biology letters
Evolutionary biology

Biol. Lett. (2010) **6**, 229–232
doi:10.1098/rsbl.2009.0688
Published online 14 October 2009

Evolution of climate niches in European mammals?

Carsten F. Dormann[1,*], Bernd Gruber[1], Marten Winter[2] and Dirk Herrmann[1]

[1]*Helmholtz Centre for Environmental Research-UFZ, Department of Computational Landscape Ecology, Permoserstrasse 15, 04318 Leipzig, Germany*
[2]*Department of Biology, Ecology and Evolution Unit, University of Fribourg, Chaussee du Musée 10, 1700 Fribourg, Switzerland*
**Author for correspondence (carsten.dormann@ufz.de).*

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 interspecific 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; Gavrilets & 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 (Gavrilets & 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

$$\mathrm{NO} = \frac{1}{N}\sum_{k}^{N}\frac{\min(\hat{y}_{ik},\hat{y}_{jk})}{\max(\hat{y}_{ik},\hat{y}_{jk})},$$

where $\hat{y}_{.k}$ is the predicted occurrence probability for the kth 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 $1 - \mathrm{NO}$. 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.

Received 24 August 2009
Accepted 24 September 2009

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.

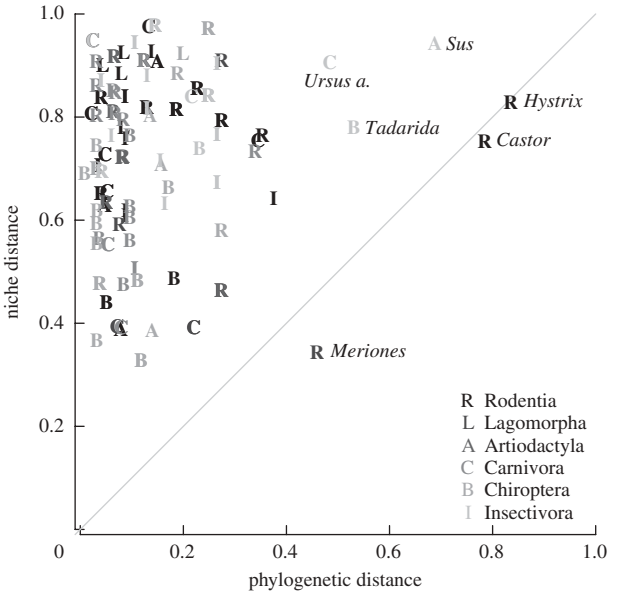

Figure 1. Climate niche distance and phylogenetic distance for a comparison of 140 mammalian sister species. Diagonal line separates niche flexible (upper left) and niche conservative (bottom right) pairs. High values for phylogenetic distance indicate species only very distantly related to any other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

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 (Olff *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.

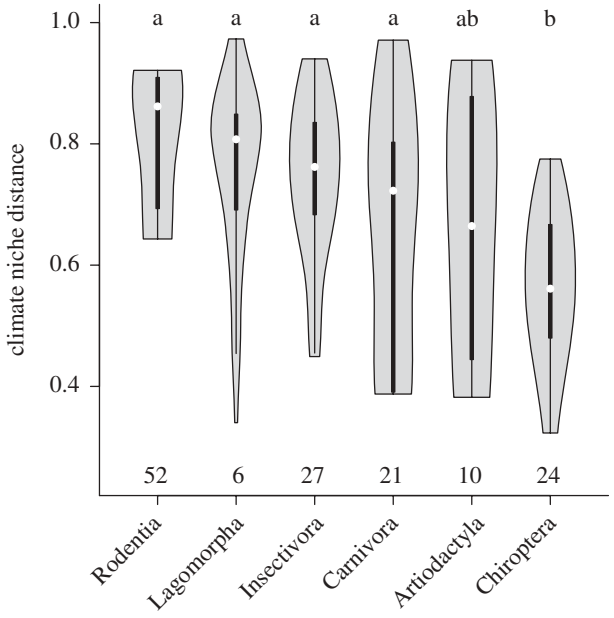

Figure 2. Violin plot of climate niche distances for the six mammalian orders. Number of species within each group is given below each bar. Groups sharing the same letter are not significantly different in Tukey's honest significant difference post hoc test (i.e. $p>0.05$).

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.

Many thanks to Michael Holyoak, Boris Schröder and an anonymous reviewer for comments on a previous version. C.F.D. and B.G. acknowledge the Helmholtz Association for funding (VN-NG-247).

