically well distinguishable and endemic to small areas (Soldati and Leo 2005, Soldati 2009), which suggests that they emerged during but not after the Pleistocene (cf. Palmer 2002 for a case study). In this respect it is important to note that the richest European country and major glacial refuge, Spain, with 560 recorded species has also the highest *NRI* (8.0) and *NTI* (2.9) scores (Fig. 1). A decreasing signal of phylogeny in the faunal composition is then compatible with a colonization of central and northern areas by species from many independent lineages.

Our results regarding the low degree of phylogenetic community composition in regional faunas contrast with many studies reporting significant phylogenetic community structure at local, ecosystem scales (reviewed by Emerson and Gillespie 2008 and Cavender-Bares et al. 2009). Our explanation of this pattern is a dependence of the strength of the phylogenetic relatedness on the spatial extent. Our study

depends on whole island and country surveys which thus contain the total regional species pools, while local and regional studies are generally based on much more limited samples from this pool. These samples are not random, but generally stem from predefined habitats and thus comprise communities of species that have already undergone competitive exclusion and habitat filtering. Both these two mechanisms might determine a significant phylogenetic community structure at the local scale if there is only a moderate correlation of phylogenetic relatedness and functional trait (Webb et al. 2002).

According to our first starting hypotheses we expected to see significant latitudinal gradients in the phylogenetic faunal composition if colonization were a non-neutral process. Indeed, *NTI* and *NRI* decreased with latitude indicating a tendency towards phylogenetic segregation in northern countries (Fig. 2). However, neither *NTI* nor *NRI* were statistically significant at the 5% error level and thus we did not find any unequivocal corroboration for our hypothesis 1. However, we can exclude a latitudinal trend towards phylogenetic clustering (Fig. 1) that might be linked to lower average temperatures (Table 2). Such a link has been inferred for microbial communities (Wang et al. 2012), ants (Machac et al. 2011), and bees (Hoiss et al. 2012). Further, the fact that the latitudinal trends in *NTI* and *NRI* towards phylogenetic segregation were linked to the latitudinal difference in species richness (Table 2) but not to factors that correlate with latitude (for instance temperature) demonstrates the importance of including possible covariates of phylogenetic community structure in the analysis of ecological gradients. It also shows that both *NTI* and *NRI* still contain species richness effects even when used in combination with a null model that accounts for differences in richness and range sizes. This richness effect might have been overlooked in previous work on phylogenetic community structure.

We were surprised to find strong longitudinal trends and U-shaped European distributions of *NRI* and *NTI* with a general decreasing tendency of *NTI* towards eastern Europe (Fig. 1C, particularly when omitting Moldavia with only 10 species, and Fig. 1D, Supplementary material Appendix 4A, B). This pattern does not coincide with post-glacial colonization but indicates differences in speciation

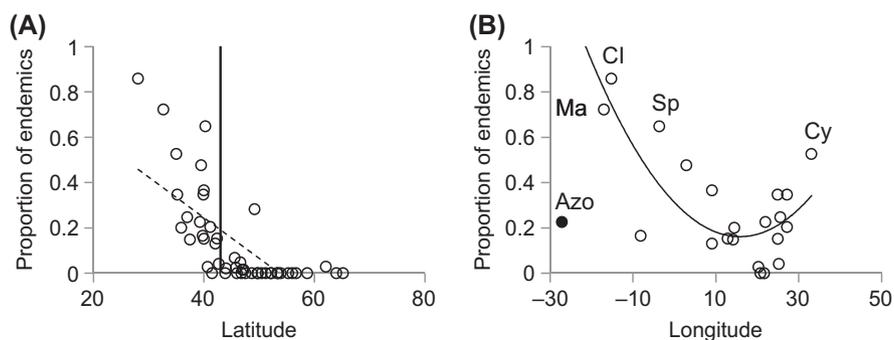


Figure 3. (A) Proportion of endemic species in 49 European islands-mainlands in dependence on latitude (linear regressions: $r = -0.67$, $p < 0.001$). The vertical line in (A) marks the average latitude of the Pyrenees and the southern part of the Alps. (B) Proportion of endemic species in 22 European islands-mainlands south of the vertical line in (A) in dependence on latitude (quadratic regression: $r^2 = 0.59$, $p < 0.001$, the quadratic term is significant at $p < 0.01$). In (B) the outlying Azores (Azo) are not included in the model. Ma: Madeira, CI: Canary Islands, SP: Spanish mainland, Cy: Cyprus.

rates with the major glacial refuges on the Iberian Peninsula and in the eastern Mediterranean region (Fattorini and Baselga 2012). Indeed, we found a strong bimodal distribution of endemics along the longitudinal transect of southern Europe (Fig. 3B) indicating two distinct centres of speciation and colonization. The high rates of European endemics in the eastern part of the Mediterranean may be also due to immigration from western Asia. We argue that these two centres cause the bimodal distribution of increased phylogenetic clustering in the western and eastern part of Europe.

