



Niche width impacts vertebrate diversification

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ABSTRACT

Aim The size of the climatic niche of a species is a major factor determining its distribution and evolution. In particular, it has been proposed that niche width should be associated with the rate of species diversification. Here, we test whether species niche width affects the speciation and extinction rates of three main clades of vertebrates: amphibians, mammals and birds.

Location Global.

Methods We obtained the time-calibrated phylogenies, IUCN conservation status, species distribution maps and climatic data for 2340 species of amphibians, 4563 species of mammals and 9823 species of birds. We computed the niche width for each species as the mean annual temperature across the species range. We estimated speciation, extinction and transition rates associated with lineages with either narrow (specialist) or wide (generalist) niches using phylogeny-based birth–death models. We also tested if current conservation status was correlated with the niche width of species.

Results We found higher net diversification rates in specialist species than in generalist species. This result was explained by both higher speciation rates (for the three taxonomic groups) and lower extinction rates (for mammals and birds only) in specialist than in generalist species. In contrast, current specialist species tended to be more threatened than generalist species.

Main conclusions Our diversification analysis shows that the width of the climatic niche is strongly associated with diversification rates and may thus be a crucial factor for understanding the emergence of diversity patterns in vertebrates. The striking difference between our diversification results and current conservation status suggests that the current extinction process may be different from extinction rates estimated from the whole history of the group.

Keywords

Diversification, diversity, generalist, latitudinal diversity gradient, niche evolution, specialist, speciation and extinction rates, vertebrates.

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INTRODUCTION

The width of the climatic niche of a species can be considered as the set of all the climatic conditions where the species is distributed (ecological realized niche, *sensu* Hutchinson, 1957; Futuyma & Moreno, 1988; Gaston 2003; Soberón, 2007). The niche width has been used in a large variety of studies, for example to model the responses of species to global change (such as in species distribution models; Guisan

& Thuiller, 2005; Thuiller *et al.*, 2008; Slatyer *et al.*, 2013). However, relatively few studies have attempted to describe the evolutionary history of the niche width at the macroevolutionary scale, and we are currently lacking a clear understanding of the evolution of the niche width and its potential effects on the rates of species diversification (i.e. speciation and extinction rates; but see Kostikova *et al.*, 2013; Litsios *et al.*, 2014; Gómez-Rodríguez *et al.*, 2015).

Several hypotheses have suggested a correlation between the niche width and the rate of species diversification, mainly in the direction of lower rates of speciation in generalist rather than specialist species. Generalist species, which are characterized by wider ecological niches, usually have larger range sizes than specialist species (Colwell & Rangel, 2009; Slatyer *et al.*, 2013). Their larger range size can accommodate a larger population size (Gaston & Blackburn, 1996), which in turn leads to a higher density-dependent dispersal probability and a potential decrease of speciation rates in generalist species because of higher gene flow (Gaston 2003). In contrast, specialist species should also have higher rates of speciation than generalist species, as habitat specialization is directly linked to speciation events in the case of adaptive radiations (for reviews see Schluter, 2000; Coyne & Orr, 2004). Given that dispersal becomes disadvantageous in specialist species adapted to a specific habitat because of a lower probability of reaching habitat of similar quality (Kisdi 2002; Parvinen & Egas, 2004), specialist species should thus contain more isolated and disconnected populations (Birand *et al.*, 2012), and ultimately should experience higher speciation rates. Finally, the frequency of specialist species is known to be higher in tropical areas (Fernández & Vrba, 2005) and these regions are also associated with high rates of speciation (Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014a).

However, the association between niche width and net diversification rate (the difference between speciation and extinction rates) is not so clear cut because other hypotheses suggest the opposite pattern, with higher rates of speciation and lower extinction rates in generalist than in specialist species. First, the larger range size of generalist species may lead to higher rates of allopatric speciation because of the higher likelihood of encountering ecological or geographical barriers (Darwin, 1859; Rosenzweig, 1995; Gaston, 2003). Second, the width of the ecological niche is related to the variety of conditions that a species can cope with (Slatyer *et al.*, 2013). Generalist species should thus be able to adapt more easily to various environmental conditions and have lower extinction rates than specialist species during climate changes. Furthermore, extinction rate may be higher in specialist species because populations are likely to be smaller and less connected (Bonte *et al.*, 2003) than in generalist species. The effects of demographic stochasticity could therefore be stronger than for generalist species and will potentially lead to local extinction in specialist species.

Although hypotheses linking niche width and rates of speciation and extinction have been formulated in the literature (Kozak & Wiens, 2010), very few studies have measured the effects of niche width on net diversification rate. Among those, Gómez-Rodríguez *et al.* (2015) detected a positive relationship between niche width and the diversification of amphibians, while Baselga *et al.* (2011) found that specialist species of zopherine beetles had higher diversification, probably due to higher rates of allopatric speciation. The other recent macroevolutionary studies interested in niche width have been rather focused either on the evolutionary dynamics

of the niche width (Kostikova *et al.*, 2013), the effect of trophic specialization on niche evolution (Litsios *et al.*, 2012) or the rate of evolution of the centroid of the niche (Pearman *et al.*, 2008; Evans *et al.*, 2009; Vieites *et al.*, 2009; Kozak & Wiens, 2010; Schnitzler *et al.*, 2012; Pyron & Wiens, 2013). Several studies have also tested whether the centroid of the niche was associated with diversification rates. For instance, temperature was shown to be positively correlated with net diversification rate in the context of both the metabolic theory of ecology (Brown *et al.*, 2004; Allen *et al.*, 2006) and the latitudinal diversity gradient (Pyron & Wiens, 2013).

