

Climatic niche evolution is not slower in threatened species

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1 **Climatic niche evolution is not slower in threatened species**

2

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19 ***Running head:*** Niche evolution and extinction risk

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24

25 **Abstract**

26 **Background:** Understanding why species go extinct has become a major goal of evolutionary
27 biology. Recent studies have suggested that both species traits and rates of evolution might
28 predict extinction probability in a changing world. Here, we tested whether species
29 conservation status correlates with recent rates of niche evolution within their lineages across
30 11,465 species of terrestrial vertebrates.

31 **Results:** We find no consistent association between rates of niche evolution and current IUCN
32 status in birds, mammals, amphibians and squamates. Our results suggest that rates of niche
33 evolution estimated over evolutionary time are a poor predictor of species extinction probability
34 at present time.

35 **Conclusions:** Our results are consistent with previous studies showing that past rates of
36 evolution are unrelated to how species will adapt to climate change in the future. This mismatch
37 might be explained by the different time scales involved, difficulties in accurately estimating
38 evolutionary rates and extinction risks, or simply the fact that the selective pressures affecting
39 biodiversity are different today than in the past.

40

41 **Keywords:** IUCN, squamates, birds, mammals, amphibians, extinction, climate change.

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50 Background

51 Understanding the reasons why some species are more threatened than others remains a major
52 challenge in evolutionary biology and conservation science [1-2]. It has been proposed that
53 some traits pre-determine species extinction risk, such as body size [3-5], generation time or
54 the rate of climatic niche evolution [6]. Preliminary results supporting such relationships are
55 also consistent with studies showing that threatened species are phylogenetically clustered in
56 the tree of life, with some clades containing more species at risk than others, likely because
57 they share similar traits [7].

58 Recent and forecasted climate change is recognized as a major extinction pressure.
59 Species that cannot keep pace with climate change by tracking favorable conditions or adapting
60 to new climatic conditions may face heightened extinction risk, whereas species that are able
61 to adapt rapidly are predicted to have lower extinction risk. The past rate of niche evolution
62 might capture species future adaptive capacity and vulnerability to climate change. Historical
63 rate of niche evolution might also act as a general proxy for species attributes related to
64 adaptation, such as genetic variance, dispersal capacities or generation time, that may affect
65 evolutionary potential today [6]. Thus, it is possible that species belonging to lineages with an
66 evolutionary history of a slow rate of climatic niche evolution might be more at risk of
67 extinction than species that descend from faster evolving lineages, irrespective of the
68 underlying extinction driver.

69 Here, we test these hypotheses using a large dataset on rates of climatic (temperature)
70 niche evolution obtained from phylogenetic trees, spatial distributions at the present-day and
71 derived from the fossil record for 11,465 species of terrestrial vertebrates (birds, mammals,
72 amphibians and squamates, [8]). We estimated rates of climatic niche evolution using an
73 evolutionary model informed by the present and past geographical distributions of species, and
74 the phylogenetic relationships within each clade during the last 270 Myr. We then evaluate

75 whether more slowly-evolving species are more at risk of extinction according to their IUCN
76 conservation status.

77

78 Results

79 Rates of niche evolution were not significantly different between threatened and non-threatened
80 species in any of the four clades examined, irrespective of the method used to estimate rates
81 (phylogenetic ANOVA, $P > 0.05$, see details in Table 1, Figure 1 & 2). The effect size were
82 small and not consistent between groups (see Table 1). We obtained similar results when
83 subsetting threatened species to those listed as threatened by climate change (Table 1).
84 Phylogenetic least squares analyses returned similar findings: the association was extremely
85 weak and inconsistent between groups ($R^2_{\text{adjust}} < 0.005$ for all groups, Sup. Mat. 1 & 2).
86 Classifying “Data Deficient” species as either threatened or non-threatened did not qualitatively
87 change the overall results (Sup. Mat. 3).

