

Evolution of climate niches in European mammals?

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Our ability to predict consequences of climate change is severely impaired by the lack of knowledge on the ability of species to adapt to changing environmental conditions. We used distribution data for 140 mammal species in Europe, together with data on climate, land cover and topography, to derive a statistical description of their realized climate niche. We then compared climate niche overlap of pairs of species, selected on the basis of phylogenetic information. In contrast to expectations, related species were not similar in their climate niche. Rather, even species pairs that had a common ancestor less than 1 Ma already display very high climate niche distances. We interpret our finding as a strong inter-specific competitive constraint on the realized niche, rather than a rapid evolution of the fundamental niche. If correct, our results imply a very limited usefulness of climate niche models for the prediction of future mammal distributions.

Keywords: niche evolution; niche model; species distribution model; mammal; phylogeny; phylogenetic signal

1. INTRODUCTION

Adaptive radiation and allopatric speciation are the key mechanisms in the creation of species diversity (Schluter 2001; Gavrillets & Losos 2009). Rapid adaptation to new or altered environmental conditions has been shown experimentally (e.g. Losos *et al.* 1998), by analysis of palaeontological data (Thompson 1998) and by comparisons of species across phylogenies (Benton 2009; Evans *et al.* 2009). Up to now, speciation has been commonly viewed as arising from adaptation to different habitats (Gavrillets & Losos 2009) and isolation (Schluter 2009), but rarely to climate (but see Evans *et al.* 2009). It could also thus be argued that the current changing climate may not have too severe consequences for species' continued existence, because they are able to adapt and evolve at a similar pace. A key question is whether phylogenetic constraints such as potential genetic and epigenetic mechanisms that restrict the evolution of new varieties within taxa (cf. Losos 2008; Wiens 2008) may be too strong to allow adaptive shifts in climate niches. Indeed, Kozak *et al.* (2006) show how

the conservation of climate niches can lead to geographical displacement and hence peripatric speciation.

Here, we investigate the degree to which terrestrial mammals overlap in their multidimensional climate niche. European mammals are particularly well suited for such an analysis because of three features: (i) a mammal supertree phylogeny has recently been published (Bininda-Emonds *et al.* 2007); (ii) a reliable database of mammal distributions within Europe (Temple & Terry 2007) is available; and (iii) mammals are species-rich enough to yield conclusive results. Together with data on climate, land cover and topography, these data allowed us to fit species distribution models to 140 native terrestrial European mammals and calculate climate niche overlap. For each species, we compared the climate niche distance and the phylogenetic distance to its closest relative. In accordance with the hypothesis of phylogenetic signal (Losos 2008), we tested the hypothesis that closely related species also share very similar climate niches. If this hypothesis is falsified this would indicate a lack of phylogenetic niche conservatism as well (Losos 2008).

2. MATERIAL AND METHODS

We combined three types of data in our analysis: distribution data on all European mammals (taken from Temple & Terry 2007), environmental information (climatic, topographic and land-cover data) and phylogenetic information (from Bininda-Emonds *et al.* 2007). Spatial data were gridded to 50 × 50 km, yielding 3037 cells from 11° to 32° E, and from 34° to 72° N. Owing to collinearity within the environmental data, we selected 13 final predictor variables from an initial set of 24 (see electronic supplementary material for a detailed description of variables and selection methods), of which five were climate variables (growing degree days over 5°C, annual precipitation, summer precipitation, temperature seasonality and residuals of absolute minimum temperature).

Distribution data were analysed using Boosted Regression Trees (BRT, following Elith *et al.* 2008). Across all species, climatic variables explained 56 per cent (1 s.d. = 15.5%) of the variation in species occurrences, confirming that the climatic niche played a dominant role in explaining distributional patterns. Spatial autocorrelation was present, but at a very short distance only, and could not be improved by methods presented in Dormann *et al.* (2007); see the electronic supplementary material. We then calculated overlap in climate niches between sister species (which were identified by cophenetic distances from the phylogenetic tree; Paradis *et al.* 2004). To do so, we computed predicted values from the BRTs to a five-dimensional climate dataset, which varied the five climate variables in 20 equidistant steps, but kept all other predictors at their median value. We then clipped the dataset to include only data points inside the five-dimensional convex hull of the 3037 European cells (i.e. the realized climate space). Our climate-niche dataset comprised 185 308 data points. Niche overlap (NO) was calculated on the basis of this hyperdimensional climate space (not as geographical overlap) as

$$NO = \frac{1}{N} \sum_k \frac{\min(\hat{y}_{ik}, \hat{y}_{jk})}{\max(\hat{y}_{ik}, \hat{y}_{jk})},$$

where \hat{y}_k is the predicted occurrence probability for the k th of N climate hypercube combinations (normalized so that $\sum \hat{y}_k = 1$, thereby correcting for different prevalences and hence mean expected occurrence probabilities) and species i or j . This index scales predicted probabilities by the maximum of both species, yielding values from 0 to 1. For niche distance, we use $1 - NO$. Using different measures of niche overlap made no difference to the outcome (see the electronic supplementary material). Finally, we used a null model to examine, whether our results were artefacts of species occupying different geographical locations and hence seemingly different climate niches. This was not the case (see the electronic supplementary material).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0688> or via <http://rsbl.royalsocietypublishing.org>.

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3. RESULTS

We found that closely related species differed widely with respect to their climate niche (figure 1). For the vast majority of comparisons, climate niche overlap was much smaller than would be expected from their phylogenetic relatedness (assuming constant mutation rates), hence we detected no phylogenetic signal with respect to climate niche distances of sister species. Across all species, a very weak phylogenetic trend was discernable, relating to 23 of the 140 species (21 positive, two negative trends; see the electronic supplementary material). This faint signal indicates that phylogenetic constraints were largely unimportant for the currently realized climate niche of European mammals.

Within the lagomorpha, rodentia and insectivora, niche distances between sister taxa were significantly greater than in the chiroptera (figure 2). However, scatter was also large within groups and precluded a more in-depth analysis.

4. DISCUSSION

Our analysis indicates high flexibility of realized climatic niches independent of phylogenetic distances. One might conclude that owing to the rapid evolution of climate niches in European mammals, climate change poses a minor threat to these species. The alternative explanation, and the more conservative one, is that the *fundamental* niche of the mammals investigated here is much wider than the *realized* niche (Kearney 2006). Competition between closely related species may have shifted the realized climate niche without requiring major evolutionary adaptations.

Apparently, climate niche space is similarly subject to character displacement as other dimensions of the niche hypervolume (size (Hutchinson 1959); (Diamond 1975); size of prey (Hespenheide 1975); forage quality (Olf *et al.* 2002); mutualistic gut microbe community (Ley *et al.* 2008); soil nutrient requirements (Tilman 1982)). Because our analysis does not comprise extinct mammal species (because both genetic and distributional data are known to a far lesser extent), we are hesitant to invoke the 'ghost of competition past' (Connell 1980) for the observed climate niche displacement. At the same time, we found no obvious convincing alternative explanation (e.g. shared pathogens, hybridization vigour, genetic drift; see Schluter 2001 for review).

From species ranges analysis it is known that mammals, as endothermic organisms, can occupy broader fundamental climate niches than insects or plants because they are able to buffer variation in climate (see also Gaston 2003). It is thus well conceivable that their fundamental climate niche is rather wide and less subject to physiological constraints than that of poikilothermic animals. Competition would thus simply act on the realized, not on the fundamental, climate niche. We speculate that a comparison with other species groups such as reptiles or insects should show a stronger phylogenetic signal.

