

1 **Climatic niche at physiological and macroecological scales:**
2 **thermal tolerance–geographic range interface and niche**
3 **dimensionality**

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23 **ABSTRACT**

24 **Aim** Under the Hutchinsonian concept of realized niche, biotic interactions and
25 dispersal limitation may prevent species from fully occupying areas that they could
26 tolerate physiologically. This can hamper transferring physiological limits into
27 climatically-defined range limits and distorts inferences of evolutionary changes of
28 adaptive limits (i.e. niche conservatism). In contrast, heritable physiological limits should
29 conform more closely to the position of the niche in the climatic hyperspace. Here we
30 hypothesize that a measure of niche position in the climatic hyperspace is more reliable
31 than niche boundaries to capture the variability and evolutionary pattern of physiological
32 tolerance.

33 **Location** Neotropic and Palaeartic.

34 **Methods** We used non-phylogenetic and phylogenetic regressions to test
35 relationships between physiological requirements and macroecological niche features (i.e.
36 based on known species distributions) among anurans. We measure physiological
37 responses through larval critical thermal maximum (CT_{\max}), and realized niche in the
38 geographical space through maximum temperature (T_{\max}) temperature variability (T_{var}),
39 and the position and breadth of niche at the climatic hyperspace. We also compare
40 evolutionary rates among these parameters using the Phylogenetic Signal-Representation
41 curve.

42 **Results** CT_{\max} is better related to niche position ($R^2 = 0.414$) than to T_{var} . Further,
43 CT_{\max} is unrelated to both T_{\max} and niche breadth. CT_{\max} and macroecological niche
44 position also show similar, high evolutionary rates, i.e. faster than Brownian motion,
45 whereas T_{\max} and T_{var} evolve slower, and niche breadth evolves at random.

46 **Main conclusions** Transferability between thermal tolerance and realized climatic
47 niche limits is weak. Only macroecological niche position in the multivariate climatic

48 hyperspace correlates with physiological tolerance. It thus appears to be more suitable to
49 describe the variability and evolutionary pattern of the species' adaptive limits. We link
50 these results to 'niche dimensionality', as manifold, interacting factors outweigh single
51 ones in demarcating the species' realized climatic niche, thereby determining the
52 conserved upper thermal limits of the species.

53

54 **Keywords:** Anuran larvae, CT_{max} , macrophysiology, phylogenetic comparative methods,
55 Phylogenetic Signal-Representation curve, thermal tolerance.

56

57 INTRODUCTION

58 George E. Hutchinson (1957) formalized the modern idea of the ecological niche,
59 defining it as an n -dimensional hypervolume that encompasses all environmental
60 conditions experienced and all the relationships played by a species. Hutchinson also
61 distinguished fundamental from realized niches, to demarcate the conditions that species
62 could live from that they do live on, respectively. He further viewed the species realized
63 niche reflected into the geographical space (Hutchinson, 1978), a property that would
64 allow addressing major questions in the interface between the ecological requirements
65 and broad-scales patterns of species distributions (Colwell & Rangel, 2009; Soberón &
66 Nakamura, 2009). These questions include patterns of species distribution, diversity
67 gradients, the assembly of ecological communities, trait evolution and speciation, species
68 invasiveness and response to global climate changes (see e.g. Wiens & Donoghue, 2004;
69 Pearman *et al.*, 2008; Wiens *et al.*, 2010, and references therein).

70 The niche–space duality also enabled the development of the field of ecological
71 niche modelling (ENM; aka. species distribution modelling), which uses environmental
72 variable and occurrence data to estimate, reconstruct, and forecast the geographic

73 distribution of the realized species niches at distinct spatial and temporal frames (Guisan
74 & Zimmermann, 2000; but see Hortal *et al.*, 2012). More recently, approaches based on
75 the niche–space duality have resorted to direct measures of physiological data as a means
76 to account for real constraints to the occurrence-based estimates of the realized niche
77 (Kearney & Porter, 2009). These techniques have been referred to as mechanistic niche
78 modelling, to distinguish from the occurrence-based, correlative niche modelling
79 (Kearney & Porter, 2009). Another vein to account for how fundamental niche features
80 are reflected into space is by assessing physiological correlates of the geographical
81 distributions of species, particularly their position and limits (Chown & Gaston, 1999;
82 Calosi *et al.*, 2010; Sunday *et al.*, 2010, 2012; Bozinovic *et al.*, 2011). This bridging
83 between macroecology and physiology has been termed ‘macrophysiology’ (Chown *et*
84 *al.*, 2004), a field that aims to describe general properties of the interface between
85 individuals’ endurance to environmental conditions and the patterns of geographical
86 distribution of their species (see also Gaston *et al.*, 2009). To avoid the misleading
87 implication that macrophysiology is an effective measure of physiological tolerance,
88 which we demonstrate it is not, herein we will use ‘macroecological niche’ to refer to
89 measures of the realized niche of the species obtained from the relationship between their
90 geographic distributions and current climatic conditions.

91 Permeating the niche-space transferability is the fact that environment changes in
92 space and time, altering the geography of species, and sometimes forcing them to modify
93 their Hutchinsonian niches (Pearman *et al.*, 2008; Colwell & Rangel, 2009). Whether
94 (and to what extent) niches change has become a key topic in current ecology (Pearman
95 *et al.*, 2008; Losos, 2008; Wiens *et al.*, 2010), which is centred around the ‘niche
96 conservatism hypothesis’, or the tendency of closely related species to share more niche
97 similarities among each other than with less related species (Wiens & Donoghue, 2004).

98 Under a phylogenetic framework (Losos, 2008; Cooper *et al.*, 2010), this balance
99 between niche evolution and niche conservatism has provided a powerful analytical tool
100 to link evolutionary theory, ecology and biogeography. Most often, studies on this topic
101 have used the distributional limits to infer patterns of macroecological niche conservatism
102 of species' tolerance to climate across large spatial and temporal scales (e.g. Roy *et al.*,
103 2009; Olalla-Tárraga *et al.*, 2011).