88

89 Discussion

90 The evolution of the climatic niche has been suggested as an important evolutionary response
91 to changing climatic conditions, allowing species to escape climate-driven extinction [6,20]. It
92 has also been proposed that the rates of niche evolution estimated from phylogenies over
93 macroevolutionary timescales might provide information on how species evolve over
94 microevolutionary timescales [4,6]. If rate of niche evolution were a general proxy for species
95 adaptive potential, historical rates of niche evolution might additionally correlate with species
96 extinction risk, irrespective of the underlying driver. Here, we show with a large dataset of
97 terrestrial vertebrates that the rate of niche evolution estimated over millions of years is a poor
98 predictor of the current conservation status of species.

99 We suggest that the lack of association between the rate of historical climate niche
100 evolution and present-day extinction risk has three potential explanations. First, the selective
101 pressures imposed by climate change might be different today than in the past. For example,
102 the speed and the geographical distribution of current climate change might not be comparable
103 to past climate change [21]. Thus, studying the evolution of species responses to past climates
104 might not help predict responses in the present day. Species currently threatened by climate
105 change are also likely to be threatened by other factors, such as anthropogenic pressures, habitat
106 destruction, fragmentation, hunting and pollution [1, 22-25]. The demographic declines, that
107 elevates extinction risk, reflect the combined effects of these multiple threats, potentially
108 blurring any relationship between the rate of niche evolution and current vulnerability.

109 Second, the timescales might be too different. It is well known that apparent rates of evolution
110 can be very different at different time scales (e.g. [26]), and metrics of deep-time niche
111 evolutionary rates might not directly relate to contemporary extinction rates and/or evolutionary
112 rescue of populations at the present time [22,27-28]. The results from our median rates on the
113 terminal branches (~1 Myr scale, Method 1) and on longer time scale (from the root to the tip,
114 Method 2) are virtually the same, but only represent average over long time scales compared to
115 the short time-scale of current global change (100 years or less, [29]). Rates of long-term
116 evolution of lineages (macroevolution) might not be associated to the rates of short-term
117 evolution, as the latter may be more related to microevolutionary processes, such as plasticity,
118 demographic dynamics or standing genetic variation [20]. Reconciling rates of evolution at
119 micro- and macroevolutionary scales remains both an empirical and a methodological challenge
120 [30].

121 Third, the estimates of evolutionary rates may be biased. For example, the present day
122 thermal niche of species, which we used to reconstruct the past, might not reflect species
123 fundamental niches, but instead their realized niche, a product of species interactions and

124 dispersal limitations [31]. This might bias our estimates of rates of historical niche evolution
125 [32]. Our study also used the mean position of the niche, which might be less informative for
126 measuring species vulnerability than other metrics such as changes in niche width. However,
127 in separate studies [8,33], it was found that niche width was more labile, and thus more difficult
128 to reconstruct than the mean position of the niche, and that fossil data were generally too scarce
129 to reconstruct the whole range of paleodistributions. Additionally, current classifications of
130 species into those threatened by climate change and those not threatened by climate change
131 may be imprecise and vary between clades, making comparisons difficult.

132 Our analyses confirm a general pattern for threatened species to be non-randomly
133 distributed across the tree of life (Figure 1 and Sup. Mat. S4), such that some clades contain
134 more threatened species than others [7]. Such phylogenetic patterning suggests that threatened
135 species likely have traits in common that make them vulnerable to present-day extinction
136 drivers. However, we do not find evidence that a slow rate of climatic niche macroevolution is
137 one such trait. Traits such as body size [3,5], range size, population size, generation time and
138 niche width [33], have been shown to correlate with extinction risk in various taxa, and still
139 provide the best suite of characters for predicting species threat status. As impacts of climate
140 change escalate, it is possible that the rates of long-term climatic niche evolution may become
141 more important in determining species future extinction risks. However, there remains a need
142 to better understand and model the causes of the mismatch between macroevolutionary rates,
143 estimated from phylogenies, and microevolutionary rates of adaptation, such as the changes in
144 allele frequency over short timescales, at the population level [26].