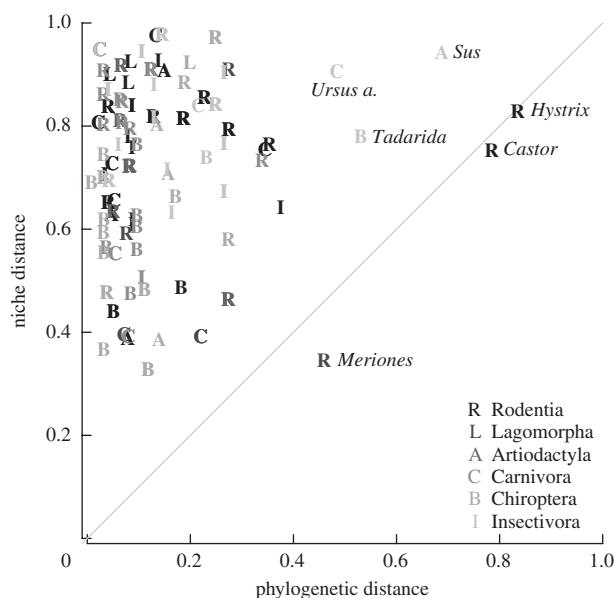


Figure 1. Climate niche distance and phylogenetic distance for a comparison of 140 mammalian sister species. Diagonal line separates niche flexible (upper left) and niche conservative (bottom right) pairs. High values for phylogenetic distance indicate species only very distantly related to any other species (e.g. crested porcupine *Hystrix cristata* and European beaver *Castor fiber*), and for niche distance, very different realized climate niches.

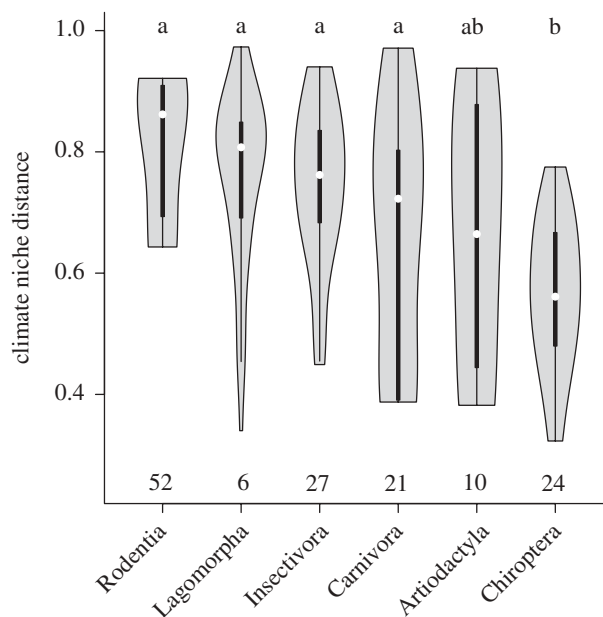


Figure 2. Violin plot of climate niche distances for the six mammalian orders. Number of species within each group is given below each bar. Groups sharing the same letter are not significantly different in Tukey's honest significant difference post hoc test (i.e. $p > 0.05$).

European mammals have been challenged by alternating climatic conditions for several million years (DeSantis *et al.* 2009). The current speed of climate change is rapid, both in geological and evolutionary terms (IPCC 2007). Depending on the interpretation of our observed large difference between the

phylogenetic and the climate niche signal, we may regard climate change as problematic or not. If we assume that climate niches have evolved to what we observed, then this would indicate rapid evolution. For plants (Sjöström & Gross 2006) as well as marsupials (Johnson *et al.* 2002), a correlation between extinction risk and phylogenetic similarity has been shown, indicating that genetic variability may not keep up with changing environments. But even the observed high degree of climate niche evolution is unlikely to suffice for European mammals to evolve *in situ* to climate change. The most recent speciation event documented within our dataset occurred almost 400 000 years ago (between the two bat species *Rhinolophus euryale* and *R. mehelyi*), or more than two ice ages before today. Such phylogenetic data, however, do not allow an investigation of climate niche changes *within* species, where most adaptation is likely to occur.

The alternative interpretation, namely that our measurement of the climate niche represents the realized rather than the fundamental climate niche, would lead to the opposite conclusion: realized climate niches bear little resemblance to the underlying fundamental niche. In this interpretation we would state that any projection of future climate change scenarios made on the basis of current distribution data alone will be misleading, because it is very likely that competition determines the niche, not the species' ability to inhabit a parameter space where it is currently not observed (see also Nogués-Bravo 2009).

Thus, while European mammals show hardly any phylogenetic signal in their climate niches, this presents no guarantee for their survival under climate change. Because mammal populations worldwide (and those in Europe are no exception) are also threatened by habitat loss, pollution and accidental mortality (Schipper *et al.* 2008), climate change is only one of several threats dormice and brown bears are facing.

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Detailed methods and additional results

accompanying “Evolution of climate niches in European mammals” by C.F. Dormann, B. Gruber, M. Winter & D. Herrmann (Biol. Lett.)

Data

Data on the distribution of European terrestrial mammals were taken from the European Mammal Assessment (Temple & Terry 2007) and were gridded into the 50 x 50 km European Environmental Agency reference grid (<http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=760>). It consists of 3037 cells from 11° to 32° East, and from 34° to 72° North. Grid cells were classified as “present” when a cell fell at least to 50% of its terrestrial area into the distribution polygon (Table A1 gives details on each species).

We selected 13 explanatory variables from an initial set of 24. In case of collinearity, one variable was selected on ecological grounds (for land cover), or a sequential regression (Graham 2003) was used to orthogonalise variables (for topography and climate). Specifically, we omitted landcover variables which we considered unimportant due to their rareness (bare ground, ice and snow, lakes, sea) and several derived measures of water availability (equilibrium and potential evapotranspiration, water deficit and water balance). We confirmed our selection by a quantification of variable importance using randomForest (Breiman 2001): The variables selected were always better than the correlated variables we omitted. Instead of altitude and slope we calculated their residuals with respect to all other variables retained (see below). This means, “residual altitude” and “residual slope” represent topographic effects *in addition to* all more direct effects correlated with topography (such as climate and landuse). Similarly, due to the high correlation of absolute minimum temperature with growing degree days (over 5°C), we calculated its residuals after linear regression against GDD5 and temperature seasonality.

The following variables were finally used as input: five climatic variables (growing degree days over 5°C, annual precipitation, summer precipitation, temperature seasonality, and residuals of absolute minimum temperature; data taken from WorldClim (Hijmans et al. 2005) or calculated from these following Levinsky et al. (2007)); two topographic variables (residuals of mean elevation, residuals of slope; based on NASA’s SRTM 30” data, available through <http://seamless.usgs.gov>); and six land-cover variables (proportion of crop, grassland, mosaic habitat, shrubland, urban and forest; data taken from Global Landcover Project URL: <http://ies.jrc.ec.europa.eu/global-land-cover-2000>). All these variables were correlated with $|r| < 0.7$.

Phylogenetic data were extracted from the second of the three supertrees published in Bininda-

Emonds et al. (2007, 2008, see Fig. A6). The analyses of all trees were almost identical (data not shown). We calculated the cophenetic distance between all 140 mammal species which were found both in the supertree and the European Mammal Assessment using the R-package ape (Paradis *et al.* 2004). Branch lengths were divided by twice the tip-root-distance, yielding a phylogenetic distance ranging from 0 (identical species) to 1 (maximum difference, approx. 96 million years). We identified for each species a sister species, i.e. the one with the shortest phylogenetic distance. For some few species we randomly choose one from the group of identically closely related species. This random decision had no discernable impact on our analysis. Some very few species were used twice as reference, due to the structure of the phylogeny (see Table A1 and the group *Sorex granarius/ araneus/ coronatus* in the phylogeny).