104 However, real limits of climatic tolerance may be loosely defined by – or even
105 divorced from – range limits, particularly for terrestrial organisms (Sexton *et al.*, 2009;
106 Buckley *et al.*, 2010 Sunday *et al.*, 2012; but see Calosi *et al.*, 2010). Multiple factors
107 govern the species' distributional range, but how they combine to define range
108 boundaries are still poorly understood (Pulliam, 2000; Gaston, 2003; Sexton *et al.*, 2009).
109 Soberón & Peterson's (2005) BAM diagram (from biotic, abiotic, and movement)
110 summarizes in part how different factors affect the species distribution at large spatial
111 scales. Besides tolerance limits (depicted by the abiotic factor), species distributions are
112 also affected by a number of biotic interactions and movement constraints, which modify
113 the geographical response of the species. If one factor falls short of others, the species
114 will fail to accomplish its potential distribution, and the characterization of any of these
115 factors from the observed distribution of the species will be distorted (see Soberón, 2007;
116 Soberón & Nakamura, 2009; Hortal *et al.*, 2012).

117 Multiple interactions of factors, rather than abiotic constraints alone, set the limits
118 of species ranges, and hence their realized niche (Soberón, 2007). However, no species
119 populations can persist for long outside its tolerance limits (which outline the species
120 fundamental niche in the first place) (see Soberón & Nakamura, 2009). Due to this, the
121 parameters of climatic tolerance of each species remain, to some extent, close to their
122 distribution in the environmental space (Hoffmann *et al.*, 2012). In addition, being a

123 heritable trait, biophysical tolerance of individuals should evolve precisely in response to
124 the species' overall position in the climatic space after a spatial and/or temporal change
125 takes place (Huey & Steverson, 1979; Huey & Kingsolver, 1993). This may suggest that
126 a given measure of the species' modelled niche that weights the position of its centroid in
127 the climatic hyperspace (hereafter niche position) over its limits should be less affected
128 by the biotic and movement constraints that affect its boundaries, thus remaining spatially
129 and phylogenetically related to the physiological features of that species. Consequently,
130 this measure of niche position should outperform climatic boundaries in summarizing
131 both the variation and the evolutionary pattern of the species' biophysical tolerance
132 (Soberón & Nakamura, 2009).

133 In the absence of true data on species physiology, Hof *et al.*, (2010) recently used
134 a macroecological measure of niche position to assess the broad-scale patterns of niche
135 conservatism among amphibians. Here, we resort to data on amphibian thermal tolerance
136 to test the hypothesis that a measure of niche position in the multidimensional climatic
137 hyperspace describes the variation in species tolerance at the level of individuals better
138 than climatic niche features drawn from either species' niche boundaries. To do this, we
139 compare physiological limits characterizing individuals within species to some
140 macroecological metrics of species' niche, in terms of both explanatory ability and
141 evolutionary rate. This latter analysis describes how traits have evolved along the
142 phylogeny, thus enabling a model-based estimation of niche conservatism/evolution. We
143 use anurans to test which macroecological niche measure (maximum air temperature,
144 temperature variability of the species' range, multivariate niche position, or niche breadth
145 at the climatic hyperspace) best explains the variation in a true measure of an individual's
146 physiological performance, the larval critical thermal maximum (CT_{max}). By doing this
147 we show the divergence between physiological and geographical (i.e. macroecological)

148 thermal limits and suggest a finer approach to describe the variability and the
149 evolutionary pattern of thermal tolerance that takes into account the multi-dimensionality
150 of the species' climatic niches.

151

152 **METHODS**

153 *Species Data*

154 We gathered data about the upper thermal limit of physiological tolerance (CT_{max}) for 47
155 species of anurans (information on 42 species comes from Duarte *et al.* [2012], and data
156 for other five species were gathered by H. Duarte, M. Tejedo, and collaborators following
157 the same protocol; see Duarte *et al.*, 2012). The five species of Caudata analysed by
158 Duarte's *et al.* (2012) study were excluded. The data employed here comprises species
159 from three communities located at distinct environmental conditions: the subtropical
160 warm Gran Chaco region, the subtropical Atlantic Forest, and Temperate Europe and
161 northern Africa (see Duarte *et al.*, 2012 for further details). However, each of these
162 species is distributed at varying geographical positions and climatic conditions, including
163 most of Neotropical and Palearctic realms (Figure S1). We should anticipate, however,
164 that the low resolution of the climatic data prevents us from refining conclusions on the
165 species' fine-tuning to particular microhabitats and local conditions. Nevertheless, our
166 aim here is to provide a broad description of how specific thermal features are expressed
167 at coarse scales, after multiple interactions with other niche dimensions have taken place.

168 Also following Duarte *et al.* (2012), we used a phylogenetic hypothesis for the 47
169 anurans according to Frost *et al.* (2006), including branch length estimation based on
170 three nuclear and two mitochondrial genes. Species missing from the phylogeny had their
171 branch lengths inferred from sister-taxa, which have, by definition, the same age of the

172 target species (see details in Duarte *et al.*, 2012, including their electronic Supporting
173 Information).

174 ***Physiological data***

175 CT_{\max} was estimated from anuran larvae under controlled trials in laboratory, following
176 Hutchison's dynamic method (Hutchison, 1961). Tadpoles were heated until individuals
177 reach the onset of muscular spasms, which was assumed as maximum thermal limit for
178 species tolerance (see details of laboratorial procedure and parameterization in Duarte *et*
179 *al.*, 2012). Fully aquatic, small anuran larvae can be considered isothermal with the
180 environment (Lutterschmidt & Hutchison, 1997a), so they are expected to mirror the
181 environmental tolerance at the species geographical limits better than adults. In addition,
182 the tadpoles of the species studied develop in temporary, shallow ponds, where
183 thermoclines are virtually absent and individuals are fully subject to the actual thermal
184 variation. Ponds temperatures, in turn, are ruled by the outer climate, which is related to
185 the macroclimatic dominion. Adults, in contrast, are capable to circumvent thermal stress
186 by actively searching for more suitable microhabitats outside the ponds – including
187 fossorial and nocturnal activity, thus their thermal tolerance limits may not match the
188 environmental limits, as those of larvae. Therefore, we can assume that anuran larvae can
189 reasonably represent the susceptibility to thermal variability of the species.