The separate analysis of different patterns of co-occurrence (Table 4, 5) highlighted the importance of dissecting multiple matrix structures in the analysis of species co-occurrence and phylogenetic structure. Recently, Gotelli and Ulrich (2012) and Ulrich and Gotelli (2012) demonstrated how treating ecological presence–absence matrices as mono-structured entities might lead to false interpretations of ecological patterns. Instead, many matrices have multiple and even seemingly contradictory substructures (Gotelli and Ulrich 2012). This fact led Ulrich et al. (2012) to develop a method of phylogenetic inference based on three distinct patterns: clumping, checkerboards, and togetherness. In the present case, we found significant positive correlations of phylogenetic distance with distance in latitude, longitude, and species richness with respect to joint presences–absences (togetherness). That means that species of identical patterns of occurrence tend to be closer in phylogeny and geographical distance than expected by chance. We did not find respective correlations for spatially segregated species pairs. At local scales the togetherness pattern is generally associated with similar environmental requirements (niche conservatism) (Stone and Roberts 1992, Ulrich et al. 2012). At regional to continental scales, togetherness is best explained by similar climatic requirements and colonization history. Under this interpretation our finding in fact re-detects that phylogenetically similar species have more often similar broad environmental requirements than expected by chance. This is the naturalization hypothesis (Darwin 1859) at larger spatial scales and indicates trait conservatism in the pattern of tenebrionid occurrence across Europe.

Interestingly the togetherness pattern vanished when comparing the observed correlation coefficients with those obtained from a null model that accounts for differences in species range sizes and mainland or island richness contained in the row and column marginal distributions of the matrix (Table 5). Niche conservatism in tenebrionids has also a richness component where phylogenetically similar species tend to have also similar range sizes. Webb and Gaston (2003) termed this phenomenon ‘range size heritability’. Indeed, we found a significant negative correlation between the phylogenetic eigenvector and the total number of islands–mainlands occupied by a certain species ($r = -0.34$, $p < 0.0001$).

In spite of the fact that the average phylogenetic relatedness as quantified by *NTI* did not significantly deviate from our random expectation (Fig. 1 A, C) and that phylogeny explained only a minor part of variance in species occurrences (Fig. 2B), our study does not unequivocally corroborate a neutral explanation of post-glacial tenebrionid

range expansion, neither in a strong (hypothesis 2a) nor in a soft version (hypothesis 2b). The average phylogenetic relatedness *NRI* was in most European islands–mainlands higher than expected by chance and on average highest in the species rich southern European countries (Fig. 1). This finding is in contrast with a strong neutral pattern that predicts random phylogenetic distributions irrespective of the position on a colonization trajectory. Further, neither *NTI* nor *NRI* significantly decreased with latitude as expected from the soft version of neutrality that relies on random dispersion only and predicts a decrease in the phylogenetic relatedness. However, the associated decrease in the importance of phylogeny to explain regional faunas and the weak tendency of *NTI* to decrease towards northern countries does also not exclude ecological drift (Hubbell 2001) as a major factor in the colonization process. Surely further studies are needed to disentangle the influence of neutral and non-neutral patterns of colonization at large spatial scale.

The present results are based on a distance matrix obtained at the level of taxonomic resolution. This method has naturally a lower power to detect non-random phylogenetic relatedness than the use of explicit phylogenetic trees that contain fewer polytomies and much better resolved information on clade distances (Whitfeld et al. 2012, but see Ricotta et al. 2012). In turn, it has a higher power than traditional species per genus ratios that are still used in the lack of appropriate phylogenies (Heino and Soininen 2007, Krug et al. 2008). Further, the inclusion of > 1300 species should theoretically allow the detection of very small signals simply due to the large number of cases. For instance, correlations in the submatrix approach were based on as many as 245786 clumped, 11367655 togetherness, and 3322126 checkerboard submatrices. At such high sample sizes even very small deviations from the null model distribution become statistically significant. Therefore, in spite of the potentially lower resolution of taxonomy based analyses, we strongly feel that our study detected the existing large scale trends in the phylogenetic faunal composition of European Tenebrionidae. If this is true the gate is open for similar comparative studies on other large arthropod groups. Additionally, we need similar studies on phylogenetically well resolved taxa like mammals, birds, or plants to compare taxon and phylogeny based analyses of the large scale spatial distribution of species.

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Supplementary material (Appendix ECOG-00188 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.