Species Distribution Models

Distribution data were analysed using boosted regression trees (BRT), following Elith *et al.* (2008). Recently, Elith & Graham (2009) have shown, through simulation, that BRT is superior to presence-only approaches such as MaxEnt (Phillips *et al.* 2006) (GLMs are too constrained by their smooth functional relationship, while GARP suffers from severe commission errors: Stockman *et al.* 2006). 70% of the data were stratified-randomly selected for training the BRT, thus maintaining equal prevalences in training and hold-out sample. On the 30% hold-out, we assessed model quality using AUC, ratio of observed to predicted presences and number and distances of predicted occurrences outside the observed range (data not shown). The latter three give an indication of how closely the BRTs follow the geographical distribution, and if they predict occurrences far away from actual presences. We additionally quantified spatial autocorrelation in model residuals but did not specifically adjust the models because the range of spatial autocorrelation was extremely short and could not be improved by a spatial model (see below). All analyses were carried out using R (R Development Core Team 2009).

Niche overlap

How to calculate niche overlap: a brief positioning of our work in the current debate

There is currently no standard way to calculate niche overlap. Two decisions of importance for our analysis are currently debated: Firstly, how to quantify overlap (i.e. which metrics to use); secondly, whether to base niche overlap on geographical overlap or on overlap in parameter space.

There are many indices to calculate the overlap of niches (Hurlbert 1978, Krebs 1989, Warren *et al.* 2008), and we use four different ones to check for robustness of our analyses: 1. a new one, defined in appendix I; 2. the Horn-Morisita-index; 3. the D-index of Schoener (1968); and, 4. the I-index (a variation of the Hellinger distance: Warren *et al.* 2008). All indices use the probability of occurrence of the two species i and j under environmental conditions k : \hat{y}_{ik} and \hat{y}_{jk} . We calculated the ratio

$\hat{y}_{ik} / \sum_{k=1}^N \hat{y}_{ik}$ to control for prevalence differences before calculating niche overlap (the sum is across all data used for calculating niche overlap).

Fundamentally, \hat{y}_{ik} values can be derived for each cell in space, and a comparison of species ranges could then serve as surrogate for niche overlap. While this approach was recommended by Warren *et al.* (2008), it suffers from a weighting in favour of common environments: Any two species co-occurring in the same and common habitat (say, a lowland agricultural grassland) will have a high overlap, even if one was able to also occur in the mountains. This is because the lowlands are far more common and thus have a greater influence on the niche overlap value. Warren *et al.* (2008) correct for this by using an environment-based null model.

Alternatively, one could predict \hat{y}_{ik} for a regular hypercube of climate variable combinations and calculate niche overlap in climate space (Graham *et al.* 2004, Knouft *et al.* 2006, Pfenninger *et al.* 2007). This automatically avoids the problem of commonness of environments. It has been criticised, however, as potentially causing a biased estimate of niche overlap, because in the hypercube certain climate variable value combinations would be used, which are not found in the study region (Warren *et al.* 2008). While this is true in principle, it is also strongly dependent on the model type of the species distribution analysis. Regression trees (such as our BRTs) extrapolate beyond the fitted range without trend, i.e. a value higher than observed will receive the same value as the highest observed (Elith *et al.* 2008, in contrast to more regression-based approaches such as GLM, GAM, SVM or MARS). Thereby an effect of beyond-the-range predictions is eliminated. Note that the example given by Warren *et al.* to illustrate this potential problem is due to their method making extremely high predictions outside the fitted range. We consider this a weakness of their species distribution modelling approach, not of the niche overlap in climate space. We follow this latter approach in our analysis, but additionally restrict niche overlap calculations to those data points of the hypercube which are inside the 5-dimensional convex hull of the original climate data. This reduces the number of points to predict to from 3.2 million to 185 308. (This severe reduction of parameter space with dimension has also been termed the ‘‘curse of dimensionality’’ by Bellman 1957.) In a previous analysis, using all hypercube points, results are qualitatively similar, but niche overlap was lower (data not shown). Predicting to ‘‘non-analogous’’ did not, however, distort the analysis as claimed by Warren *et al.*, indicating that it was indeed more to do with their modelling approach.

Finally, depending on the methods used, niche overlap comparisons may be closer to investigating ‘‘niche equivalency’’ or closer to ‘‘niche similarity’’ (Warren *et al.* 2008). Our approach (based on niche overlap in climate space) is much closer to ‘‘niche equivalency’’ than the cross-prediction tests of niche similarity (e.g. Peterson *et al.* 2002).

Niche overlap calculations

To calculate climate niche overlap, we predicted probability of occurrence of each species for a multi-dimensional climate parameter space. To do so, we produced a data set with equidistant sequences of 20 points along each of the five climate parameters, from the lowest to the highest observed value, i.e. a five-dimensional hypercube with 20^5 (=3.2 million) different parameter combinations. We then clipped the data set to include only data points inside the 5-D convex hull of the 3037 European cells (i.e. the realised climate space). Our climate-niche data set now comprised 185 308 data points. Values for non-climatic variables were set to their median value. Next, we used the predicted probabilities for the hypercube sample to compare sister species. The similarity in the climate parameter space is an unbiased estimator of climate niche overlap, while geographic overlap is confounded not only by land-use and topographic variables, but also by the frequency of climate variable combinations. In our hypercube sample, each climate combination occurs exactly once.

Climate niche overlap between sister species was calculated in four ways. One (henceforth termed niche overlap) calculates the proportion of the niche space occupied by *both* species of the total niche space occupied by *any* of the two species:

$$NO = \frac{1}{N} \sum_k \min(\hat{y}_{ik}, \hat{y}_{jk}) / \max(\hat{y}_{ik}, \hat{y}_{jk}),$$

where \hat{y}_k is the predicted value for the k th of N climate hypercube combinations (normalised so that $\sum \hat{y}_k = 1$, thereby

correcting for different prevalences and hence mean expected occurrence probabilities) and species i or j . This index scales predicted probabilities by the maximum of both species, yielding values from 0 to 1. For niche distance, we use $1-NO$. Secondly, we used the Morisita-Horn index, the I-index and the D-index, which yields a very similar picture (see next section for formulae and results).

To investigate whether climate niche overlap may occur as an artefact of the unique climate conditions of the geographical species ranges, we analysed the overlap of each species with the combined niche of both sister species. The results (below) indicate that this was not the case.

Additional results and the null model approach

Analysis using the Morisita-Horn-index, the I-index and the D-index

The Morisita-Horn index is defined as (Wolda 1981, Krebs 1989):

$$MH = 1 - \frac{2 \sum_{k=1}^N \hat{y}_{ik} \hat{y}_{jk}}{\left(\frac{\sum_{k=1}^N \hat{y}_{ik}^2}{\left(\sum_{k=1}^N \hat{y}_{ik} \right)^2} + \frac{\sum_{k=1}^N \hat{y}_{jk}^2}{\left(\sum_{k=1}^N \hat{y}_{jk} \right)^2} \right) \sum_{k=1}^N \hat{y}_{ik} \sum_{k=1}^N \hat{y}_{jk}}$$

(definitions of symbols as in the formula for NO , appendix I). It allows the calculation of distances for any type of positive valued abundance information, thus also for probabilities (Oksanen *et al.* 2009).