Here, we used the largest data sets available for vertebrates, including species distribution maps and phylogenetic trees, to test whether niche width is associated with the rate of diversification. Vertebrates are an ideal taxonomic group for studying the evolution of niche breadth and its impact on species diversification. Vertebrate species encompass endothermic and ectothermic species that are widely distributed on earth, with extreme variations in niche width, spanning a broad range of ecological tolerances from the Sahara Desert to Antarctica. We investigated the evolution of niche width in birds, mammals and amphibians and tested whether the niche width was associated with diversification rates. In addition, we tested if there was an association between niche width and current extinction risk using the IUCN conservation status of the species sampled. Our study has implications for conservation as the niche width is directly linked to the breadth of ecological conditions that species will be able to tolerate in the face of climatic change. It also contributes to a global understanding of the evolution of the ecological niche in vertebrates and other organisms.

MATERIALS AND METHODS

Phylogenies

We used published phylogenetic trees of 5020 species of mammals (Bininda-Emonds *et al.*, 2007; Fritz *et al.*, 2009; Kuhn *et al.*, 2011), 9993 species of birds (Jetz *et al.*, 2012; <http://birdtree.org>) and 2871 species of amphibians (Pyron & Wiens, 2011, 2013). The use of the phylogenetic tree from Bininda-Emonds *et al.* (2007; hereafter referred to as Bininda-Emonds trees) has been recently criticized (Meredith *et al.*, 2011; Faurby & Svenning, 2015). We therefore also used two other recent phylogenetic trees of mammals (Faurby & Svenning, 2015; Hedges *et al.*, 2015) to confirm that our diversification results were robust to different time calibrations and topologies. These two trees contain respectively 4160 (Faurby & Svenning, 2015; hereafter referred to as Faurby trees) and 3738 species of mammals (Hedges *et al.*, 2015; hereafter referred to as Hedges tree) and focus only on species for which we have molecular data.

Phylogenetic data for the birds and for two studies on mammals (Faurby and Bininda-Emonds trees) were available as posterior distributions of trees. We built maximum credibility trees for these three data sets using TREEANNOTATOR (included in BEAST v.1.7.5; Drummond & Rambaut, 2007)

and we used both the maximum credibility tree and 100 trees sampled randomly from the posterior distributions for the diversification analyses. No tree distributions were available for the amphibian data or the Hedges tree of mammals. We thus only used the single tree provided by the authors for the diversification analyses.

Distribution and climatic data

The species distribution maps for 10,242 species of birds were obtained from BirdLife International and NatureServe (<http://www.birdlife.org/datazone/home>, accessed January 2015). The species distribution maps for 5286 species of mammals and 6299 species of amphibians were downloaded from the IUCN Red List website (<http://www.iucnredlist.org>, accessed May 2015). The final numbers of species with both phylogenetic and distribution data were 9823 for birds, 4563 for mammals (3838 for the Faurby tree and 3292 for the Hedges tree) and 2340 species for amphibians. We used the R package *raster* to plot species distributions and to compute mean annual temperature from the BIO1 WorldClim climatic layer (at a resolution of 2.5 arcmin; Hijmans *et al.*, 2005; <http://www.worldclim.org>).

Climatic niche width was calculated as the difference between the minimum and the maximum temperatures found among the cells of each species distributions (data available on Dryad). We also extracted the minimum and maximum latitude for each species.

Niche width characterization

We used the median niche width of each clade to assign species to two distinct categories: 'specialist' and 'generalist'. Species with a niche width smaller than the median were assigned to the 'specialist' category, while species with a larger niche width were categorized as 'generalist'. As the median value differentiating 'specialist' and 'generalist' categories changed between birds, mammals and amphibians, the analyses were run for each clade independently.

Diversification analysis

We tested if niche width was associated with speciation rate (λ), extinction rate (μ) or net diversification rate ($r = \lambda - \mu$), by following the methodological pipeline used in Rolland *et al.* (2014b). Character-dependent diversification analyses (FitzJohn, 2012) were run using the maximum credibility tree for the three taxonomic groups. To account for transitions between generalist and specialist species along branches and during speciation events, we used the cladogenetic state speciation and extinction model (ClasSE; Goldberg & Igić, 2012), implemented in the *diversitree* R package 0.9-7 (FitzJohn, 2012). This model, which is a refinement of the binary-state speciation and extinction (BiSSE) model (Maddison *et al.*, 2007), accounts for four different speciation parameters. Two parameters are symmetrical speciation rates, i.e. a species gives rise to two descendants with no change in character state (λ_{SSS} for the specialist symmetrical speciation