145

146 **Methods**

147 *Rates of climatic niche evolution*

148 The rates of climatic niche evolution, reflecting evolution of the mean annual temperature, were

149 obtained from Rolland *et al.* [8], and was computed using a Brownian motion model
150 encompassing 18,066,914 geo-localized present-day occurrences for 11,465 species and more
151 than 25,814 fossil occurrences for 829 genera (see [8] for more details). This comparative
152 method estimates rate of evolution by first reconstructing ancestral character given the trait
153 values of species at present day and in the past using fossil data. For example, the method has
154 recently been used to reconstruct episodes of latitudinal range expansions and contractions
155 using the current and fossil occurrences of New World monkeys [9]. To reconstruct the mean
156 climatic niche for each node of the phylogenies of birds [10], mammals [3,11-12], amphibians
157 [13] and squamates [14], we first reconstructed the paleolatitude and the paleoaltitude of all the
158 nodes of the phylogeny with present day and fossil data. Information on the past distribution of
159 fossils were integrated in the Brownian motion model as soft calibrations for the reconstruction
160 of past latitude, while a simple Brownian motion (with no fossil information) was used for
161 reconstructing past altitude. Then, we determined the temperature corresponding to each node
162 of the phylogeny, for each latitude-altitude combination using an altitude-latitude grid of
163 temperature at the present time from the mean annual temperature Worldclim layer [15]. We
164 then rescaled this grid using a global paleoclimate model (based on the curves of [16-18]) to
165 get a historical temperature grid matching to the age of each node in phylogeny (see
166 supplementary material of [8] for more details). This grid was then used to obtain a temperature
167 value for each paleolatitude and paleoaltitude at each node of the phylogeny.

168 The rate of niche evolution for each phylogenetic branch was computed as the difference
169 between the climatic niche of the descendant and the ancestor, divided by the branch length.

170 We used three different methods to compute a per-species rate of niche evolution. The first
171 method uses only the rate of niche evolution of the most recent branch leading to each species
172 at the present time. The second method computes, for each species, the median rate along all
173 the branches from the tip to the root of the tree. The third method also considers all the branches

174 from the tip to the root, but it weights the rate of each branch by a factor representing its
175 relatedness to the species (at present time). For example, the rate of the most recent branch (i.e.
176 from the species at the present-time to its most recent ancestor) was multiplied by a factor of 1,
177 the rate of the second most recent branch (i.e. from the first ancestor to the second ancestor)
178 was multiplied by a factor of 1/2, the rate of the third most recent branch was multiplied by a
179 factor of 1/3 and so on to the root of the tree (see Figure 1). We then computed the sum of the
180 weighted rates and divided by the sum of all the weightings. This latter method (inspired from
181 the diversification rate metric *DR* from [10]) gives more weight to the recent branches than to
182 old branches and represents an intermediate between the first and the second method.

183

184 *Conservation status*

185 We used the IUCN conservation status of each species (<http://www.iucnredlist.org>) as a proxy
186 for its probability of extinction. We obtained IUCN status for 5840 species of birds, 2922
187 species of mammals, 1125 species of amphibians, 987 species of squamates for which rates of
188 niche evolution were estimated. First, we classified species as: threatened versus not threatened
189 (as in [7]): species with status “endangered” (EN), “extinct in the wild” (EX), “critically
190 endangered” (CR), and “vulnerable” (VU) considered as threatened, while species with status
191 “nearly threatened” (NT), “least concerned” (LC) and “data deficient” (DD) classified as non-
192 threatened. Second, we assigned a continuous value to the conservation status with LC = 1, NT
193 = 2, DD = 3, VU = 4, EN = 5, CR = 6, EW = 7 and EX = 8. Data deficient species are considered
194 between threatened and not threatened because species might be in both categories (as described
195 in <https://www.iucnredlist.org/resources/summary-statistics>).

196 Finally, we identified the list of threatened species (status EN, EX, CR or VU) for which climate
197 change was listed as a threat according to IUCN Red List criteria version 3.1. This included
198 151 birds, 71 mammals, 43 amphibians and 7 squamates for which rates of niche evolution

199 were estimated.