The D- and I-indices are defined as (Warren *et al.* 2008):

$$D = 1 - \frac{1}{2} \sum_{k=1}^N |\hat{y}_{ik} - \hat{y}_{jk}|$$

and

$$I = 1 - \frac{1}{2} \sqrt{\sum_{k=1}^N (\sqrt{\hat{y}_{ik}} - \sqrt{\hat{y}_{jk}})^2}$$

Fig. A1 shows that the results are near-identical for these indices.

Spatial autocorrelation

As with all spatial data, residual spatial autocorrelation (SAC) is a potentially relevant issue (Dormann 2007). It may arise from various sources, most noticeably from biological causes (dispersal limitation, source-sink dynamics, spill-over effects), from omission of relevant

environmental drivers (e.g. prey abundance) or from model mis-specification. The modelling approach chosen here (Boosted Regression Trees), can only address the last problem. It offers high flexibility in the fitting of statistical relationships, particularly non-linear relationships (including thresholds) and interactions between explanatory variables. On the other hand, BRT cannot be combined readily with any of the methods correcting for spatial autocorrelation that are currently available (Dormann *et al.* 2007). One could thus “only hope” to have reduced residual spatial autocorrelation compared to more traditional GLM approaches.

To investigate of spatial autocorrelation, we build GLMs (including quadratic effects and interactions) from the most important variables in the BRT models. Next, we used the very flexible approach of Spatial Eigenvector Mapping (Griffith & Peres-Neto 2006, Dormann *et al.* 2007) to reduce the residual spatial autocorrelation of this GLM. In Fig. A2 we illustrate the findings for two species, one rather common and widespread (the European fox *Vulpes vulpes*) and a local endemic species (*Acomys minous*). This figure shows that BRT has the shortest range of spatial autocorrelation (i.e. the distance when Moran’s I drops to approximately zero), and considerably less SAC than the GLM. The spatial correction of SEVM is able to reduce SAC at the very short distance (one to four grid cell), but is still inferior to BRT’s in any of the longer distances.

Across all species, residual spatial autocorrelation is still prevalent (Fig. A3), with mean range of 4.6 grid

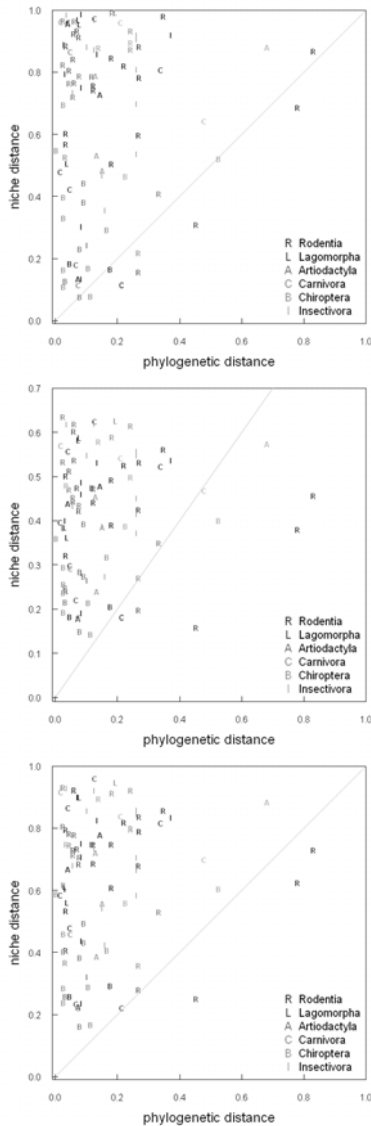


Fig. A1. Morisita-Horn-, I- and D-index depiction of fig. 1. While scaling (of the y-axis) and the position of the out-species changes slightly, the overall picture is highly similar.

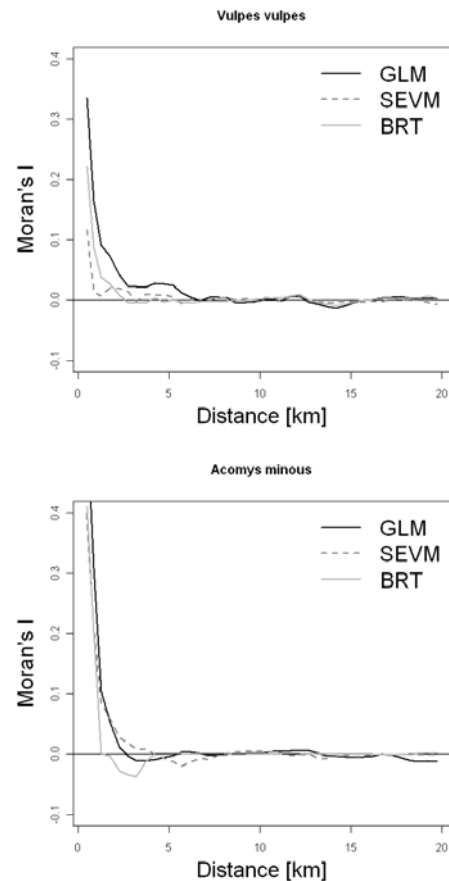


Fig. A2. Corelograms depicting spatial autocorrelation (as Moran’s I) in model residuals for two species.

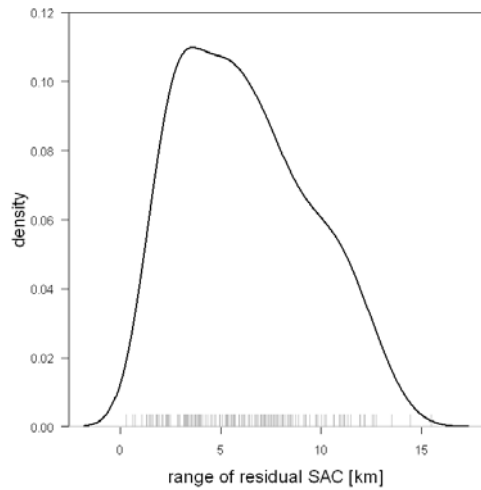


Fig. A3. Density plot of range of spatial autocorrelation across all modelled species (in km). Rug at the bottom indicates data points. *Vulpes vulpes* and *Acomys minous* have a range of 2.3 and 1.3 km, respectively.

cells (i.e. approximately 250 km). We tried, for some species, to find spatial eigenvectors correlated with BRT residuals and include those in the BRT to reduce its SAC. Neither for *Vulpes vulpes* nor for *Acomys minous* did this alter the SAC in residuals noticeably (data not shown). We are thus not aware of any way to reduce spatial autocorrelation while maintaining the high model fit of BRT. Overall, while BRT is not able to remove spatial autocorrelation (as neither does SEVM), we regard the huge reduction compared to the GLM as indication of appropriateness of our method in the face of spatial autocorrelation.

Null models for niche overlap

Our approach may be liable to type II errors, i.e. two species may be described as non-overlapping in their climate niche although they really are. Imagine, for example, the case of the European Brown Hare (*Lepus europaeus*) and its sister species the Corsican Brown Hare (*Lepus corsicanus*). If both species shared the same climate niche but just happened to be spatially separated, we might find a low niche overlap because Corsica has a very different climate variable correlation structure than the rest of Europe. To investigate the effects of spurious non-overlap, we adopted the following procedure:

We combined the presence-points of two sister species, fitted a boosted regression tree to the combined data, calculated the multidimensional climate niche for the combined data and then calculated the overlap of each species with the combined climate niche. If the two species were completely and truly separated in climate space, then we would expect an average overlap of each species with the combined of 0.5 (measured by Morisita-Horn), since each species contributes equally to the new pseudo-species' niche. That is exactly what we found (Fig. A4).