190 Threshold temperature limits such as CT_{\max} are important parameters for
191 describing the Hutchinsonian fundamental niche as they set hard boundaries for animal
192 survivorship (Huey & Steverson, 1979; Lutterschmidt & Hutchison, 1997b). Besides,
193 there is a correspondence between upper thermal resistance and optimal temperature of
194 performance in lizards (Huey *et al.* 2009) and in tadpoles (Katzenberger, M & Tejedo, M,
195 unpublished results). So, variation in CT_{\max} , not only may provide insights on species'

196 fundamental niche position through thermal tolerance itself but also can be a proxy of
197 optimal performance and then explaining sub-lethal viability of species. However,
198 according to its earlier definition, CT_{max} is “the thermal point at which locomotory
199 activity becomes disorganized and the animal loses its ability to escape from conditions
200 that will promptly lead to its death” (Cowles & Bogert, 1944). Therefore, it remains
201 challenging to determine the ecological meaning of the CT_{max} of the larval stage for the
202 anuran species as a whole, and out of controlled laboratorial experiences. Indeed, this is a
203 frequent problem with other organisms used as physiological models (e.g. Castañeda et
204 al. 2012; Ribeiro *et al.*, 2012; also reviewed in Terblanche et al. 2011). Probably even
205 lower temperatures could cause other sub-lethal distresses in nature, including
206 developmental disorders or decrease the ability to forage or to evade from predators, thus
207 undermining the viability of the populations (Huey & Stevenson, 1979). In addition,
208 CT_{max} is a complex function of experimental heating rates, and usually information of
209 field heating rates is absent (Ribeiro *et al.*, 2012). In this sense, we should assume that,
210 whichever is the outdoor ecological meaning of acute measures of CT_{max} , it should be
211 linearly correlated with an actual measure of thermal tolerance to higher temperatures.

212 ***Macroecological data***

213 We gathered data on the geographic distribution of all species from the ‘Global
214 Amphibian Assessment’ database (IUCN, 2009). Maximum air temperature of species
215 distribution (T_{max}) was calculated as the mean of the maxima among grid cells within
216 each species’ range (see below). Temperature variability (T_{var}) was characterized by the
217 range (T_{max} minus T_{min}) in temperature. We used average measures instead of, say, the
218 maximum of the cells maxima, to circumvent errors in climatic measurements within
219 some species’ range (particularly larger ones).

220 For the multivariate macroecological niche measurement (see below), we
221 assembled a set of seven environmental descriptors widely recognized as direct or
222 indirect limiting factors constraining the climatic niche of amphibians (mean actual
223 evapotranspiration – AET, mean potential evapotranspiration – PET, maximum
224 temperature of the warmest month, minimum temperature of the coldest month, annual
225 range of temperature, mean annual precipitation, and annual range in precipitation).
226 These environmental variables were drawn from interpolated surfaces of time data series
227 (AET and PET from Willmott & Matsuura, 2001; and the others from Hijmans *et al.*,
228 2005). Both the species' geographical range and the environmental variables were
229 projected onto a grid cell system of 1°×1° resolution covering the geographic region
230 outlined by the distribution of all 47 species together, i.e. parts of the Neotropics and the
231 Palearctic. Each grid cell defined a sample unit for estimating the environmental
232 maximum temperature and the multivariate niche features.

233 We used the Outlying Mean Index (OMI; Doledec *et al.*, 2000) to obtain
234 macroecological measures of niche position and breadth in the multivariate climatic
235 hyperspace. OMI is a multivariate ordination technique that calculates the
236 hypervolumetric space of species niche (i.e. a subset of the Hutchinsonian niche in the
237 multidimensional space) according to the selected factors (e.g. environmental variables).
238 OMI characterizes niche breadth, 'niche marginality', 'inertia' – which provides an
239 estimate of niche overlap – and 'residual' variation – which describes the variation in the
240 niche breadth unrelated to the variables of the model. Niche breadth is measured as the
241 dispersion of the sampling units of each species at the multivariate climatic hyperspace,
242 whereas niche marginality describes the amount of differentiation of the species niche
243 relative to a theoretical, average niche that is drawn from the environmental data inputted
244 (Doledec *et al.*, 2000), so it can be interpreted as a measure of niche position in the

245 climatic hyperspace (see also Hof *et al.*, 2010). Because niche marginality measures the
246 ecological distance of each species relative to an average, theoretical niche, species
247 similarly distant to this mid-point but at opposite points of a niche axis will have similar
248 marginality values. We thus used the species scores along the first axis of the OMI
249 ordination (which encompassed 92.35% of the variation among all axes) as a measure of
250 niche position.

251 The macroecological and physiological data we use involve measures at two very
252 different scales and levels of biological organization. Therefore, some unavoidable
253 assumptions are required. For instance, that the CT_{\max} of the individuals are
254 representative of the entire species; that the geographical range of each species is
255 assumed to describe the distribution of its breeding populations; and that the climatic
256 variables are good enough to reflect suitable conditions for the studied species. Although
257 hard for the data at hand, these assumptions are nonetheless common for virtually all
258 broad-scale studies, especially for our case. This is because we are precisely focused on
259 the possibility of identifying macroscale correlates of the species variability in a
260 physiological property that is shared by all individuals of the species.

261 ***Phylogenetic Comparative Analysis***

262 We first ran ordinary least square (OLS) regression of CT_{\max} against each
263 macroecological niche feature (T_{\max} , T_{var} position, and breadth) independently to test if
264 physiological tolerance and climatic niche parameters at the macroscale are capable to
265 explain each other in a direct way. This could help determining, for example, if CT_{\max}
266 could systematically approximate the environmental maximum temperature of the species
267 or other niche description. We do not expect, however, CT_{\max} and T_{\max} to coincide

268 because T_{\max} may underestimate the maximum body temperature of individual
269 amphibians. Instead, we question whether CT_{\max} and T_{\max} are in some way correlated.

270 Next, we evaluated if these features are related to each other while accounting for
271 phylogenetic autocorrelation, which can bias significance tests of standard statistical
272 techniques such as OLS, when applied to cross-species data. We analysed the
273 phylogenetic signal using Phylogenetic Signal-Representation (PSR) curves (Diniz-Filho
274 *et al.*, 2012) for each trait, as also a means to access their intrinsic evolutionary rate
275 through the phylogeny. PSR curve is built upon the eigenvectors from the phylogenetic
276 eigenvector regression (PVR; Diniz-Filho *et al.*, 1998), in which the models fit (R^2) of
277 successive PVRs of accumulated eigenvectors are plotted against the phylogenetic
278 representation that is given by the accumulated percentage of the corresponding
279 eigenvalues (λ %). The shape of the curve describes the model of evolution of the trait
280 across the phylogeny. A PSR curve near the reference 45° line indicates an evolutionary
281 pattern equivalent to the Brownian motion of trait evolution (Fig. 1), whereas a curve
282 bending below the reference line implies a stronger phylogenetic signal, which can be
283 described by an Ornstein-Uhlenbeck (O-U) process, or by a low lambda model
284 (Freckleton *et al.*, 2002). In contrast, models of accelerated divergence should generate
285 PSR curves traced above the reference line (see Diniz-Filho *et al.*, 2012 for further
286 details). In comparative terms, the trait evolution either slower or faster than an assumed
287 model can be indicative of niche conservatism or niche evolution, respectively (Wiens *et*
288 *al.*, 2010; Cooper *et al.*, 2010). We used permutations to test the evolutionary model of
289 each trait against a null (random) and a neutral (Brownian motion) model of trait
290 evolution. Departures from these models denote accelerated ($PSR_{\text{area}} > 0.0$) or O-U
291 process ($PSR_{\text{area}} < 0.0$).