200

201 *Association between the rate of niche evolution and the conservation status*

202 We used phylogenetic ANOVA [19] using the *phylANOVA* function in the R package *phytools*
203 with 1000 simulations to test for an association between the rate of niche evolution and
204 conservation status. This method evaluates whether mean rates of niche evolution are
205 significantly different between threatened and non-threatened species controlling for
206 phylogeny. We also ran phylogenetic generalized least squares regression between the rates of
207 niche evolution and the continuous values of the conservation status using the *crunch* function
208 of R package *caper*. Finally, we tested whether the rate of niche evolution was different for
209 species explicitly listed as threatened by climate change versus non-threatened species.

210

211 Conclusion

212 In this study, we show that the current extinction risk of species (represented by their
213 conservation status) is not associated with the rate of niche evolution of their past lineage. We
214 propose that these results might be due either to the fact that current climate changes at a faster
215 rate than in the past or that the timescales involved might be too different to estimate
216 comparable rate of evolution between the past and the present. Future studies aiming at
217 forecasting species adaptation to current climate change using their past evolutionary history
218 will have to determine the causes of this mismatch of scale which relates to the difficult task of
219 bridging micro and macroevolution.

220

221 Declarations

222 **Ethics approval and consent to participate**

223 Not applicable

224

225 **Consent for publication**

226 Not applicable

227

228 **Availability of data and materials**

229 Data to run the analyses are available in the supplementary material of [8]. Conservation status
230 are available at the IUCN website (<http://www.iucnredlist.org>).

231

232 **Competing interests**

233 Nicolas Salamin and Daniele Silvestro are associate editors of this journal.

234

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238

239 **Author's contributions**

240 J.R. designed the study, ran the analyses and wrote the first draft of the manuscript. J.R., J. D.,
241 Da. Si., N.S., Do. Sc. contributed to edit the manuscript.

242

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245

246 **Abbreviations**

247 Not applicable

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373 **Table 1. Per-species rates of niche evolution (in °C per million years) are not significantly**
374 **different between threatened and non-threatened species of birds, mammals, squamates**
375 **and amphibians.** The rate of niche evolution was computed using three methods: in the first
376 method, we took the rate computed from the most recent (terminal) branch of the tree. In the
377 second method, we used the median of the rate computed along the branches, from the leaves
378 to the root. In the third method, we computed the weighted average rate from the leaves to the
379 root, giving more weight to the branches closest to the present. Mean, median and standard
380 deviation (sd) of rates of niche evolution are shown for the three methods and the four clades
381 for non-threatened species, all threatened species in the dataset and species listed as threatened
382 by climate change. In bold, F-values and P-values of the phylogenetic ANOVA are given for
383 the comparisons (1) between non-threatened and all threatened species in the dataset, and (2)
384 between species threatened by climate change and non-threatened species in the dataset.

		Non-threatened species			Threatened species (all)					Threatened species (climate)				
		Mean	Median	sd	Mean	Median	sd	F-Value	P-value	Mean	Median	sd	F-Value	P-value
Method 1	Birds	3.73	0.74	58.5	4.6	0.83	34.21	0.1	0.936	3.23	0.95	14.64	0.01	0.975
	Mammals	3.03	0.75	15	2.34	0.69	7.45	0.82	0.745	2.78	0.75	8.93	0.02	0.935
	Amphibians	0.58	0.3	3.15	0.44	0.29	0.56	0.46	0.822	0.41	0.2	0.71	0.13	0.88
	Squamates	0.79	0.35	2.34	0.58	0.31	1.44	0.69	0.696	0.97	0.65	1.23	0.04	0.896
Method 2	Birds	0.91	0.88	0.3	0.92	0.88	0.52	0.66	0.85	0.95	0.88	0.43	2.64	0.599
	Mammals	1.02	0.93	0.43	0.9	0.72	0.4	28.57	0.051	0.96	0.89	0.47	1.43	0.505
	Amphibians	0.56	0.49	0.16	0.54	0.49	0.14	2.32	0.572	0.48	0.46	0.13	11.02	0.082
	Squamates	0.64	0.6	0.29	0.66	0.56	0.33	0.24	0.837	0.92	0.6	0.5	6.07	0.066
Method 3	Birds	3.25	2.11	16.2	3.41	2.16	9.32	0.04	0.957	3.11	2.32	4.34	0.01	0.985
	Mammals	5.18	2.59	8.56	4.14	2.2	6.45	5.27	0.407	3.79	1.96	5.63	1.85	0.474
	Amphibians	1.21	0.86	1.23	1.27	0.8	1.36	0.44	0.823	1.37	0.85	1.08	0.67	0.715
	Squamates	1.12	0.95	0.9	1.02	0.9	0.58	1.14	0.624	1.21	1.05	0.54	0.07	0.863