This finding generally confirms our assumption that non-overlapping species really occupy different climate space and that our results (in the main text) are not a mere artefact of environmental conditions differing between their ranges.

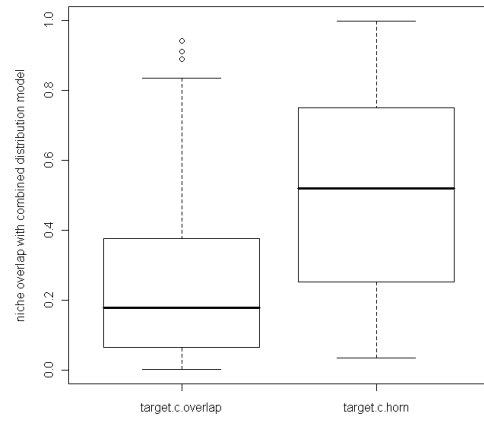


Fig. A4. Niche overlap between species and the hypothetical super-species resulting from the combination of the target and its sister species. Expected values for the Morisita-Horn (right box plot) is 0.5.

Fig. A5 presents the values for all 140 comparisons. While on average their value is 0.5 (for Morisita-Horn), they scatter across the entire graph. This means that the effect of a rare species contributing to the combined niche (i.e. values closer to 0 on the x-axis) is unpredictable, i.e. it does not systematically affect our results.

The situation is slightly more complex for the niche overlap-index, which includes the absolute probabilities of occurrence values. (We could not derive an expected value for this index analytically.) Similar to the Morisita-Horn index, there is no systematic effect of rare or common species on the estimation of niche overlap (Fig. A4).

Across all comparisons, Morisita-Horn-overlap of each species with the combined is 0.5 (Fig. A4). Although there are cases where the overlap is considerably higher (particularly when one species is far more abundant than the other and hence also dominates the combined climate niche), this gives us confidence that our findings are no statistical artefact.

Phylogenetic trends in climate niche distance

Our study focused on the question, whether climate niche overlap is maintained between sister species. One could, however, address a wider question on niche distances through phylogeny. This is more challenging, because we have no date for the extinct species, so that we are unable to trace the evolution of the climatic niche back through the phylogenetic tree. Still, we can analyse all possible extant species comparisons ($140 \times (140-1) / 2 = 9730$) and investigate this pattern as a function of phylogenetic distance. This section presents the results of this comparison.

Fig. A6 shows the phylogenetic trend for climate niche distance for each species. Across all 140 species, linear lines dominate, and most are horizontal. More formally, we carried out a Spearman rank correlation for each of these panels, the results of which are depicted in Fig. A7. Of the 140 comparisons, 23 were significant (21 positive and 2 negative).

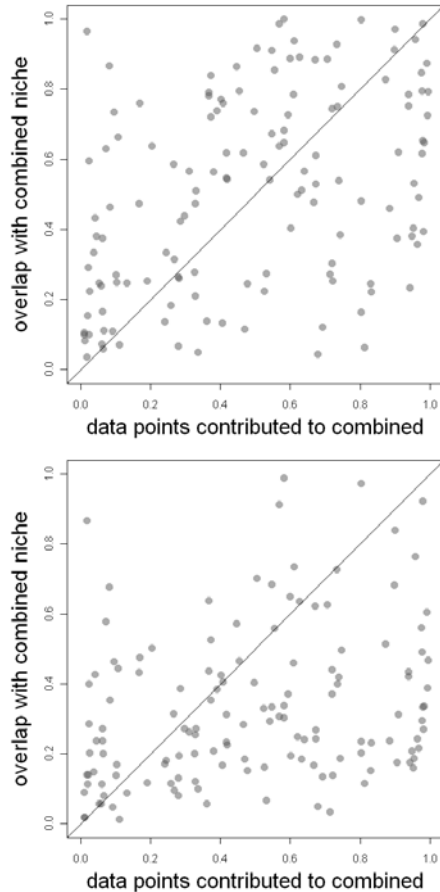


Fig. A5. Null model analysis for Morisita-Horn overlap (upper) and niche overlap (lower). Niche overlap of each species with the combined data as a function of their contribution to the combined data set. In principle, one could expect a species that contributes 30% to the combined data also to overlap to 30% with the “combined niche”. These points would be on the 1:1 line. The majority of points falls below this line (for niche overlap) or at least no pattern suggests a dominance by the more prevalent of the two combined species (for Morisita-Horn overlap). A species contributing only 10 to 110 points will have lower expected overlap than the sister species contributing the remaining 100. Thus, the expected overlap is $N_i/(N_i + N_j)$, where N_i is number of observations for species i .

To get an estimate of the overall importance of phylogeny, we calculated the overall trend across the 9730 comparisons (realising that doing so we violated the assumption of independence of data points). This regression indicates a significant trend of climate niche distance with phylogenetic distance (Fig. A8).

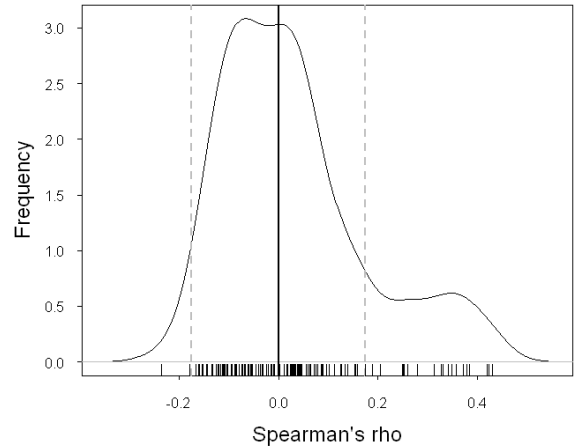


Fig. A7. Distribution of correlation coefficients for the 140 species in Fig. A6. Dashed grey lines indicate thresholds for significance ($P < 0.05$).

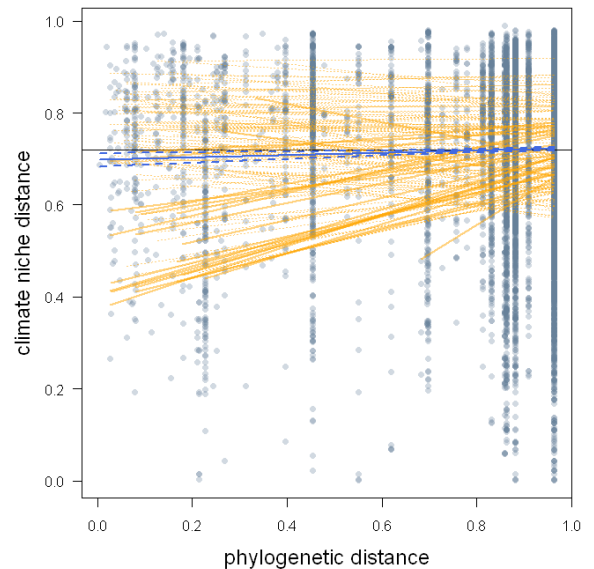


Fig. A8. All pairwise comparisons ($140 \times (140-1) / 2 = 9730$) of climate niche distance as a function of phylogenetic distance. Orange lines indicate per-species regressions (dotted and thin if not significant according to Spearman's rank test). Blue lines are regression (+/- 95% CI) through all points (climate niche distance = $0.698 + 0.025 \times \text{phylogenetic distance}$, $F_{1, 9728} = 8.4$, $P < 0.01$, $R^2_{\text{adj}} = 0.00076$), and black horizontal line is the grand mean of climate niche distance (0.719).