292 Finally, we tested the associations among traits using a Phylogenetic Generalized
293 Linear Models (PGLS), with maximum likelihood estimation for λ (Freckleton *et al.*,
294 2002). Analyses were run using the PVR and caper packages in R 2.14, R Core
295 Development Team 2010.

296 RESULTS

297 Species' CT_{\max} varied from 35.42 to 44.73°C ($\bar{x} \pm SD = 40.29 \pm 2.20$), whereas
298 geographically-measured T_{\max} was considerably lower, as expected, varying between
299 18.76 and 35.63°C (29.94 ± 4.31). T_{var} varied from 12.45° to 40.54°C. The multivariate
300 macroecological niche breadth and position (in terms of departure from the theoretical
301 average niche) were slightly higher for some Neotropical species (e.g. *Dendropsophus*
302 *minutus*, *Hypsiboas raniceps* and *Trachycephalus venulosus*) than they were for other
303 species (Fig. S2).

304 According to OLS regressions, CT_{\max} was unrelated to T_{\max} ($R^2 = 0.0008$; $F =$
305 0.0385 ; $P = 0.845$), though its ability in predicting T_{var} was significant, but weak ($R^2 =$
306 0.105 ; $F = 6.394$; $P = 0.0150$). In contrast, a significant and substantial amount of
307 variation in macroecological niche position within the climatic hyperspace was explained
308 by CT_{\max} ($R^2 = 0.414$; $F = 31.840$; $P \ll 0.001$), although not by niche breadth ($R^2 =$
309 0.013 ; $F = 0.604$; $P = 0.441$). However, these results may be affected by phylogenetic
310 signal in data.

311 The PSR curves showed that CT_{\max} and macroecological niche position had
312 evolutionary rates slightly, but significantly faster than Brownian motion (CT_{\max} , PSR_{area}
313 $= 0.037$; $p < 0.001$; niche position, $\text{PSR}_{\text{area}} = 0.026$, $p < 0.001$). In contrast, T_{\max} and T_{var}
314 showed slower rates. Both patterns were described by the O-U processes (T_{\max} , $\text{PSR}_{\text{area}} =$

315 $-0.196, p < 0.001$; $T_{\text{var}}, \text{PSR}_{\text{area}} = -0.070, p < 0.001$), whereas the evolutionary pattern of
316 realized niche breadth did not differ from random ($\text{PSR}_{\text{area}} = -0.237, p = 0.10$) (Fig. 1).

317 Because of the phylogenetic signal in data, it is worthwhile to apply comparative
318 analyses to test for relationships among variables. Despite this signal, however, PGLS
319 analyses provided similar results to OLS. These included a non-significant between CT_{max}
320 and the T_{max} ($\beta = -0.064 \pm 0.038; p = 0.095$), a weak, though significant, relationship of
321 CT_{max} to T_{var} ($\beta = -0.079 \pm 0.039; p = 0.023$), and a non-significant relationship between
322 CT_{max} and niche breadth ($\beta = 0.067 \pm 0.739; p = 0.992$). On the other hand, we found a
323 positive, highly significant explanation of macroecological niche position by CT_{max} ($\beta =$
324 $1.965 \pm 0.073; P \ll 0.001$) (Table 1; Fig. 2).

325 **DISCUSSION**

326 The ability of physiological tolerance limits (e.g. CT_{max}) to describe geographical range
327 limits (e.g. T_{max}) – and *vice versa* – has been the “holy grail” of ecophysiology (and, more
328 recently, of macrophysiology). Physiological tolerance limits are informative on the
329 susceptibility of species to rapid climatic changes in terms of the maximum amount of
330 heat they can withstand (Duarte *et al.*, 2012). Thus, knowing the relationship between
331 tolerance and range limits would allow both (i) using individuals physiological
332 parameters to infer species distributional shifts during climatic changes (reviewed in
333 Bozinovic *et al.*, 2011), and (ii) inferring species tolerances based on their geographical
334 distributions. The latter is in fact a fairly common practice (e.g. Roy *et al.*, 2009; Olalla-
335 Tàrraga *et al.*, 2011), despite the lack of knowledge about how physiological tolerance
336 relates with current species distributions. Strikingly, our results evidence that upper
337 physiological limits alone may fail in characterizing macroecological (i.e. geographical)
338 climatic boundaries of species’ distributions, such as maximum air temperature or a

339 multivariate measure of niche breadth within the climatic hyperspace. Conversely, a
340 climatic parameter that reflects realized variability (T_{var}) can be better described by CT_{max}
341 than a single climatic limit (Clusella-Trullas et al. 2011), although this explanatory ability
342 was weak in our case.

343 It can be argued that the lack of or low predictability of T_{max} and T_{var} is due to
344 other climatic parameters being more important for defining the thermal limits of the
345 studied species in the geographical space (e.g. Addo-Bediako *et al.*, 2000; Sunday *et al.*,
346 2010). However, the rationale of the physiological–geographical transferability of
347 climatic tolerance, as has been applied, builds upon the assumption that tolerance limits
348 define some boundaries of the species fundamental niche and, as species ranges reflect
349 their niche at the geographical space, tolerance and range boundaries should mirror one
350 another (Calosi *et al.*, 2010). However, there is more in a species’ distribution than
351 climatic requirements. Besides various sources of noise in tolerance estimates that can be
352 anticipated (Terblanche *et al.*, 2011; Castañeda *et al.*, 2012; Ribeiro *et al.*, 2012),
353 geographical ranges reflect the limits of the macroecological niche after it interacts with a
354 series of other recent and historical factors, particularly biotic interactions and constraints
355 to movement (i.e. biogeographical processes and occupancy dynamics; Hortal *et al.*,
356 2010), that conform the realized niche (i.e. the BAM diagram of Soberón & Peterson,
357 2005; see Soberón, 2007; Soberón & Nakamura, 2009; Godsoe, 2010). When the
358 geographical projection of these three dimensions (biotic, abiotic and movement) fails to
359 fully overlap with each other, the species will inhabit only a subset of its potentially
360 suitable area, and hence the response to a single dimension will fail to predict the whole
361 species’ distribution (see discussion in Hortal *et al.*, 2012). As a consequence, the
362 physiological–geographical transferability would only be possible in the particular case in
363 which these three dimensions fully coincide in the geographic space.