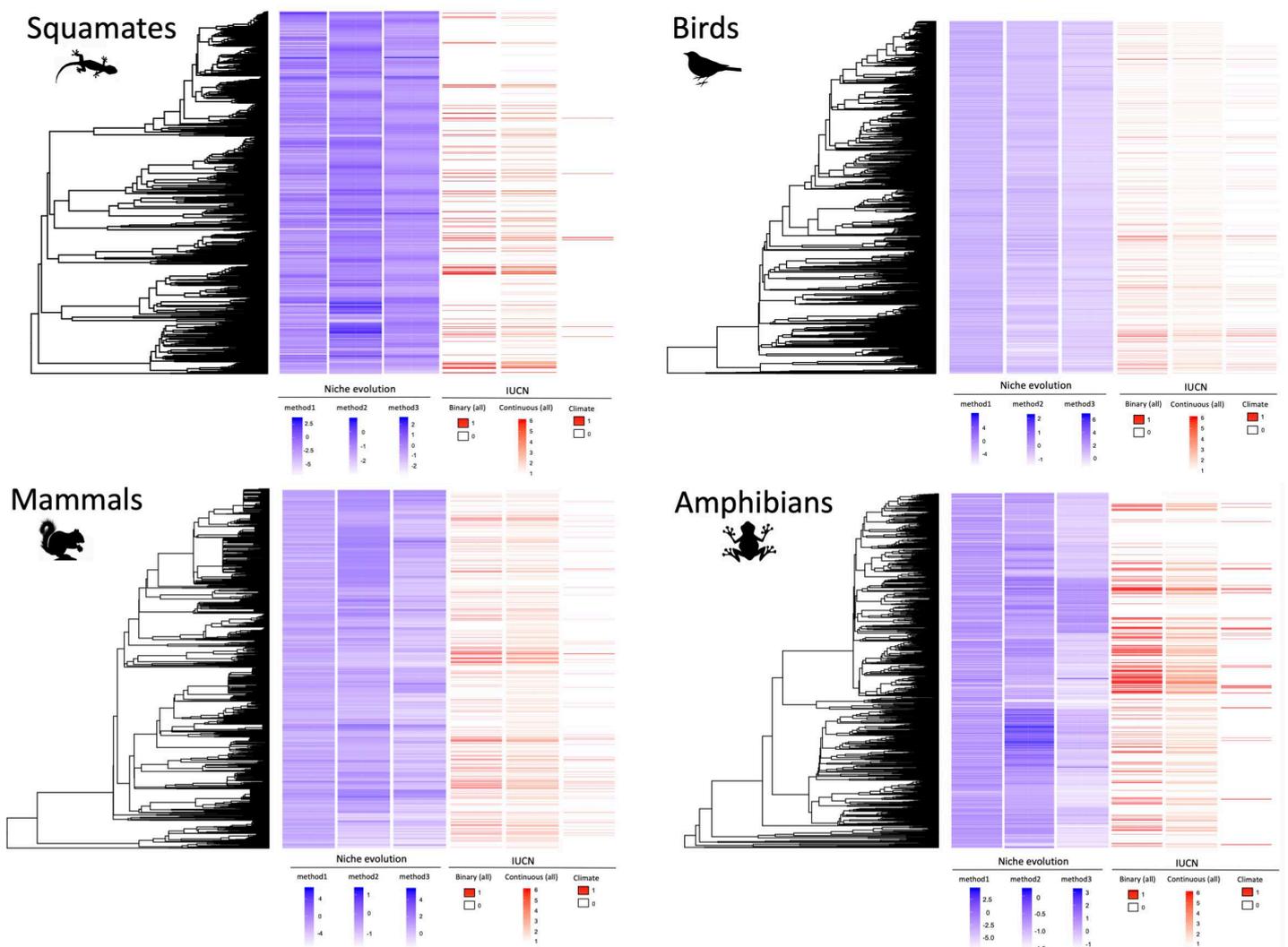
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389 **Figure 2. Comparison between the rate of thermal niche evolution for each of the three**
 390 **methods (blue) and conservation status (red) aligned to the phylogenetic tree for birds,**
 391 **mammals, amphibians and squamates.** Our study shows that threatened species are
 392 phylogenetically clustered (see also Sup. Mat. 4), but that there is no strong association between
 393 rates of niche evolution and conservation status. Rates of niche evolution were log transformed.
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Climatic niche evolution is not slower in threatened species