rate and λ_{GGG} for the generalist symmetrical speciation rate), while two parameters are asymmetrical speciation rates, i.e. a species gives rise to two descendants and one of the descendants has a different character state from its ancestor (λ_{SSG} for the specialist asymmetrical speciation rate, i.e. one specialist species gives rise to one specialist and one generalist species, and λ_{GSG} for the generalist asymmetrical speciation rate, i.e. one generalist species gives rise to one specialist and one generalist species). We did not consider the possibility that a generalist species diversifies into two specialist daughter species (λ_{GSS}) or alternatively that a specialist species diversifies into two generalist daughter species (λ_{SGG}), because these parameters were biologically unrealistic (their estimates were in any case close to zero; results not shown). The ClasSE model also includes two extinction rates (μ_S for specialist and μ_G for generalist species) and two parameters for anagenetic transition rates between specialist and generalist states that were not associated with speciation events ($q_{G \rightarrow S}$ and $q_{S \rightarrow G}$). We tested a total of 16 different models. Eight of these models considered asymmetrical speciation rates ($\lambda_{GSG} \neq 0$ and $\lambda_{SSG} \neq 0$) and eight did not ($\lambda_{GSG} = \lambda_{SSG} = 0$). In each of these sets of eight models, four accounted for different symmetrical speciation rates ($\lambda_{GGG} \neq \lambda_{SSS}$) between specialist and generalist character, while four other models considered equal symmetrical speciation rates between specialist and generalist character ($\lambda_{GGG} = \lambda_{SSS}$). In each set of these four models we tested two models with different extinction rates between specialist and generalist character ($\mu_G \neq \mu_S$) and two models with equal extinction rates ($\mu_G = \mu_S$). Finally, in each of these two models, the rates of anagenetic change from generalist to specialist was allowed to be different than from specialist to generalist ($q_{G \rightarrow S} \neq q_{S \rightarrow G}$), or the same ($q_{G \rightarrow S} = q_{S \rightarrow G}$). Overall, the models supporting an effect of niche width on diversification rates had either differential speciation rates ($\lambda_{SSS} \neq \lambda_{GGG}$ or $\lambda_{GSG} \neq \lambda_{SSG}$, or both) or differential extinction ($\mu_G \neq \mu_S$), or both, between generalist and specialist character, regardless of the anagenetic transition rates. All analyses were run accounting for incomplete taxon sampling (FitzJohn *et al.*, 2009). The sampling fractions were similar between specialist and generalist species, and when compared with the total number of species (from BirdLife International for birds, Wilson & Reeder (2005) for mammals and the current amphibian taxonomic list at <http://www.amphibiaweb.org/>) they were 9823/10242 = 0.96 for birds, 4563/5416 = 0.84 for Bininda-Emonds tree of mammals (3838/5416 = 0.71 for the Faurby tree and 3292/5416 = 0.61 for the Hedges tree) and 2340/7424 = 0.315 for amphibians. We first chose the best model using the Akaike information criterion (AIC; Burnham & Anderson, 2002). When the AIC difference was less than two between the first and the second model, we followed the procedure of Rolland *et al.* (2014b) and selected the simplest model (with fewer parameters).

Second, we performed Markov chain Monte Carlo (MCMC) analyses on the best model to obtain credibility intervals around parameter estimates. MCMC analyses were

run with an exponential prior and the chain was initiated with parameters obtained by maximum likelihood (as suggested by FitzJohn, 2012). We chose a 500-step burn-in and a length of 20,000 steps for the MCMC chain. We found that the MCMC converged quickly and the values of the parameters estimated did not vary substantially along the chain.

Robustness of diversification analyses

We assessed if our results were affected by high levels of Type I errors by comparing our empirical results with diversification analyses performed on simulated data (as recommended by Rabosky & Goldberg, 2015). We used the following four-step procedure.

1. For each of the three groups, we simulated 100 trait data sets using the *sim.history* function in the *phytools* R package. The transitions matrix Q used the transition rates obtained by the model with different transition rates but equal diversification rates between states. The values of these transition rates were also confirmed by a diversification-independent approach (*fit.continuous* in the *geiger* R package). This procedure maintains the phylogenetic signal present in the trait and uses meaningful transition rates obtained from the real data sets.

2. We fitted two different models, one that allows for an association between the character states and diversification and one that does not. The model accounting for different diversification rates between character states was chosen using the model selection procedure on empirical data described previously (e.g. see the best fitting model for each group shown in Tables S1–S3 in the Supporting Information). This model either accounted for differential speciation ($\lambda_{SSS} \neq \lambda_{GGG}$ or $\lambda_{GSG} \neq \lambda_{SSG}$, or both) or differential extinction rates ($\mu_G \neq \mu_S$), or both. The second model was the constant rate model that does not account for a differential diversification rate (for which $\lambda_{GGG} = \lambda_{SSS}$, $\lambda_{GSG} = \lambda_{SSG} = 0$, $\mu_G = \mu_S$ and $q_{G \rightarrow S} = q_{S \rightarrow G}$). We fitted these two models for each of the 100 simulated data sets and for the empirical data.

3. We then estimated the difference between the AIC (ΔAIC) of the two models for each of the 100 simulated data sets and for the empirical data.

4. We plotted the resulting distribution of ΔAIC for the simulated data and compared it with the ΔAIC obtained for the empirical data. If the empirical value fell within, or to the left of, the distribution (indicating similar or lower ΔAIC value), then we considered that the model performance was poor, because the difference in model fit (ΔAIC) was not different for the simulated and observed traits. In contrast, if the empirical value fell to the right of the distribution (higher ΔAIC values), we considered that the model performance was good, because there is more support with the empirical data than with the simulations for a model that allows for an association with diversification. This latter case indicates that niche width has a strong effect on

diversification and that this effect is not due to a particular shape of the phylogeny (Rabosky & Goldberg, 2015).

A second potential bias in our analyses could be due to misassignment of species into the categories ‘generalist’ and ‘specialist’. We assessed the robustness of our categorization in two ways. Because we previously estimated the niche width of migratory birds using both their breeding and their wintering ranges, we might have overestimated the niche width of these species, and consequently we also might have made mistakes in their assignment. Thus, we ran all the diversification models a second time with a phylogenetic tree containing only the sedentary species to remove any effects of the misassignment. We removed all migratory bird species from the phylogenetic tree using the migratory status information from BirdLife International and NatureServe. The range of each species is coded in these databases using several annotated polygons. Following Somville *et al.*, (2013), we classified a species as migratory if it occurred at least once in a breeding season polygon or in a non-breeding season polygon (coded 2 or 3 in BirdLife International and NatureServe databases; see Rolland *et al.*, 2014b, for more details). Among the 10,172 species of birds with both migratory behaviour and environmental data, 8222 species were considered as non-migratory based on this criterion. Finally, 7961 species (sampling fraction $7961/10,242 = 0.78$) were also present in the phylogenetic tree of birds and could be used in the diversification analyses.

A second potential source of bias in our assignment of species into specialists and generalists was that we considered the niche width as the difference between minimum and maximum values of the mean annual temperature (BIO1; Hijmans *et al.*, 2005) in the range of the species. As temperature can fluctuate throughout the year, especially at high latitude, the assignment based on mean annual temperature might underestimate the niche width. We therefore ran a second diversification analysis for all three groups with niche width estimated as the difference between the maximum value of the species range in the warmest month (BIO5; Hijmans *et al.*, 2005) and the minimum value of the coldest month (BIO6; Hijmans *et al.*, 2005). The assignment of species with this new measurement changed for 11.7% of the birds, 15.6% of the mammals and 24.3% of the amphibians.