364 The same reasoning made for T_{\max} and T_{var} applies to niche breadth. This latter
365 measure summarizes the range of environmental conditions that are experienced by each
366 species. Thus, it is also related to the conditions in the boundaries of the regions where
367 the species are distributed. Our results also show that T_{\max} , T_{var} , and niche breadth may
368 differ from CT_{\max} in their evolutionary rates. In fact, there is evidence of both faster and
369 slower rates of evolution for either physiological (Huey & Kingsolver, 1993; Angilletta *et*
370 *al.*, 2002; Kellermann *et al.*, 2012) or macroecological (Pearman *et al.*, 2008) niche
371 features. Within a clade, different features in the same clade may also evolve at specific
372 rates, or yet have varying rates through evolutionary time (Pearman *et al.*, 2008).
373 Therefore, the observed patterns of trait evolution are contingent to the trait and the clade
374 involved. However, different rates – or amounts – of trait change can yield different
375 conclusions on patterns of niche conservatism/evolution for these traits, which in turn can
376 indicate different evolutionary processes (Cooper *et al.*, 2010). Flawed inferences of trait
377 change may therefore misguide conclusions on the evolutionary process of that trait.
378 Since the evolutionary pattern observed in T_{\max} , T_{var} , and niche breadth should
379 incorporate other factors affecting distributional range, then these macroecological niche
380 parameters – that depict the boundaries of the response of the species to climate – may
381 lead to inaccurate conclusions on the actual evolutionary pattern of thermal tolerance, if
382 taken as a measure of such aspect of the fundamental niche.

383 A caveat of our results comes from the quality of the macroecological data used. It
384 is possible, for example, that coarse range maps are poor descriptors of both the
385 geographical (Hurlbert & White, 2005) and climatic limits of the species (which are also
386 coarse). In such case, the poor ability of climatic limits measured in the geographical
387 space (e.g. T_{\max} or T_{var}) to describe physiological limits could be an artefact caused by
388 deficiencies in the data. The same problem would affect the estimation of the

389 evolutionary rate through the PSR curve. That is, because most species share part of their
390 distribution, it would be possible that an overall low ability in discriminating their
391 climatic boundaries make their climatic limits to be most similar than expected by chance
392 (i.e. Brownian motion), thus resulting in a more conserved pattern of trait evolution. In
393 fact, some of these caveats are related to the scaling issue referred before, for we are
394 dealing with variables that stand at contrasting spatial scales (pond *vs.* continent) and
395 levels of organization (individuals *vs.* species). In addition, our physiological data comes
396 from tadpoles, whereas macroecological data characterize terrestrial environments of
397 adults. Although the broad-scale distributions of both larvae and adults should coincide,
398 we overlook possible, particular developmental modifications in the physiological
399 machinery of each species.

400 From the physiological standpoint, some important information needed to discuss
401 species tolerance limits is also missing. Species' physiological limits are defined by the
402 pool of physiological tolerance limits of the individuals, including acclimation and inter-
403 individual plasticity in critical temperatures, and are expected to vary according to the
404 conditions of their position in the species' range (Huey & Stevenson, 1979; Hoffmann *et*
405 *al.*, 2012). However, we only have individual limits under acute change, i.e. a subset of
406 the range of thermal tolerances that characterize the entire species.

407 From a macroecological point of view, there is still the challenge of identifying
408 the species' range limits accurately, even for well-known species. Many factors besides
409 those summarized in the Soberón & Peterson's (2005) BAM scheme are known to cause
410 the species' range to behave dynamically. They include, for example, population's
411 source-sink dynamics (Pulliam, 2000), adaptation at peripheral distributions, Allee effect,
412 among many others (see e.g. Sexton *et al.*, 2009). The dynamic nature of range limits is
413 common even during environmentally stable periods, and may often hamper their clear

414 demarcation (Gaston, 2003), especially in the context of the realized niche (i.e.
415 presupposing non-negative population growth rates). In addition, species abundance tends
416 to clump around the centroid of the environmental space, thus making suboptimal sites
417 placed farther from this environmental optimum to represent the species inherited niches
418 poorly (Martinez-Meyer *et al.*, 2013). Therefore, discriminating between niche
419 conservatism and niche evolution from the species distributional limits is, at least,
420 problematic because of the coarseness of range maps, the dynamic nature of geographic
421 ranges, and the decay of niche optimality towards its boundaries, particularly when
422 inference about niche conservatism comes from single variables. This is expected
423 because these inferences may take into account the sort of factors involved in range
424 determination that prevents the species to occupy suitable regions.

425 We have shown, however, that a multivariate description of the species climatic
426 niche – its position in the climatic hyperspace – may provide a reasonable
427 characterization of both among-species variability and the evolutionary rate of
428 physiological tolerance. Although this measure of niche position also derives from the
429 climatic domain defined by the species' distribution (thus being subject to the same
430 sources of error of both range maps and climatic data layers), species range boundaries
431 seem to be better described by combined rather than single climatic parameters
432 (Kellermann *et al.*, 2012; Smith, 2012). Accordingly, combinations of factors (e.g.
433 temperature and humidity) and properties of these factors (e.g. total amounts, variability,
434 range) impose direct and indirect limits to the species niche, thus outperforming single
435 parameters in demarcating their position in this climatic hyperspace.

436 What our findings emphasize beyond any doubts is the importance of taking into
437 account the multiple dimensions of the modelled niche while studying niche conservatism
438 or niche evolution. Although dimensionality is a central part of Hutchinson's (1978)

439 concept of the niche, it is often seen as a caveat to understand the conservatism/evolution
440 of particular niche dimensions (e.g. Peterson, 2011). Of course, pooling in as many
441 factors as possible to describe the niche may be of little help to understand its
442 evolutionary dynamics, particularly because of data collinearity. But we provide
443 empirical evidence that relying on a single dimension may not only be insufficient, but
444 rather misleading (see Godsoe, 2010 for an in-depth discussion on the caveats of
445 identifying niche features from incomplete environmental measurements). Taking into
446 account dimensionality in studies of niche dynamics may improve our understanding on
447 the variability and evolution of fundamental attributes (e.g. physiological) of the species,
448 which ultimately determine their endurance across temporally and spatially changing
449 conditions. In addition, this approach may circumvent the problem of dealing with
450 macroecological variables that are more subject to external constraints, such as climatic
451 boundaries or niche breadth drawn from the species' geographical distribution. This
452 leaves the question on the number of niche dimensions that should be included in the
453 macroecological niche description (Godsoe, 2010), which depends on the context and the
454 taxon involved. If our approach proves useful, defining the modelled niche dimensions to
455 be studied would be a necessary step for any investigations of niche evolution. Here,
456 making available additional data on the fundamental properties of physiological
457 endurance of species, together with a proper manner to handle them, is of critical
458 importance.