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Supplementary Material

Sup. Mat. 1. Rate of niche evolution is not slower for the species threatened compared to non-threatened species. In this analysis, phylogenetic least squares regressions were performed using the variance-covariance matrix corresponding to each phylogenetic tree. Even if some p-values were significant, the slopes were not consistent between clades and the overall proportion of variance explained by IUCN was very low $R^2_{\text{adjust}} < 0.005$.

Clade	Method	Estimate	Std. Error	t value	P-value		R^2_{adjust}
Birds	method 1	2.45	1.078	2.273	0.023	*	0.001
	method 2	2.64×10^{-4}	0.001	0.249	0.804		-1.61×10^{-4}
	method 3	0.335	0.296	1.132	0.258		4.82×10^{-5}
Mammals	method 1	-0.748	0.238	-3.142	0.002	**	0.003
	method 2	-3.48×10^{-3}	0.002	-1.589	0.112		0.001
	method 3	-0.159	0.081	-1.959	0.050		0.001
Amphibians	method 1	-5.78×10^{-2}	0.046	-1.25	0.211		0.001
	method 2	8.87×10^{-4}	0.001	0.806	0.421		-3.12×10^{-4}
	method 3	2.09×10^{-2}	0.022	0.963	0.336		-6.53×10^{-5}
Squamates	method 1	0.197	0.074	2.672	0.008	**	6.19×10^{-3}
	method 2	8.65×10^{-3}	0.005	1.89	0.059		2.60×10^{-3}
	method 3	5.47×10^{-2}	0.028	1.979	0.048	*	2.95×10^{-3}

417 **Sup. Mat. 2. Rate of niche evolution is not slower for the species threatened by climate**
 418 **change compared to non-threatened species.** In this analysis, phylogenetic least squares
 419 regressions were performed using the variance-covariance matrix corresponding to each
 420 phylogenetic tree. The slope were not consistent between clades and the overall proportion of
 421 variance explained by IUCN was very low $R^2_{\text{ajust}} < 0.005$.

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Clade	Method	Estimate	Std. Error	t value	P-value	R^2_{ajust}
Birds	method 1	-0.8984	1.5726	-0.571	0.568	0.000
	method 2	0.00014	0.00164	0.087	0.931	0.000
	method 3	0.03013	0.43956	0.069	0.945	0.000
Mammals	method 1	-0.649	0.3728	0.0818	0.082	0.001
	method 2	-0.002743	0.00384	-0.714	0.476	0.000
	method 3	-0.06018	0.13729	-0.438	0.661	0.000
Amphibians	method 1	-0.04981	0.11777	-0.423	0.672	-0.001
	method 2	-0.00406	0.00241	-1.683	0.093	0.002
	method 3	-0.02363	0.03634	-0.65	0.516	-0.001
Squamates	method 1	0.005235	0.166281	0.031	0.975	-0.001
	method 2	0.004747	0.011079	0.428	0.668	-0.001
	method 3	-0.01581	0.06498	-0.243	0.808	-0.001