IUCN and extinction risk at the present time

We found the IUCN conservation status on the IUCN Red List website (<http://www.iucnredlist.org>, accessed May 2015) for 9261 bird, 4551 mammal and 1859 amphibian species from the previous set of species with phylogenetic and niche width information. We tested for a link between niche width and IUCN status. According to the IUCN Red List, species are classified into eight major groups: EX (extinct), EW (extinct in the wild), CR (critically endangered), EN (endangered), VU (vulnerable), NT (near threatened), LC (least concern) and DD (data deficient). We considered that species in the categories CR, EN and VU were threatened and that

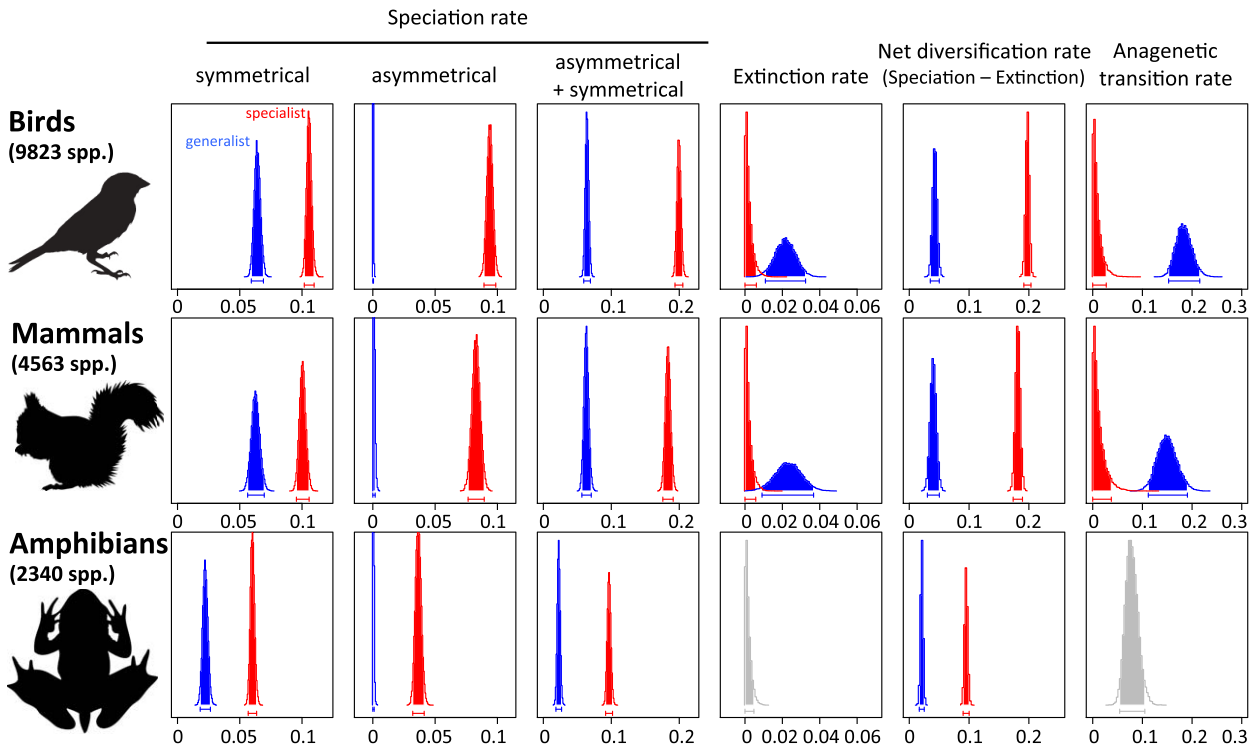


Figure 1 Speciation, extinction and transition rates associated with niche width obtained from the best-fitting models for birds, mammals and amphibians. Maximum credibility intervals were obtained by Markov chain Monte Carlo analysis with a chain of 20,000 generations. Estimates for the generalist character are shown in blue and those for the specialist character are shown in red. Grey distributions are used for models assuming the same estimates for generalists and specialists.

species in NT or LC were not threatened. EX, EW and DD species were not considered here. Using a generalized least square regression (the *gls* function implemented in the *nlme* R package), we assessed for the three groups if threatened species tend to have a narrower temperature tolerance than non-threatened species. We accounted for the non-independence between species due to their shared evolutionary history with a correlation structure derived from the phylogenetic tree assuming a Brownian motion model of evolution, and estimated Pagel's λ (Pagel, 1999) with the *corPagel* function of the *ape* R package.

RESULTS

The median of the thermal niche width was smaller for amphibians (10.6 °C) than for mammals (16.5 °C) or birds (19.2 °C), which suggests that amphibian species are more specialist in terms of thermal tolerance than mammal and bird species (Fig. S1).

Diversification analyses

For the three groups, our diversification analyses showed that net diversification rates were higher in specialist species (birds $r = 0.2 \text{ Myr}^{-1}$, mammals $r = 0.184 \text{ Myr}^{-1}$, amphibians $r = 0.096 \text{ Myr}^{-1}$) than in generalist species (birds $r = 0.064 \text{ Myr}^{-1}$, mammals $r = 0.063 \text{ Myr}^{-1}$, amphibians $r = 0.02 \text{ Myr}^{-1}$; Fig. 1, Tables S1–S3).