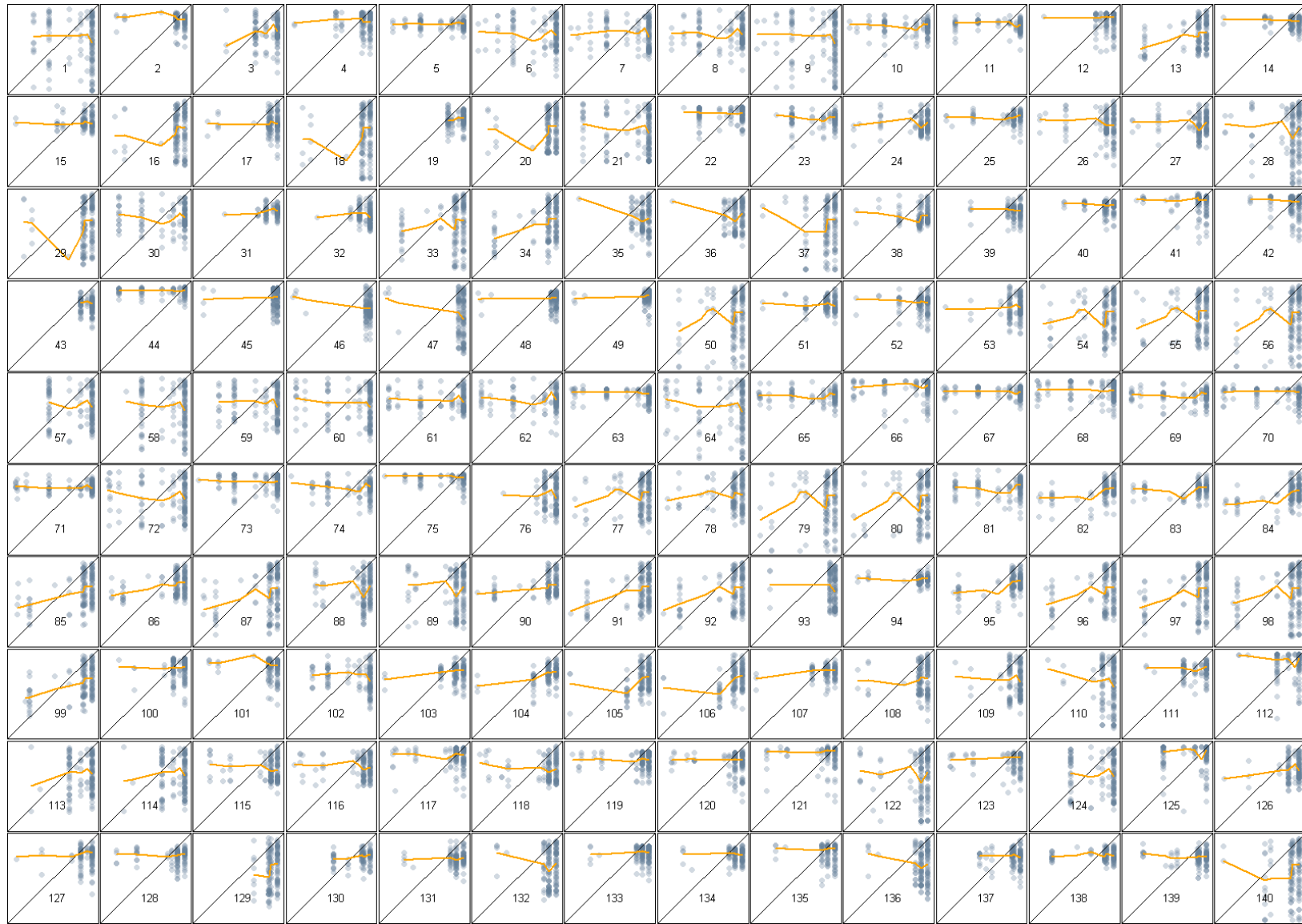


Fig. A6. Climate niche distance for each species against phylogenetic distance (both axes scaling from 0 to 1). Coloured lines are lowess-smoothers to guide the eye. Numbers refer to species code (Table A4).

Table A1. Species under investigation in this study, their prevalence, sister species, niche overlap (NO, H, D and I index), cophenetic distance and node age. Note that while we give niche overlap values here, the figures in the main paper give niche distances (i.e. 1 – niche overlap). Last column gives significance levels and direction of phylogenetic trend (Spearman rank correlation, see fig. A6; empty cell indicate n.s.).