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434 **Sup. Mat. 3. Table showing the association between rate of niche evolution and IUCN**
 435 **status.** In this analysis, we considered “Data Deficient” species as threatened species, and it
 436 did not change the results presented in the main text of the manuscript (Table 1).

		Non-threatened species			Threatened species (all)					Threatened species (climate)				
		Mean	Median	sd	Mean	Median	sd	F-Value	P-value	Mean	Median	sd	F-Value	P-value
Method 1	Birds	3.73	0.74	58.5	4.56	0.83	33.93	0.09	0.95	3.23	0.95	14.64	0.01	0.979
	Mammals	2.97	0.76	14.9	2.82	0.67	10.17	0.05	0.918	2.71	0.73	8.64	0.02	0.923
	Amphibians	0.59	0.31	3.21	0.43	0.28	0.55	0.69	0.741	0.4	0.2	0.7	0.15	0.878
	Squamates	0.8	0.36	2.37	0.55	0.29	1.3	1.29	0.627	0.97	0.65	1.23	0.04	0.883
Method 2	Birds	0.91	0.88	0.3	0.92	0.88	0.52	0.79	0.826	0.95	0.88	0.43	2.65	0.606
	Mammals	1.02	0.93	0.43	0.92	0.74	0.41	25.05	0.028	0.95	0.85	0.47	2.12	0.384
	Amphibians	0.56	0.49	0.16	0.55	0.49	0.15	1.52	0.637	0.48	0.47	0.13	9.99	0.093
	Squamates	0.64	0.6	0.29	0.66	0.56	0.33	0.25	0.825	0.92	0.6	0.5	6.16	0.057
Method 3	Birds	3.25	2.11	16.2	3.4	2.16	9.24	0.04	0.954	3.11	2.32	4.34	0.01	0.975
	Mammals	5.08	2.6	8.41	4.86	2.27	7.87	0.29	0.832	3.64	1.93	5.47	2.19	0.364
	Amphibians	1.21	0.85	1.24	1.26	0.83	1.31	0.34	0.836	1.4	0.85	1.09	0.96	0.665
	Squamates	1.13	0.95	0.91	1.02	0.91	0.57	1.42	0.609	1.21	1.05	0.54	0.06	0.857

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454 **Sup. Mat. 4. Strong phylogenetic signal in extinction risk.** Phylogenetic signal (Pagel's
455 lambda) was computed for the four phylogenies using the continuous values of IUCN
456 conservation status at the tips. We used the *phylosig* function of the *R* package *phytools* to test
457 whether lambda estimated from the data was significantly different than 0. LogL is the log-
458 likelihood for lambda estimated from the data and LogL0 is the log-likelihood for Lambda=0.
459 Our results suggest that Lambda is significantly different than 0 in all clades (P<0.001), and
460 thus that there is a strong phylogenetic signal in species vulnerability.

Clade	Lambda	LogL	LogL0	P-value
Birds	0.473	-7965.9	-8256.7	1.67×10^{-128}
Mammals	0.548	-8448.1	-8708.1	4.43×10^{-115}
Amphibians	0.728	-1969.3	-2102.8	4.91×10^{-60}
Squamates	0.393	-1462.8	-1507.7	2.79×10^{-21}