Speciation rates were higher in specialist species (birds $\lambda_s = \lambda_{SSS} + \lambda_{SSG} = 0.2 \text{ Myr}^{-1}$, mammals $\lambda_s = 0.184 \text{ Myr}^{-1}$, amphibians $\lambda_s = 0.096 \text{ Myr}^{-1}$) than in generalist species (birds $\lambda_G = \lambda_{GGG} + \lambda_{GSG} = 0.064 \text{ Myr}^{-1}$, mammals $\lambda_G = 0.063 \text{ Myr}^{-1}$, amphibians $\lambda_G = 0.022 \text{ Myr}^{-1}$). This was due to both higher rates of symmetrical speciation in specialist (birds $\lambda_{SSS} = 0.105 \text{ Myr}^{-1}$, mammals $\lambda_{SSS} = 0.099 \text{ Myr}^{-1}$, amphibians $\lambda_{SSS} = 0.060 \text{ Myr}^{-1}$) than in generalist species (birds $\lambda_{GGG} = 0.064 \text{ Myr}^{-1}$, mammals $\lambda_{GGG} = 0.063 \text{ Myr}^{-1}$, amphibians $\lambda_{GGG} = 0.022 \text{ Myr}^{-1}$) and higher rates of asymmetrical speciation in specialist (birds $\lambda_{SSG} = 0.095 \text{ Myr}^{-1}$, mammals $\lambda_{SSG} = 0.085 \text{ Myr}^{-1}$, amphibians $\lambda_{SSG} = 0.032 \text{ Myr}^{-1}$) than in generalist species (birds $\lambda_{GSG} = 3 \times 10^{-7} \text{ Myr}^{-1}$, mammals $\lambda_{GSG} = 1 \times 10^{-6} \text{ Myr}^{-1}$, amphibians $\lambda_{GSG} = 7 \times 10^{-8} \text{ Myr}^{-1}$). The presence of cladogenetic changes in the niche width was strongly supported against a model accounting for only anagenetic changes (we found large ΔAIC for the three groups between the best model with cladogenetic changes and the best model without cladogenetic changes; ΔAIC birds = 687.6, ΔAIC mammals = 177.7, ΔAIC amphibians = 62).

In birds and mammals, extinction rates were lower for specialist species (birds $\mu_s = 2 \times 10^{-9} \text{ Myr}^{-1}$, mammals $\mu_s = 2 \times 10^{-7} \text{ Myr}^{-1}$) than generalist species (birds $\mu_G = 0.022 \text{ Myr}^{-1}$, mammals $\mu_G = 0.024 \text{ Myr}^{-1}$). In contrast, the rates of extinction in amphibians were equal between specialist and generalist species ($\mu_G = \mu_s = 4.00 \times 10^{-7} \text{ Myr}^{-1}$).

For birds and mammals, anagenetic rates of transition from generalists to specialists were higher than in the opposite direction (birds $q_{G \rightarrow S} = 0.018 \text{ Myr}^{-1}$, mammals $q_{G \rightarrow S} = 0.015 \text{ Myr}^{-1}$; birds $q_{S \rightarrow G} = 7 \times 10^{-7} \text{ Myr}^{-1}$, mammals $q_{S \rightarrow G} = 5 \times 10^{-7} \text{ Myr}^{-1}$), while they were not different for amphibians (amphibians $q_{S \rightarrow G} = q_{G \rightarrow S} = 0.008 \text{ Myr}^{-1}$).

In birds and mammals, running the same selection of models on 100 trees randomly sampled from the original posterior distribution of trees gave very similar results to those with maximum credibility trees. The same best-fitting model was selected in 94% of cases for birds and in 100% of cases for mammals. This model contained different symmetrical and asymmetrical speciation rates and different extinction and transitions rates between the two niche width types (Tables S4 & S5). Specialist species showed higher net diversification rates due to higher speciation rates (mean and standard deviation for birds $\lambda_S = 0.204 \pm 0.001 \text{ Myr}^{-1}$ and for mammals $\lambda_S = 0.184 \pm 0.006 \text{ Myr}^{-1}$) and lower extinction rates (mean and standard deviation for birds $\mu_S = 6.03 \times 10^{-6} \pm 3.06 \times 10^{-5} \text{ Myr}^{-1}$ and for mammals $\mu_S = 1.9 \times 10^{-6} \pm 6.09 \times 10^{-6} \text{ Myr}^{-1}$) than generalist species (mean speciation rate and standard deviation for birds $\lambda_G = 0.065 \pm 0.001 \text{ Myr}^{-1}$, and mammals $\lambda_G = 0.063 \pm 0.002 \text{ Myr}^{-1}$; extinction rate for birds $\mu_G = 0.019 \pm 0.007 \text{ Myr}^{-1}$, and mammals $\mu_G = 0.023 \pm 0.004 \text{ Myr}^{-1}$). We also found that anagenetic rates of transition were consistent with the analyses on the maximum credibility trees, with higher transition rates from generalists to specialists than in the opposite direction (mean and standard deviation for birds $q_{G \rightarrow S} = 0.018 \pm 0.001 \text{ Myr}^{-1}$, mammals $q_{G \rightarrow S} = 0.015 \pm 0.001 \text{ Myr}^{-1}$; birds $q_{S \rightarrow G} = 2.39 \times 10^{-6} \pm 4.8 \times 10^{-6} \text{ Myr}^{-1}$, mammals $q_{S \rightarrow G} = 2.29 \times 10^{-6} \pm 5.61 \times 10^{-6} \text{ Myr}^{-1}$).

The diversification analyses based on the two additional mammal trees further confirmed that our results were robust to variations in topology and time calibration of the tree. We also found higher net diversification rates in specialist species than in generalist species for both Faurby and Hedges trees (Tables S6 & S7). This higher net diversification rate was due to higher speciation rates (in both trees) and to lower extinction rates in specialist species (only in the Faurby tree). Analyses on the posterior distribution of 100 Faurby trees were also very consistent with these results (Table S8), since 86% of the trees supported higher net diversification rates in specialist species, due to higher symmetrical and asymmetrical speciation rates, compared with generalist species. Although we found a large difference between the extinction rates associated with specialist and generalist species in the maximum credibility tree of Faurby ($\mu_S = 6 \times 10^{-6} \text{ Myr}^{-1}$ and $\mu_G = 0.053 \text{ Myr}^{-1}$), only 59% of the trees supported differential extinction rates between niche width types, and models with differential extinction rates were not supported using the Hedges tree.