nr	name	group	N	sister	cophenetic	nodeage	NO	Horn	D-index	I-index	trend
1	<i>Acomys minous</i>	Rodentia	11	5	0.96	92	0.54	0.84	0.72	0.8	
2	<i>Alces alces</i>	Artiodactyla	868	18	0.7	67	0.1	0.27	0.22	0.52	
3	<i>Allactaga major</i>	Rodentia	29	111	0.96	92	0.24	0.02	0.14	0.44	
4	<i>Alopex lagopus</i>	Carnivora	68	140	0.96	92	0.06	0.04	0.08	0.43	
5	<i>Apodemus agrarius</i>	Rodentia	952	6	0.7	67	0.18	0.26	0.31	0.56	
6	<i>Apodemus alpicola</i>	Rodentia	45	7	0.27	26	0.35	0.4	0.47	0.68	
7	<i>Apodemus flavicollis</i>	Rodentia	1893	6	0.27	26	0.35	0.4	0.47	0.68	
8	<i>Apodemus mystacinus</i>	Rodentia	117	5	0.7	67	0.18	0.26	0.31	0.56	
9	<i>Apodemus sylvaticus</i>	Rodentia	2182	6	0.04	3	0.17	0.19	0.26	0.55	
10	<i>Apodemus uralensis</i>	Rodentia	434	6	0.04	3	0.17	0.19	0.26	0.55	
11	<i>Arvicola sapidus</i>	Rodentia	400	21	0.45	44	0.19	0.49	0.39	0.61	
12	<i>Atelerix algirus</i>	Insectivora	214	35	0.45	44	0.08	0.14	0.17	0.47	
13	<i>Barbastella barbastellus</i>	Bats	1491	98	0.96	92	0.52	0.83	0.71	0.79	+++
14	<i>Canis aureus</i>	Carnivora	538	15	0.03	2	0.2	0.52	0.42	0.6	
15	<i>Canis lupus</i>	Carnivora	878	14	0.03	2	0.2	0.52	0.42	0.6	
16	<i>Capra ibex</i>	Artiodactyla	22	17	0.27	26	0.37	0.04	0.33	0.56	
17	<i>Capra pyrenaica</i>	Artiodactyla	20	16	0.27	26	0.37	0.04	0.33	0.56	
18	<i>Capreolus capreolus</i>	Artiodactyla	2377	2	0.7	67	0.1	0.27	0.22	0.52	
19	<i>Castor fiber</i>	Rodentia	586	1	0.7	67	0.25	0.31	0.38	0.62	
20	<i>Cervus elaphus</i>	Artiodactyla	1789	29	0.45	44	0.62	0.87	0.77	0.82	
21	<i>Chionomys nivalis</i>	Rodentia	232	11	0.45	44	0.19	0.49	0.39	0.61	
22	<i>Cricetulus migratorius</i>	Rodentia	183	23	0.18	17	0.21	0.22	0.21	0.47	
23	<i>Cricetus cricetus</i>	Rodentia	529	22	0.18	17	0.21	0.22	0.21	0.47	
24	<i>Crociodura leucodon</i>	Insectivora	1125	25	0.12	11	0.16	0.25	0.25	0.51	
25	<i>Crociodura russula</i>	Insectivora	811	24	0.12	11	0.16	0.25	0.25	0.51	
26	<i>Crociodura sicula</i>	Insectivora	20	24	0.08	7	0.39	0.02	0.41	0.61	
27	<i>Crociodura suaveolens</i>	Insectivora	1355	24	0.08	7	0.25	0.02	0.29	0.55	
28	<i>Crociodura zimmermanni</i>	Insectivora	11	24	0.08	7	0.39	0.74	0.6	0.72	
29	<i>Dama dama</i>	Artiodactyla	1822	20	0.45	44	0.62	0.87	0.77	0.82	
30	<i>Dinaromys bogdanovi</i>	Rodentia	36	11	0.45	44	0.19	0.15	0.25	0.51	
31	<i>Dryomys nitedula</i>	Rodentia	689	32	0.06	6	0.15	0.18	0.18	0.47	
32	<i>Eliomys quercinus</i>	Rodentia	961	31	0.06	6	0.15	0.18	0.18	0.47	-
33	<i>Eptesicus bottae</i>	Bats	19	34	0.04	4	0.56	0.82	0.74	0.82	
34	<i>Eptesicus serotinus</i>	Bats	1997	33	0.04	4	0.56	0.82	0.74	0.82	+++
35	<i>Erinaceus concolor</i>	Insectivora	107	36	0.06	6	0.3	0.2	0.4	0.6	
36	<i>Erinaceus europaeus</i>	Insectivora	1657	35	0.06	6	0.3	0.2	0.4	0.6	
37	<i>Felis chaus</i>	Carnivora	15	38	0.06	6	0.35	0.58	0.52	0.7	
38	<i>Felis silvestris</i>	Carnivora	871	37	0.06	6	0.35	0.58	0.52	0.7	
39	<i>Galemys pyrenaicus</i>	Insectivora	80	131	0.96	92	0.36	0.08	0.17	0.46	
40	<i>Genetta genetta</i>	Carnivora	559	42	0.78	75	0.25	0.19	0.18	0.48	
41	<i>Gulo gulo</i>	Carnivora	270	54	0.91	87	0.03	0.03	0.04	0.38	
42	<i>Herpestes ichneumon</i>	Carnivora	271	40	0.78	75	0.25	0.19	0.18	0.48	
43	<i>Hystrix cristata</i>	Rodentia	199	1	0.83	80	0.18	0.13	0.27	0.54	
44	<i>Lemmus lemmus</i>	Rodentia	307	81	0.96	92	0.09	0.21	0.25	0.53	
45	<i>Lepus capensis</i>	Lagomorpha	208	46	0.04	3	0.08	0.04	0.1	0.41	
46	<i>Lepus corsicanus</i>	Lagomorpha	48	47	0.37	35	0.12	0.03	0.1	0.42	
47	<i>Lepus europaeus</i>	Lagomorpha	2068	46	0.03	3	0.1	0.11	0.17	0.46	
48	<i>Lepus granatensis</i>	Lagomorpha	233	46	0.03	3	0.1	0.11	0.17	0.46	
49	<i>Lepus timidus</i>	Lagomorpha	964	46	0.37	35	0.22	0	0.01	0.32	
50	<i>Lutra lutra</i>	Carnivora	2709	77	0.96	92	0.61	0.88	0.78	0.82	
51	<i>Lynx lynx</i>	Carnivora	780	52	0.33	32	0.28	0.04	0.13	0.44	

nr	name	group	N	sister	cophenetic	nodeage	NO	Horn	D-index	I-index	trend
52	<i>Lynx pardinus</i>	Carnivora	30	51	0.33	32	0.28	0.04	0.13	0.44	
53	<i>Marmota marmota</i>	Rodentia	79	126	0.96	92	0.41	0.07	0.27	0.53	
54	<i>Martes foina</i>	Carnivora	1791	55	0.03	3	0.61	0.82	0.76	0.78	
55	<i>Martes martes</i>	Carnivora	2222	54	0.03	3	0.61	0.82	0.76	0.78	
56	<i>Meles meles</i>	Carnivora	2563	77	0.96	92	0.61	0.88	0.78	0.82	
57	<i>Meriones tristrami</i>	Rodentia	45	1	0.91	87	0.66	0.69	0.75	0.84	
58	<i>Mesocricetus newtoni</i>	Rodentia	16	22	0.91	87	0.09	0.12	0.16	0.47	
59	<i>Micromys minutus</i>	Rodentia	1674	1	0.96	92	0.54	0.84	0.72	0.8	
60	<i>Microtus agrestis</i>	Rodentia	1884	62	0.13	13	0.28	0.09	0.31	0.58	
61	<i>Microtus arvalis</i>	Rodentia	1386	66	0.25	24	0.09	0.08	0.08	0.4	
62	<i>Microtus cabreræ</i>	Rodentia	47	60	0.13	13	0.28	0.09	0.31	0.58	
63	<i>Microtus duodecimcostatus</i>	Rodentia	235	67	0.15	15	0.37	0.19	0.22	0.49	
64	<i>Microtus felteni</i>	Rodentia	17	65	0.15	15	0.19	0.16	0.27	0.56	
65	<i>Microtus gerbei</i>	Rodentia	84	64	0.15	15	0.19	0.16	0.27	0.56	
66	<i>Microtus guentheri</i>	Rodentia	138	61	0.25	24	0.09	0.08	0.08	0.4	
67	<i>Microtus lusitanicus</i>	Rodentia	114	63	0.15	15	0.37	0.19	0.22	0.49	
68	<i>Microtus multiplex</i>	Rodentia	55	63	0.86	83	0.28	0.01	0.05	0.36	
69	<i>Microtus oeconomus</i>	Rodentia	608	60	0.08	7	0.21	0.16	0.27	0.55	
70	<i>Microtus savii</i>	Rodentia	130	64	0.86	83	0.15	0.28	0.29	0.55	
71	<i>Microtus subterraneus</i>	Rodentia	960	63	0.86	83	0.2	0.03	0.06	0.37	
72	<i>Microtus thomasi</i>	Rodentia	60	63	0.08	7	0.16	0.32	0.31	0.56	
73	<i>Mus macedonicus</i>	Rodentia	218	74	0.07	6	0.2	0.18	0.19	0.47	
74	<i>Mus spicilegus</i>	Rodentia	223	73	0.13	12	0.1	0.09	0.13	0.43	
75	<i>Mus spretus</i>	Rodentia	387	73	0.13	12	0.14	0.03	0.07	0.36	
76	<i>Muscardinus avellanarius</i>	Rodentia	1378	31	0.96	92	0.27	0.59	0.47	0.65	
77	<i>Mustela erminea</i>	Carnivora	2054	79	0.48	46	0.61	0.88	0.78	0.82	
78	<i>Mustela lutreola</i>	Carnivora	92	80	0.55	53	0.45	0.13	0.54	0.71	
79	<i>Mustela nivalis</i>	Carnivora	2799	77	0.48	46	0.61	0.88	0.78	0.82	
80	<i>Mustela putorius</i>	Carnivora	1953	78	0.55	53	0.45	0.13	0.54	0.71	
81	<i>Myopus schisticolor</i>	Rodentia	271	44	0.96	92	0.09	0.21	0.25	0.53	
82	<i>Myotis blythii</i>	Bats	1056	85	0.62	59	0.44	0.87	0.74	0.78	+++
83	<i>Myotis capaccinii</i>	Bats	520	82	0.02	2	0.4	0.62	0.57	0.73	+++
84	<i>Myotis emarginatus</i>	Bats	1244	82	0.11	10	0.38	0.68	0.59	0.67	+++
85	<i>Myotis myotis</i>	Bats	1540	82	0	0	1	1	1	1	+++
86	<i>Myotis mystacinus</i>	Bats	1589	82	0.11	10	0.38	0.68	0.59	0.67	+++
87	<i>Myotis nattereri</i>	Bats	2160	82	0.62	59	0.24	0.42	0.41	0.63	++
88	<i>Neomys anomalus</i>	Insectivora	1312	89	0.34	33	0.5	0.76	0.68	0.73	
89	<i>Neomys fodiens</i>	Insectivora	2205	88	0.34	33	0.5	0.76	0.68	0.73	
90	<i>Nyctalus lasiopterus</i>	Bats	618	91	0.03	3	0.45	0.67	0.6	0.74	++
91	<i>Nyctalus leisleri</i>	Bats	1712	90	0.03	3	0.64	0.88	0.81	0.82	+++
92	<i>Nyctalus noctula</i>	Bats	1811	90	0.03	3	0.38	0.6	0.54	0.71	+++
93	<i>Oryctolagus cuniculus</i>	Lagomorpha	1427	45	0.96	92	0.08	0.01	0.05	0.37	
94	<i>Ovis aries</i>	Artiodactyla	676	16	0.96	92	0.2	0.21	0.28	0.55	
95	<i>Pipistrellus kuhlii</i>	Bats	1054	96	0.53	51	0.34	0.71	0.59	0.68	+++
96	<i>Pipistrellus nathusii</i>	Bats	1818	97	0.23	22	0.68	0.92	0.83	0.86	++
97	<i>Pipistrellus pipistrellus</i>	Bats	2198	96	0.23	22	0.68	0.92	0.83	0.86	++
98	<i>Plecotus auritus</i>	Bats	2085	99	0.03	3	0.52	0.83	0.71	0.79	
99	<i>Plecotus austriacus</i>	Bats	1328	98	0.03	3	0.52	0.83	0.71	0.79	+++
100	<i>Pteromys volans</i>	Rodentia	210	109	0.23	22	0.12	0.01	0.09	0.41	
101	<i>Rangifer tarandus</i>	Artiodactyla	61	2	0.96	92	0.3	0.52	0.44	0.61	
102	<i>Rattus rattus</i>	Rodentia	1866	1	0.96	92	0.42	0.78	0.64	0.73	—
103	<i>Rhinolophus blasii</i>	Bats	325	104	0.17	16	0.26	0.21	0.3	0.57	
104	<i>Rhinolophus euryale</i>	Bats	1030	107	0.23	22	0.31	0.45	0.41	0.64	+++
105	<i>Rhinolophus ferrumequinum</i>	Bats	1351	104	0.11	11	0.41	0.83	0.71	0.76	+++