459 Our results may also foster discussion on the differences between correlative and
460 mechanistic niche models (Kearney & Porter, 2009; Buckley *et al.*, 2010). On the one
461 hand, physiological limits of species may fail in predicting their climatic limits, either
462 currently or after potential range shifts, thus supporting previous reservations about the
463 accuracy of mechanistic models in estimating realized niches (Buckley, 2010; Buckley *et*

464 *al.*, 2010). On the other hand, the link of a physiological feature (i.e. CT_{max}) to the
465 macroecological climatic niche position of species reinforces the importance of
466 considering studies on species' fundamental traits to advance the field of species
467 distribution modelling (Kearney & Porter, 2009; Buckley, 2010; Buckley *et al.*, 2010).
468 Nonetheless, and despite the problems of using correlative models of species distributions
469 to describe adaptations to climate (see Hortal *et al.*, 2012), our results point out that
470 multivariate descriptions of climatic niche are needed to address questions on the
471 conservatism or evolution of upper adaptive limits (Peterson *et al.*, 1999; Araújo &
472 Peterson, 2012).

473 Hof's *et al.* (2010) proposition on broad-scale evolutionary pattern of species'
474 climatic tolerance drawn from a similar macroecological measure of niche position finds
475 empirical support in our study. However, the differences in taxonomic resolution and
476 comprehensiveness impair a direct comparison between their results and ours. In fact, it is
477 possible that our findings are benefited by particular features of amphibians. In general,
478 among ectotherms, upper thermal limits (e.g. CT_{max}) are less spatially variable and more
479 phylogenetically constrained than other physiological responses, such as lower thermal
480 limits (reviewed in Hoffmann *et al.*, 2012). If this is the case of amphibians, Hof's *et al.*
481 (2010) results on the general tendency for retaining the realized climatic niche in the
482 geographical space, together with ours, suggest an explanation to the parallelism between
483 CT_{max} and macroecological niche position. Accordingly, the ecological and evolutionary
484 'hardness' of the upper boundary of the tolerance to temperature makes it more closely
485 related to the climatic hyperspace where the species' multidimensional niche is centred.

486 A final issue that is critical for the interpretation of our results is phylogenetic
487 scale. Depending on the scale investigated, one can draw distinct conclusions on the
488 species adaptability to changing climates and inferences of niche conservatism/evolution

489 (Losos, 2008; Pearman *et al.*, 2008; Peterson, 2011). Our dataset covers species with
490 varied phylogenetic distances, from deep temporal distances (than 200 Myr, between
491 Alytidae/Pelobatidae and the remaining clades) to relatively close ones (such as the
492 species within the *Leptodactylus* genera, separated ca. 5 Myr) (Wiens, 2011; Figure S3).
493 It is likely that our results on evolutionary rates reflect average large phylogenetic
494 distances among clades (e.g. families or genera), and for this scale, larger amounts of
495 fundamental niche change may be the standard expectation. In this case, the term “faster”
496 as employed here is only relative to the other traits investigated and to the evolutionary
497 model of reference, i.e. the Brownian motion model. It does not imply that anurans are
498 capable to track rapid climatic changes, in shorter time scales (e.g. decades or hundreds
499 of years).

500 **CONCLUDING REMARKS**

501 By combining physiological experimental data, macroecological and phylogenetic data
502 coupled with evolutionary models, we have shown that both the variability and the
503 evolutionary pattern of physiological limits, such as CT_{\max} , may be loosely described by
504 the variables that characterize the realized limits of species distributions, such as T_{\max} ,
505 T_{var} , or niche breadth. These findings challenge the transferability of physiological data
506 into the geographical space, warning for the usage of macroecological environmental
507 limits measured from species distribution ranges as indicators of tolerance in studies on
508 both the effects of climatic shifts on species distributions and niche
509 conservatism/evolution. Supporting our claim is the fact that species range limits, and
510 hence their realized niche, are also determined by other factors different from climate
511 (e.g. abiotic, biotic, movement, population dynamic and intraspecific variability).

512 In contrast, we show that the among-species variability and evolutionary pattern
513 of CT_{\max} can be better described by a multivariate measure of the macroecological niche
514 position in the climatic hyperspace. We attribute this result to the lower lability of both
515 upper thermal limits and species niche as a whole, which may be linked to the interaction
516 of multiple environmental factors in exerting direct and indirect constraints on the species
517 distribution and realized niche, a property that permeates the definition of niche since
518 Hutchinson (1957), i.e. the multi-dimensionality of the niche. Our results also warn for
519 some applications of mechanistic and correlative species distribution modelling (i.e.,
520 niche modelling), regarding inferences of realized niches and patterns of niche
521 conservatism, respectively. Further studies involving closely related species – for which
522 fundamental attributes of the Hutchinsonian niche (e.g. physiology, interaction, and
523 dispersal limitations) are known – are of primer importance to understand their effect on
524 the evolutionary and spatial dynamics of the niche.

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691 **BIOSKETCHES**

692 **Sidney F. Gouveia, Joaquín Hortal, Fernanda A. S. Cassemiro and José Alexandre**

693 **F. Diniz-Filho** work on different aspects of biogeography, macroecology and

694 macroevolution.

695 **Miguel Tejedo, Helder Duarte and Carlos A. Navas** work on ecophysiology and

696 evolutionary physiology.

697 **TABLES**

698 **Table 1.** Phylogenetic Generalized Least Squares (PGLS) models between CT_{\max} and
 699 macroecological niche traits. λ is the index that transforms the trait phylogeny to fit a
 700 Brownian motion model. β = models slope; ε = standard error.