Robustness of diversification results

Our robustness analysis suggests that the effect of niche width was much stronger than expected by chance. Models

fitted from empirical data were strongly supported compared with models fitted from simulated traits at the tips of the phylogeny. In all groups we found that the ΔAIC value (the difference between the AIC of the model that does not account for differential diversification rates between specialist and generalist characters and the AIC of the model accounting for differential diversification rates; see Material and Methods for more details) obtained from empirical data was much larger than the distribution of ΔAIC values obtained from simulations (Fig. 2). The same results were also found for the two additional mammal phylogenies (Faurby and Hedges) (Fig. S2).

Overall, we found that our diversification results were also robust to variation in the assignments of 'specialist' and 'generalist' categories. The best-fitting model on the phylogeny containing only sedentary bird species was exactly the same as with the full bird data set, with very similar speciation, extinction and transition rates (Table S9). We also found higher speciation rates and lower extinction rates in specialist species for the three groups when the niche width was defined as the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month (Tables S10–S12).

IUCN

For birds, 21% of the species considered as specialist were threatened compared with only 4% of generalist species. For mammals, 31% of specialist species were threatened and only 8% of generalist species. Finally, for amphibians, 39% specialist species were threatened compared with 17% of generalist species. We also obtained highly significant negative slopes of the generalized least square linear model ($P < 10^{-16}$), indicating that the niche width was much narrower for threatened species than for non-threatened species in all three groups (Fig. 3).

DISCUSSION

Relatively few studies have investigated the evolution of niche width and its impact on diversification rates (Baselga *et al.*, 2011; Kostikova *et al.*, 2013; Gómez-Rodríguez *et al.*, 2015). Here, based on large mammal, amphibian and bird data sets, we show that niche width is an important factor affecting species diversification. More particularly, climatic specialization increased speciation rates in all groups and decreased extinction rates in birds and mammals.

Speciation

We detected higher speciation rates in specialist species in the three groups due to higher symmetrical and asymmetrical speciation rates. There might be several explanations for this relationship between niche breadth and symmetrical speciation rate. First, as specialist species are likely to have poorer dispersal capacities than generalist species, populations of species with a narrow niche are less likely to be well connected (Kisdi, 2002; Bonte *et al.*, 2003; Baselga *et al.*, 2011; Birand

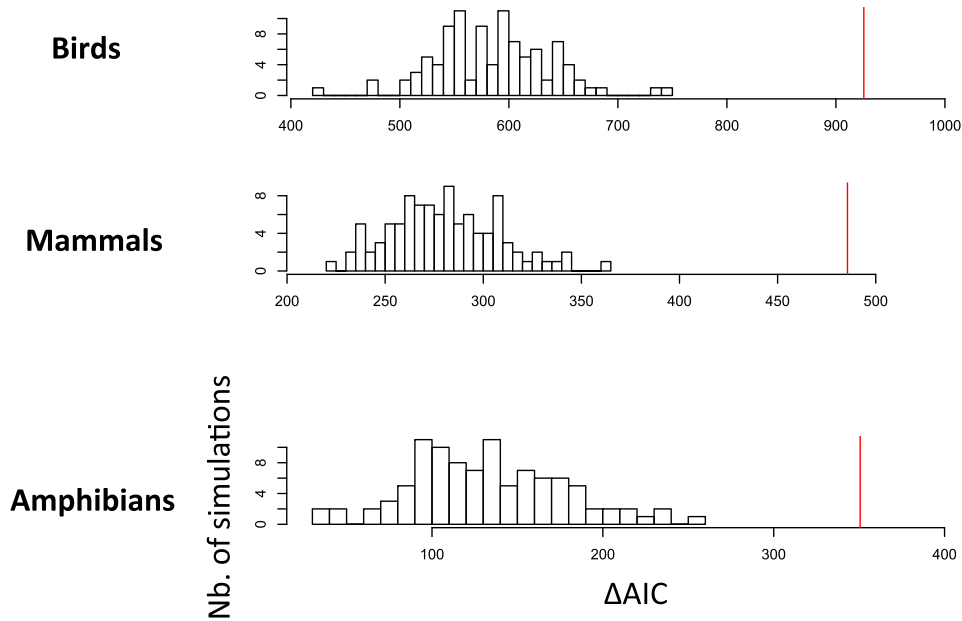


Figure 2 Test of the robustness of the data concerning Type I error in states, speciation and extinction (SSE) models: comparison between empirical data and simulations. The x-axis represents ΔAIC , which is the difference between the Akaike information criterion (AIC) of the model with no difference in diversification rates between generalist and specialist character and the AIC of the model accounting for differential diversification rates between characters. We compare here the ΔAIC value obtained from empirical data (shown in red) and the distribution of ΔAIC values obtained from simulations (shown in black). We show that the ΔAIC value obtained from empirical data sets (for birds, mammals and amphibians) is much higher than the distribution of ΔAIC values obtained from simulated data.

et al., 2012). Higher spatial isolation may, with time, lead to the emergence of reproductive barriers and consequently to the creation of new species (Baselga *et al.*, 2011). Divergence and local adaptation might also be increased in isolated populations, leading to the creation of new species (Kirkpatrick & Barton, 1997). In contrast, generalist species have larger range sizes than specialist species (a pattern supported by our data in Fig. S3; Colwell & Rangel, 2009; Slatyer *et al.*, 2013, Boucher-Lalonde *et al.*, 2016), and probably higher dispersal rates (Gaston, 2003). The increased connectivity

existing between populations of generalist species can thus hamper speciation. Another explanation is that specialist species are mainly distributed in tropical areas, consistent with the latitude–niche width hypothesis (MacArthur, 1965; Janzen, 1967; Addo-Bediako *et al.*, 2000; Fernández & Vrba, 2005). This hypothesis is consistent with additional analyses of our data set showing that there is a significant relationship between niche width and absolute latitude in all groups (Fig. S4). The association between temperature niche width and diversification may thus be highly correlated with the