nr	name	group	N	sister	cophenetic	nodeage	NO	Horn	D-index	I-index	trend
106	<i>Rhinolophus hipposideros</i>	Bats	1606	104	0.23	22	0.3	0.24	0.33	0.59	+++
107	<i>Rhinolophus mehelyi</i>	Bats	401	104	0.05	4	0.3	0.37	0.37	0.61	+
108	<i>Rupicapra rupicapra</i>	Artiodactyla	62	16	0.96	92	0.62	0.47	0.61	0.76	
109	<i>Sciurus anomalus</i>	Rodentia	99	110	0.08	8	0.53	0.47	0.63	0.75	
110	<i>Sciurus vulgaris</i>	Rodentia	2300	109	0.08	8	0.53	0.47	0.63	0.75	
111	<i>Sicista betulina</i>	Rodentia	534	112	0.88	85	0.16	0.1	0.2	0.5	
112	<i>Sicista severtzovi</i>	Rodentia	33	111	0.09	9	0.03	0.66	0.4	0.58	
113	<i>Sicista strandi</i>	Rodentia	12	111	0.09	9	0.03	0.66	0.4	0.58	
114	<i>Sicista subtilis</i>	Rodentia	41	111	0.88	85	0.16	0.1	0.2	0.5	
115	<i>Sorex alpinus</i>	Insectivora	196	116	0.26	25	0.37	0.64	0.57	0.73	
116	<i>Sorex araneus</i>	Insectivora	1879	119	0.26	25	0.13	0.01	0.07	0.38	
117	<i>Sorex caecutiens</i>	Insectivora	404	120	0.37	36	0.19	0.13	0.26	0.53	
118	<i>Sorex coronatus</i>	Insectivora	377	116	0.26	25	0.24	0.26	0.32	0.57	
119	<i>Sorex granarius</i>	Insectivora	38	116	0.26	25	0.13	0.01	0.07	0.38	
120	<i>Sorex isodon</i>	Insectivora	156	117	0.37	36	0.19	0.13	0.26	0.53	
121	<i>Sorex minutissimus</i>	Insectivora	266	122	0.03	3	0.06	0.12	0.14	0.45	
122	<i>Sorex minutus</i>	Insectivora	2387	121	0.03	3	0.06	0.12	0.14	0.45	
123	<i>Sorex samniticus</i>	Insectivora	87	116	0.81	78	0.12	0.21	0.23	0.5	
124	<i>Spalax graecus</i>	Rodentia	20	125	0.08	8	0.03	0.12	0.1	0.42	
125	<i>Spalax zemni</i>	Rodentia	50	124	0.08	8	0.03	0.12	0.1	0.42	
126	<i>Spermophilus citellus</i>	Rodentia	188	127	0.08	8	0.31	0.11	0.25	0.52	
127	<i>Spermophilus suslicus</i>	Rodentia	73	126	0.08	8	0.31	0.11	0.25	0.52	
128	<i>Sumcus etruscus</i>	Insectivora	666	24	0.96	92	0.29	0.53	0.46	0.61	
129	<i>Sus scrofa</i>	Artiodactyla	2075	2	0.96	92	0.06	0.12	0.12	0.43	+
130	<i>Tadarida teniotis</i>	Bats	673	13	0.96	92	0.23	0.48	0.4	0.6	++
131	<i>Talpa caeca</i>	Insectivora	117	132	0.13	12	0.24	0.3	0.33	0.58	
132	<i>Talpa europaea</i>	Insectivora	1777	131	0.13	12	0.1	0.16	0.18	0.46	
133	<i>Talpa levantis</i>	Insectivora	59	131	0.04	3	0.33	0.03	0.08	0.4	
134	<i>Talpa occidentalis</i>	Insectivora	130	131	0.04	3	0.33	0.03	0.08	0.4	
135	<i>Talpa romana</i>	Insectivora	57	131	0.13	12	0.1	0.16	0.18	0.46	
136	<i>Talpa stankovici</i>	Insectivora	14	131	0.13	12	0.24	0.3	0.33	0.58	
137	<i>Ursus arctos</i>	Carnivora	605	41	0.96	92	0.1	0.36	0.3	0.53	
138	<i>Vespertilio murinus</i>	Bats	1298	13	0.96	92	0.26	0.54	0.44	0.61	
139	<i>Vormela peregusna</i>	Carnivora	134	77	0.88	85	0.16	0.04	0.16	0.46	
140	<i>Vulpes vulpes</i>	Carnivora	2879	4	0.96	92	0.06	0.04	0.08	0.43	

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