CT_{\max} vs.	λ	β	$\pm \varepsilon$	F -value	p -value
T_{\max}	0.980	0.064	0.038	2.9	0.09
T_{var}	0.964	-0.079	0.039	4.1	0.02
Niche position	1.00	1.965	0.073	717.6	2.2×10^{-16}
Niche breadth	0.969	0.067	0.739	0.0	0.99

701

702 **FIGURE CAPTIONS**

703 **Figure 1.** Phylogenetic Signal Representation (PSR) curves showing the evolutionary
704 rates of critical thermal maximum (CT_{max}), geographical maximum temperature (T_{max}),
705 temperature variability (T_{var}), niche marginality (the 1st axis of OMI – Outlying Mean
706 Index) and niche breadth for 47 anurans. Lighter and darker grey bands are the
707 confidence intervals for the neutral (Brownian motion) and null (random) expectations,
708 respectively (Diniz-Filho *et al.*, 2012). Note that CT_{max} and OMI 1st axis have very similar
709 patterns of evolution (i.e., slightly faster than Brownian motion).

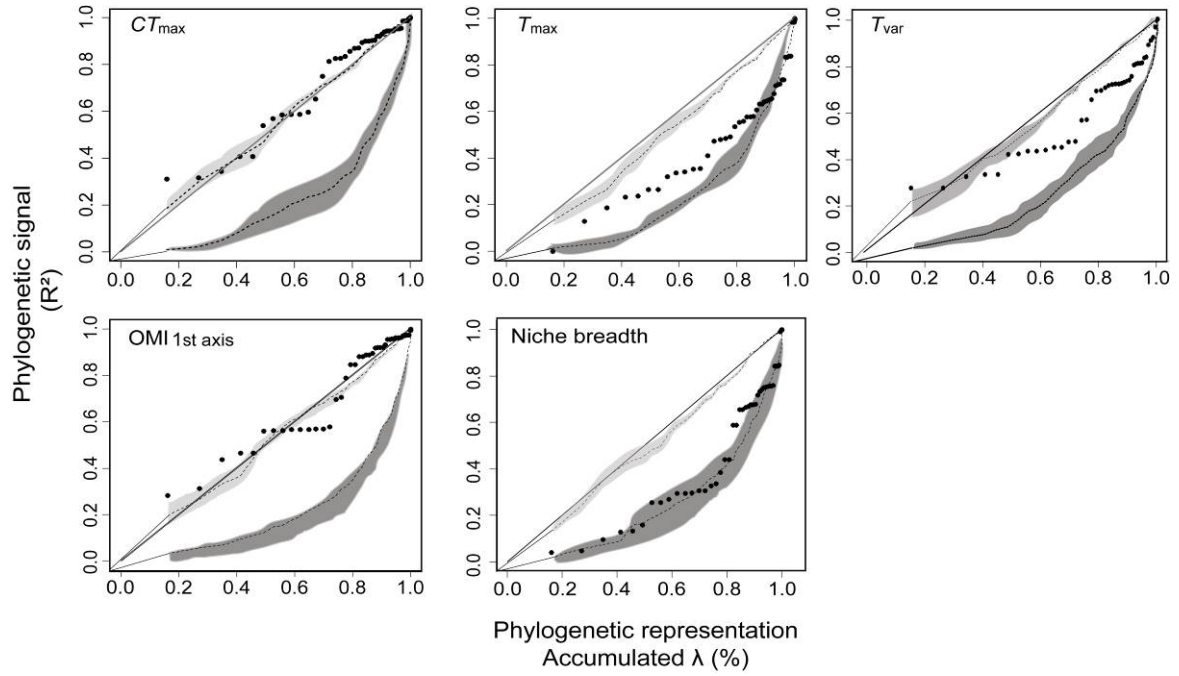
710

711 **Figure 2.** Phylogenetic Generalized models between the anuran larvae CT_{max} and
712 macroecological climatic niche features: a = niche position (the 1st axis of OMI –
713 Outlying Mean Index); b = T_{max} ; c = T_{var} ; d = niche breadth.

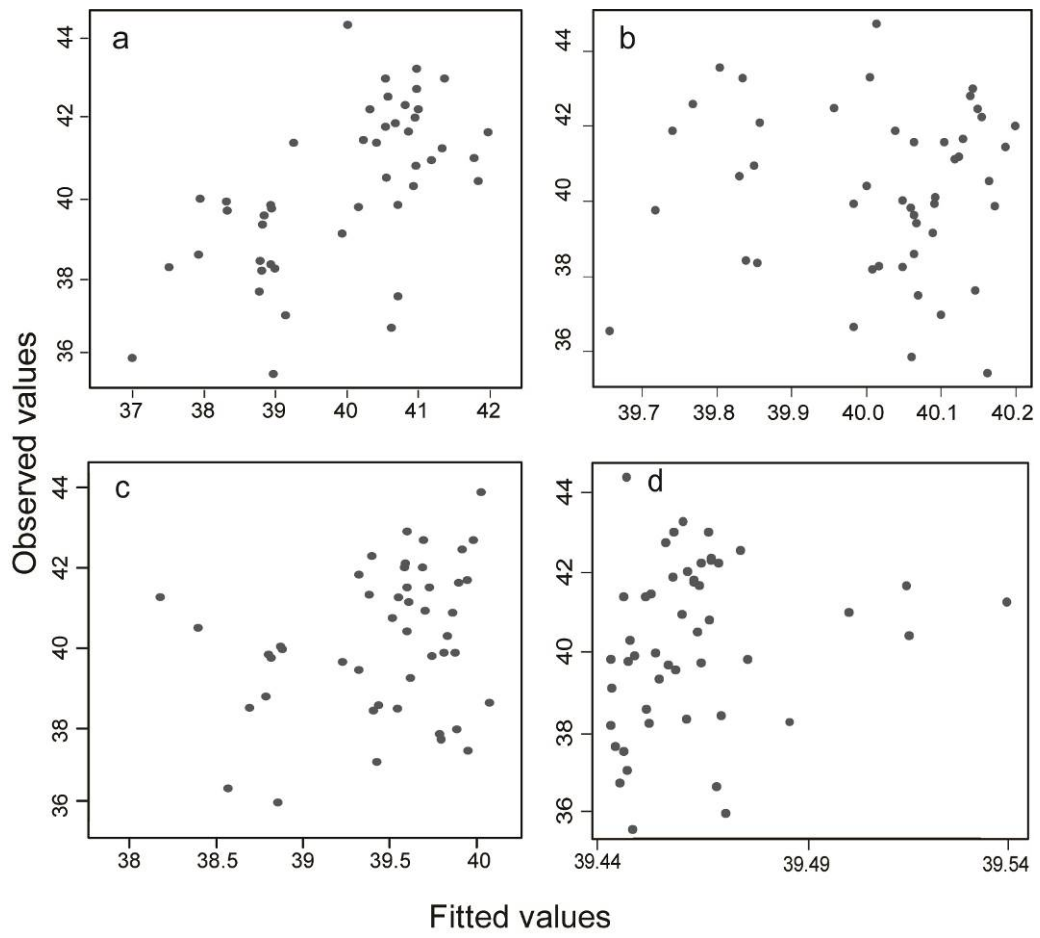
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715 **FIGURES**