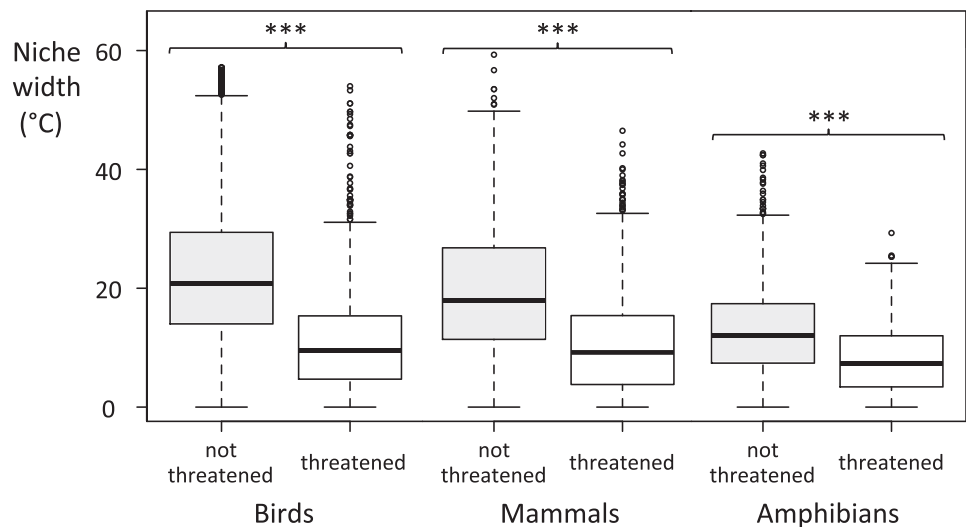


Figure 3 Niche width of threatened (white) and non-threatened (grey) species according to the IUCN conservation status of birds, mammals and amphibians. Differences in niche width between non-threatened species and threatened species were highly supported according to generalized least square linear models in the three groups ($P < 10^{-16}$).

latitudinal diversity gradient. Indeed, specialist species may experience warmer climates (Rohde, 1992), a higher-productivity habitat (Currie *et al.*, 2004) and more complex biotic interactions (Schemske *et al.*, 2009), which will lead to increased speciation rates (Cardillo, 1999; Pyron & Wiens, 2013; Rolland *et al.*, 2014a). We also found that there were high asymmetrical speciation rates in specialist species, which suggests that many specialist species diversified into one specialist species and one generalist species. This result could indicate that speciation through niche divergence may be a more important process than previously thought (Gómez-Rodríguez *et al.*, 2015). Our results could indicate that tropical specialist species may have given rise simultaneously to one generalist species that dispersed to temperate areas (with wider climate variability) and one specialist species that remained in the tropics. This process of creation of species from the tropics to the temperate regions is consistent with the Jablonski's 'out of the tropics' theory (2006), which stipulates that diversity is generated in the tropics and exported toward higher latitudes.

Our results concerning speciation rates challenge the recent study of Gómez-Rodríguez, *et al.* (2015), who showed that the niche width of amphibian families is positively correlated with diversification rates when niche width is estimated as the range of temperature and precipitation across all species in a family. This correlation was strongly reduced when the family niche width was estimated as the mean of all species in a family. The pattern found by Gomez-Rodríguez *et al.* can be artefactual given that it is expected that the total niche width of a family will always increase with the number of species in the family (although they attempted to test for this bias). Given that the temperature variables (BIO1, BIO5 and BIO6) are the same between the two studies, the discrepancy between our results and theirs is likely to come from a difference in methodology, such as the diversification metric that they used (Magallon & Sanderson, 2000), which was based on present diversity and age of the clades. This approach likely oversimplifies the process of diversification because it does not model extinction processes nor take into account the tree structure and cladogenetic changes of characters, which have been shown here to be a crucial factor in niche-related speciation events. It is thus possible that their method had less statistical power to detect a significant relationship between niche width and diversification rates as it reduces the data to several family-level points that are necessarily coarse summaries of the full history of the diversification process. Another advantage of our approach is its direct use of the niche width at the species level in the analyses. We can therefore depict finer differences between species, which is not the case in the study of Gomez-Rodríguez *et al.*, that used total or mean measures per species to represent the niche of families. Finally, it is also possible that our methodology is biased toward detecting significant relationships (Type I error; as suggested by Rabosky & Goldberg, 2015),

but we carefully tested for this potential bias as described in the section 'Limitations and robustness of the results'.

Extinction

Although the estimation of extinction rates from phylogenies alone is highly debated (Rabosky, 2010), our diversification analysis detected lower extinction rates in specialist than in generalist species in birds and in two of the phylogenetic trees of mammals (Bininda-Emonds and Faurby), which contradicts our expectations that generalist species are more prone to survive than specialist species during periods of climate change such as glaciation events. These results may be indirectly linked to the fact that generalist species are preferentially found at higher latitudes (Janzen, 1967; Dynesius & Jansson, 2000; Fig. S4), where lineages have higher extinction rates, whatever the size of their niche (Rolland *et al.*, 2014a). Similarly, the low extinction rates found in specialist species could be due to the higher climate stability in tropical areas (Dynesius & Jansson, 2000). These results concerning extinction rates are counterintuitive, because, at present, our results also suggest that specialist species are more threatened than generalist species, which is in line with recent studies showing that specialist species living in small geographical ranges have higher extinction rates (Harris & Pimm, 2008). This discrepancy may suggest that the dynamics of extinction in the whole history of the groups are different from those observed at present (probably influenced by human-related factors and current climate change).