Benton, M. J. 2009 The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**, 728–732. (doi:10.1126/science.1157719)

Bininda-Emonds, O. R. P. *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507. (doi:10.1038/nature05634)

Connell, J. H. 1980 Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**, 131–138. (doi:10.2307/3544421)

DeSantis, L. R. G., Feranec, R. S. & MacFadden, B. J. 2009 Effects of global warming on ancient mammalian communities and their environments. *PLoS ONE* **4**, e5750. (doi:10.1371/journal.pone.0005750)

Diamond, J. M. 1975 Assembly of species communities. In *Ecology and evolution of communities* (eds M. Cody & J. M. Diamond), pp. 342–444. Harvard, MA: Belknap Press.

Dormann, C. F. *et al.* 2007 Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628. (doi:10.1111/j.2007.0906-7590.05171.x)

Elith, J., Leathwick, J. R. & Hastie, T. 2008 A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813. (doi:10.1111/j.1365-2656.2008.01390.x)

Evans, M. E. K., Smith, S. A., Flynn, R. S. & Donoghue, M. J. 2009 Climate, niche evolution, and diversification of the 'bird-cage' evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *Am. Nat.* **173**, 225–240. (doi:10.1086/595757)

Gaston, K. J. 2003 *Structure and dynamics of geographic ranges*. Oxford, UK: Oxford University Press.

Gavrilets, S. & Losos, J. B. 2009 Adaptive radiation: contrasting theory with data. *Science* **323**, 732–737. (doi:10.1126/science.1157966)

Hespenheide, H. A. 1975 Prey characteristics and predator niche width. In *Ecology and evolution of communities* (eds M. Cody & J. M. Diamond), pp. 158–180. Harvard, MA: Belknap Press.

Hutchinson, G. E. 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–158. (doi:10.1086/282070)

IPCC 2007 Climate Change 2007. The physical science basis. In *Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change* (eds S. Solomon, D. Qin, M. Manning, M. Marquis, K. Averyt, M. Tignor, H. L. Miller Jr, Z. Chen), p. 996. Cambridge, UK: Cambridge University Press.

Johnson, C. N., Delean, S. & Balmford, A. 2002 Phylogeny and the selectivity of extinction in Australian marsupials. *Anim. Conserv.* **5**, 135–142. (doi:10.1017/S1367943002002196)

Kearney, M. 2006 Habitat, environment and niche: what are we modelling? *Oikos* **115**, 186–191. (doi:10.1111/j.2006.0030-1299.14908.x)

Kozak, K. H. & Wiens, J. J. 2006 Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**, 2604–2621.

Ley, R. E. *et al.* 2008 Evolution of mammals and their gut microbes. *Science* **320**, 1647–1651. (doi:10.1126/science.1155725)

Losos, J. B. 2008 Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**, 995–1003. (doi:10.1111/j.1461-0248.2008.01229.x)

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. & Rodríguez-Schettino, L. 1998 Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118. (doi:10.1126/science.279.5359.2115)

Nogués-Bravo, D. 2009 Predicting the past distribution of species climatic niche. *Global Ecol. Biogeogr.* **18**, 521–531. (doi:10.1111/j.1466-8238.2009.00476.x)

Olff, H., Ritchie, M. E. & Prins, H. H. T. 2002 Global environmental controls of diversity in large herbivores. *Nature* **415**, 901–904. (doi:10.1038/415901a)

Paradis, E., Claude, J. & Strimmer, K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)

Schipper, J. *et al.* 2008 The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**, 225–230. (doi:10.1126/science.1165115)

Schluter, D. 2001 Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372–380. (doi:10.1016/S0169-5347(01)02198-X)

Schluter, D. 2009 Evidence for ecological speciation and its alternative. *Science* **323**, 737–741. (doi:10.1126/science.1160006)

Sjöström, A. & Gross, C. L. 2006 Life-history characters and phylogeny are correlated with extinction risk in the Australian angiosperms. *J. Biogeogr.* **33**, 271–290. (doi:10.1111/j.1365-2699.2005.01393.x)

Temple, H. J. & Terry, A. 2007 *The status and distribution of European mammals*, p. 48. Luxembourg: Office for Official Publications of the European Communities.

Thompson, J. N. 1998 Rapid evolution as an ecological process. *Trends Ecol. Evol.* **13**, 329–332. (doi:10.1016/S0169-5347(98)01378-0)

Tilman, D. 1982 *Resource competition and community structure*. Princeton, NJ: Princeton University Press.

Wiens, J. J. 2008 Commentary on Losos (2008): niche conservatism deja vu. *Ecol. Lett.* **11**, 1004–1005. (doi:10.1111/j.1461-0248.2008.01238.x)