716 **Figure 1**



718 **Figure 2**



719

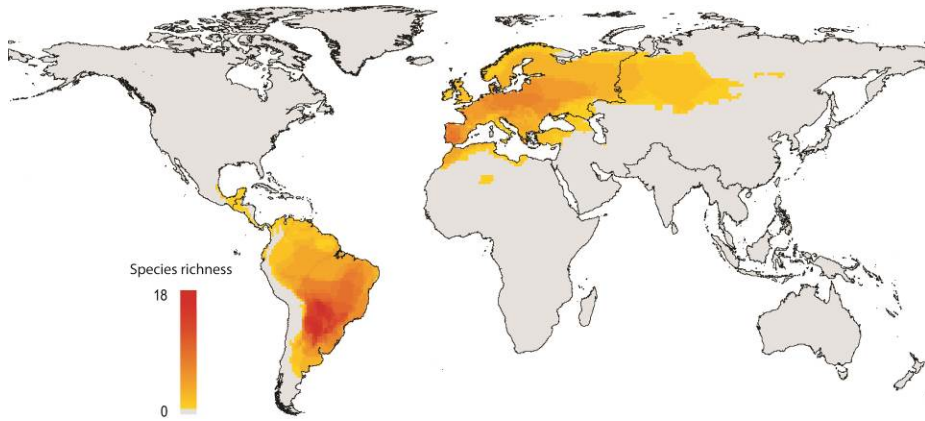
720 **SUPPLEMENTARY FIGURE LEGENDS**

721 **Figure S1.** Spatial distribution and local richness after overlapping the extent of
722 distribution of all 47 anurans onto a cells grid of $1^\circ \times 1^\circ$ resolution.

723 **Figure S2.** Interspecific variability of climatic niche traits (CT_{\max} ; T_{\max} ; T_{var} ; niche
724 position and niche breadth) among 47 anurans. Species are ordered alphabetically.

725 **Figure S3.** Non-ultrametric phylogeny for 47 anurans, after Frost (2006). Different
726 colours denote different families.

727 **Figure S1**

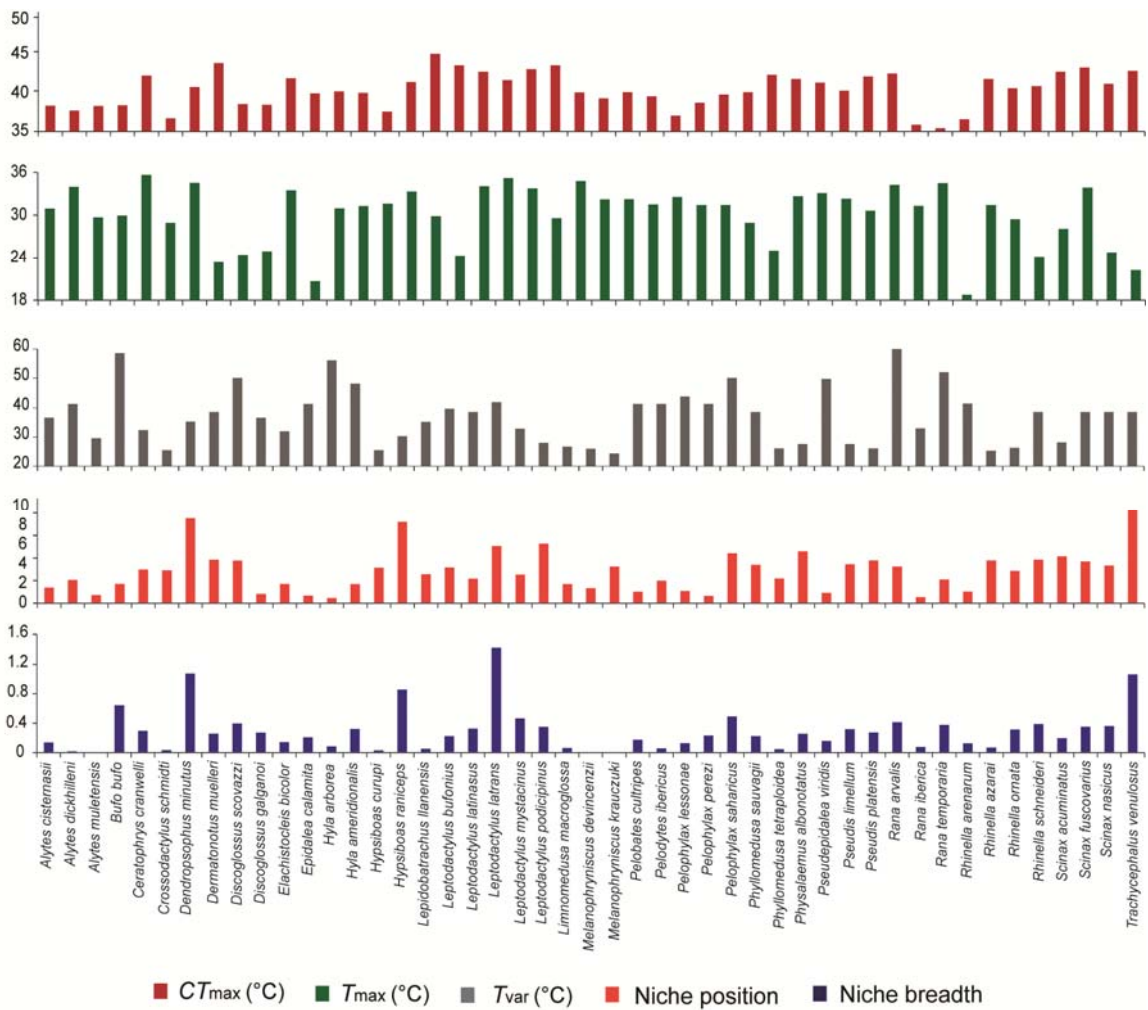


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730

731 **Figure S2**



732

733