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Figures

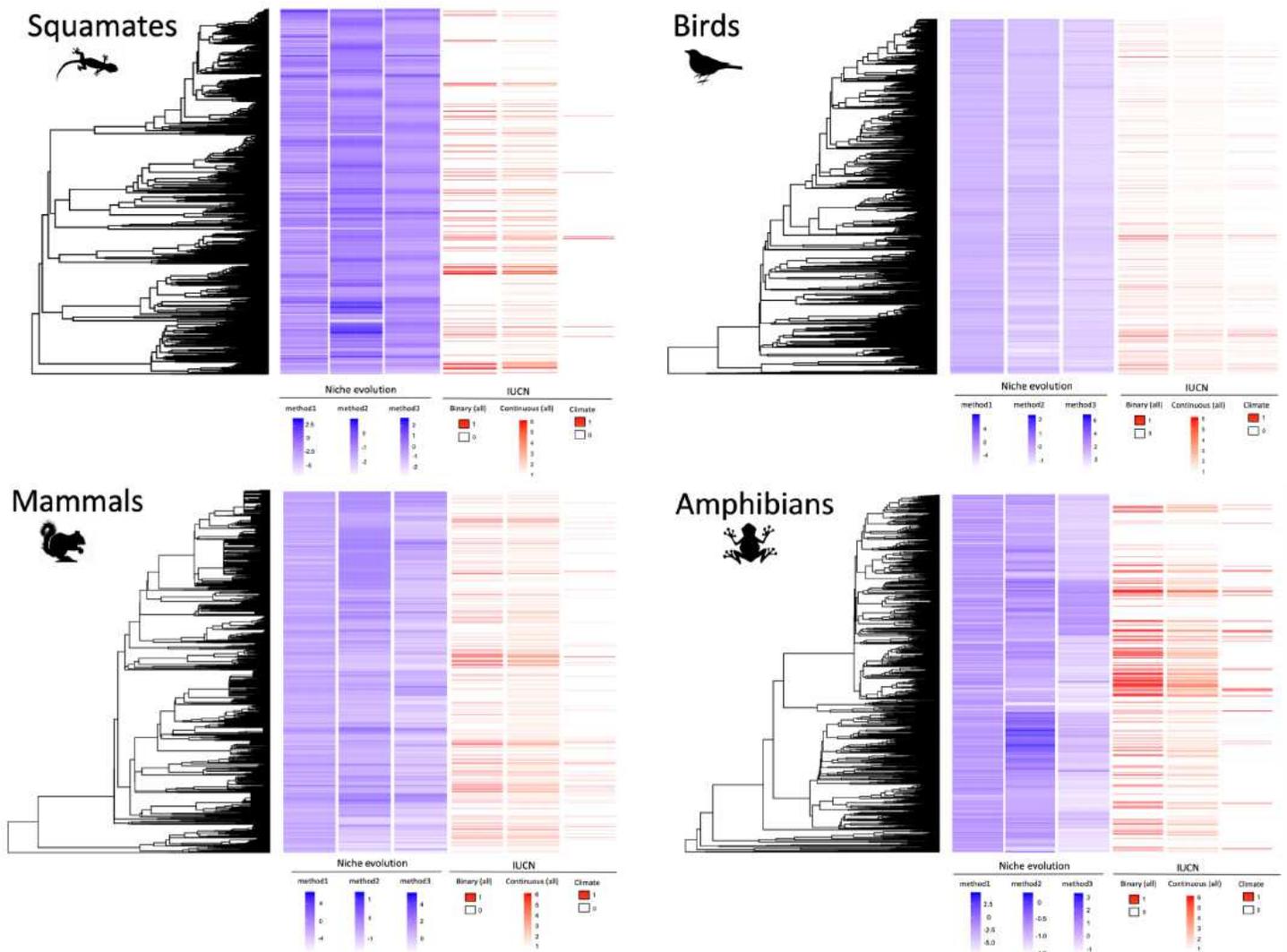


Figure 2

Comparison between the rate of thermal niche evolution for each of the three methods (blue) and conservation status (red) aligned to the phylogenetic tree for birds, mammals, amphibians and squamates. Our study shows that threatened species are phylogenetically clustered (see also Sup. Mat. 4), but that there is no strong association between rates of niche evolution and conservation status. Rates of niche evolution were log transformed.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.pdf](#)