We found the same pattern in extinction rates for birds and mammals (Bininda-Emonds and Faurby trees) but detected no difference in extinction rates between specialist and generalist species in amphibians. It might be possible that we lacked statistical power to detect the signal of extinction for the latter group (Rabosky, 2010), although the large size of the amphibian phylogeny that we used (2340 species) should be sufficient. It is thus possible that extinction does not vary much between generalist and specialist species in amphibians. Given our contradictory results on extinction in mammals and the fact that the Hedges tree and the distribution of trees from Faurby only found weak support for differential extinction, it is also possible that generalist and specialist mammals do not differ much in their extinction rates. The difference between specialist and generalist net diversification rates could thus mainly be due to differences in speciation rates in this group.

Limitations and robustness of the results

Recently, the states, speciation and extinction (SSE) class of models, which contain the ClaSSE model used in this study, have provoked a controversial debate. Rabosky & Goldberg (2015) showed that in some cases particular shapes of phylogenies might bias the method, resulting in the detection of a spurious relationship (Type I error) between the trait and diversification rates. For instance, Type I error may be the result of unexpected variation of diversification rates through time independent of character states. We assessed whether our

results were biased using two approaches. (1) The three independent groups of vertebrates gave similar results. Because birds, mammals and amphibians have different evolutionary histories, it seems very unlikely that all three phylogenies are giving the same results and are biased in the same direction. (2) Using 100 simulations of the character states on the tips of the phylogeny we tested that our data set was not biased towards finding falsely significant associations between niche width and diversification rates. We found that the effect of niche width on diversification rates observed in the data was much stronger than the effect expected by chance. These two approaches strongly supported that our diversification results were not affected by Type I error.

A second problem with SSE models is Type II error (i.e. false negatives). This type of error may occur when there are few transitions of the trait of interest in the phylogeny (i.e. lack of replication; FitzJohn & Maddison, 2015), when the phylogeny contains fewer than 300 species or if the proportion of one character state is very small compared with the other state (<10%; Davis *et al.*, 2013). To optimize the number of replications and the tree size we used the largest phylogenies available (over 2000 species). We also considered that there are the same number of specialist and generalist species at the present time (50% specialist and 50% generalist species). Our study design thus met the requirements of our diversification methodology, and our results should not be influenced by Type II errors.

Finally, a common limitation of studies of ecological niches is that we are only measuring the realized niche of the species, which is obtained from presence data in the field. The fundamental niche of a species (i.e. its physiological tolerances) is likely to be significantly larger. If there is any systematic bias in the difference between fundamental and realized niche this could have direct implications for our niche characterization (specialist/generalist) and our diversification analyses. We also acknowledge that future studies would do better to use direct species occurrences data rather than the polygons used here to define the niche (as in Thuiller *et al.*, 2004; Treier *et al.*, 2009), especially where the spatial heterogeneity of the environmental variable is high such as in mountainous regions. It should, however, be noted that compiling world-wide occurrences for the c. 20,000 species in our study is currently not tractable.

CONCLUSION

The evolution of the climatic niche is central to improving our understanding of how species adapt to novel environments (Losos & Ricklefs, 2009). Our results suggest that niche width is a major factor affecting species diversification in birds, mammals and amphibians. A small thermal niche width promotes net diversification rates, increases speciation and decreases extinction rates. We also show that speciation events are associated with the evolution of niche width, because specialist species tend to simultaneously create generalist and specialist species. Overall, our study gives a first insight into how the characteristics of the ecological niche have a deep impact on the diversification of vertebrates.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1 Histogram of the niche width values for birds, mammals and amphibians.

Figure S2 Test of the robustness of the data concerning Type I error in states, speciation and extinction models: comparison between empirical data for mammals (Hedges and Faurby trees) and simulations.

Figure S3 Relationship between the niche width (°C) and the range size (km²) (log-transformed).

Figure S4 Relationship between the niche width (°C) and the absolute latitude (degrees).

Table S1 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for birds.

Table S2 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for mammals.

Table S3 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for amphibians.

Table S4 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models on 100 birds phylogenies randomly sampled from the distribution of Jetz *et al.* (2012).

Table S5 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models on 100 mammals phylogenies randomly sampled from the distribution of Kuhn *et al.* (2011).

Table S6 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models on the maximum credibility tree of mammals built from 500 trees of the posterior distribution of trees given by Faurby & Svenning (2015).

Table S7 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models on the Hedges *et al.* (2015) phylogeny of mammals.

Table S8 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models on 100 mammals phylogenies randomly sampled from the posterior distribution of trees obtained in Faurby & Svenning (2015).

Table S9 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for a bird phylogeny of 7961 species for which migratory species have been removed.

Table S10 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for birds. The niche width has been defined here as the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month.

Table S11 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for mammals. The niche width has been defined here as the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month.

Table S12 Speciation, extinction and transition rates associated with generalist and specialist character for the 16 models for amphibians. The niche width has been defined here as the difference between the maximum temperature of

the warmest month and the minimum temperature of the coldest month.

BIOSKETCH

Jonathan Rolland is now a post-doctoral researcher in the group of **Nicolas Salamin** in the University of Lausanne, Switzerland. He took his PhD in Paris (France) at the Ecole Polytechnique and at the Museum of Natural History, supervised by Hélène Morlon and Frédéric Jiguet. His interests cover a wide range of areas in ecology and evolution, including population genetics, niche modelling, phylogenetics, biogeography, macroevolution and conservation. One of his favourite topics of research is to understand the emergence of diversity patterns such as the latitudinal diversity gradient.

Author contributions: J.R. and N.S. conceived the ideas. J.R. collected and analysed the data. J.R. wrote the first draft. J.R. and N.S. revised and corrected the manuscript.

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