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

Sidney F. Gouveia^{1,2*}; Joaquín Hortal³; Miguel Tejedo⁴; Helder Duarte⁴; Fernanda A. S.
Cassemiro⁵; Carlos A. Navas⁶; José Alexandre F. Diniz-Filho¹

¹ *Departamento de Ecologia, ICB, Universidade Federal de Goiás, Cx.P. 131, 74001-970
Goiânia, GO, Brazil.*

² *Departamento de Ecologia, CCBS, Universidade Federal de Sergipe, Av. Marechal
Rondon s/n, 49100-000 São Cristóvão, SE, Brazil.*

³ *Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias
Naturales, CSIC, Madrid, Spain.*

⁴ *Departamento de Ecología Evolutiva, Estación Biológica de Doñana, CSIC, Seville,
Spain.*

⁵ *Systema Naturae - Consultoria Ambiental LTDA Goiânia, GO, Brazil.*

⁶ *Departamento de Fisiologia, Instituto de Biociências, Universidade de São Paulo, São
Paulo, SP, Brazil.*

* Author for correspondence. E-mail: sgouveia@ufs.br

Running title: Physiological and macroecological thermal niches.

Article type: Research paper

ABSTRACT

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

Location Neotropic and Palaearctic.

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

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

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

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

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

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

METHODS

Species Data

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

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

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

Physiological data

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

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

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

Macroecological data

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

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

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

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

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

Phylogenetic Comparative Analysis

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

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

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

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

RESULTS

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

CONCLUDING REMARKS

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

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

ACKNOWLEDGEMENTS

We thank Jorge Lobo, Raúl García Valdés, David Currie, Alberto Jiménez-Valverde and three anonymous reviewers for comments and suggestions; Regan Early and Ignacio Morales-Castilla for inviting SFG to express these ideas to enlightening audiences at the Museo Nacional de Ciencias Naturales de Madrid, and Universidad de Alcalá, Spain. SFG was supported by a CAPES doctoral internship abroad (PDSE 0278-12-2). JH was funded by a Spanish MICINN Ramón y Cajal grant and by the CSIC/CNPq cooperation grant P2011BR0071. MT was funded by Spanish AECID grants A/016892/08, A/023032/09 and the Spanish MICINN grant CGL2009-12767-C02-02. CAN was funded by the State of São Paulo Science Foundation grant PFPMCG/PRONEX 2008/57687-0, and JAFDF has been continuously supported by several CNPq and CAPES grants.

REFERENCES

- Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the National Academy of Sciences USA*, **267**, 739–745.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.
- Angilletta, M.J., Niewiarowski, P.E. & Navas, C.A. (2002) The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, **27**, 249–268.
- Bozinovic, F., Calosi, P. & Spicer, J.I. (2011) Physiological Correlates of Geographic Range in Animals. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 155–179.
- Buckley, L.B. (2010) The range implications of lizard traits in changing environments. *Global Ecology and Biogeography*, **19**, 452–464.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041–1054.
- Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C. & Atfield, A. (2010) What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, **79**, 194–204.
- Castañeda, L.E., Calabria, G., Betancourt, L.A., Rezende, E.L. & Santos, M. (2012) Measurement error in heat tolerance assays. *Journal of Thermal Biology*, **37**, 432–437.

- Chown, S.L. & Gaston, K.J. (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Review of the Cambridge Philosophical Society*, **74**, 87–120.
- Chown, S.L., Gaston, K.J. & Robinson, D. (2004) Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology*, **18**, 159–167.
- Clusella-Trullas, S., Blackburn, T.M. & Chown, S.L. (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, **177**, 738–51.
- Colwell, R.K. & Rangel, T.F.L.V.B. (2009) Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences USA*, **106**, 19651–19658.
- Cooper, N., Jetz, W. & Freckleton, R.P. (2010) Phylogenetic comparative approaches for studying niche conservatism. *Journal of Evolutionary Biology*, **23**, 2529–2539.
- Cowles, R.B. & Bogert, C.M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, **83**, 265–296.
- Diniz-Filho, J.A.F., Rangel, T.F., Santos, T. & Bini, L.M. (2012) Exploring Patterns of Interspecific Variation in Quantitative Traits Using Sequential Phylogenetic Eigenvector Regressions. *Evolution*, **66**, 1079–1090.
- Diniz-Filho, J.A.F., Sant'Ana, C.E.R. & Bini, L.M. (1998) An Eigenvector method for estimating phylogenetic inertia. *Evolution*, **52**, 1247–1262.
- Doledec, S., Chessel, D. & Gimaret-Carpentier, C. (2000) Niche separation in community analysis: a new method. *Ecology*, **81**, 2914–2927.
- Duarte, H., Tejedo, M., Katzenberger, M., Marangoni, F., Baldo, D., Beltrán, J.F., *et al.*, (2012) Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Global Change Biology*, **18**, 412–421.

- Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.
- Frost, D.R., Grant, T., Faivovich, J., Haddad, C.F.B., Bain, R.H., Haas, A., *et al.*, (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**, 1–370.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press. Oxford, UK.
- Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., *et al.*, (2009) Macrophysiology: a conceptual reunification. *The American Naturalist*, **174**, 595–612.
- Godsoe, W. (2010) I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. *Oikos*, **119**, 53–60.
- Guisan, A. & Zimmermann, N. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hijmans, R.J., Cameron, S.E. Parra, J.L. Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hof, C., Rahbek, C. & Araújo, M.B. (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, **32**, 242–250.
- Hoffmann, A.A., Chown, S.L. & Clusella-Trullas, S. (2012) Upper thermal limits in terrestrial ectotherms: how constrained are they? *Functional Ecology*, *in press*.
- Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2012) Basic questions in biogeography and the (lack of) simplicity of species distributions: Putting species distribution models in the right place. *Natureza & Conservação*, **10**, 108–118.

609 Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E. & Álvarez, H.J. (2009)
 610 Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the*
 611 *Royal Society B – Biological Sciences*, **276**, 1939–1948.
 612 Huey, R.B. & Kingsolver, J.G. (1993) Evolution of resistance to high temperature in
 613 ectotherms. *The American Naturalist*, **142**, 21–46.
 614 Huey, R.B. & Stevenson, R.D. (1979) Integrating thermal physiology and ecology of
 615 ectotherms: a discussion of approaches. *The American Zoologist*, **19**, 357–366.
 616 Hurlbert, A.H. & White, E.P. (2005) Disparity between range map- and survey-based
 617 analyses of species richness: patterns, processes and implications. *Ecology Letters*, **8**,
 618 319–327.
 619 Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harbor Symposium of*
 620 *Quantitative Biology*, **22**, 415–427.
 621 Hutchinson G.E. (1978) *An introduction to population biology*. Yale University Press,
 622 New Haven, CT.
 623 Hutchison, V.H. (1961) Critical thermal maximum in salamanders. *Physiological*
 624 *Zoology*, **43**, 92–125.
 625 IUCN (2009) *Global Amphibian Assessment*. Conservation International and
 626 NatureServe, Washington, DC. Available at: <http://www.globalamphibians.org>
 627 (accessed November 2010).
 628 Kearney, M.R. & Porter, W.P. (2009) Mechanistic niche modelling: combining
 629 physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–
 630 350.
 631 Kellermann, V., Overgaard, J., Hoffmann, A.A., Fløjgaard, C., Svenning, J.-C. &
 632 Loeschcke, V. (2012) Upper thermal limits of *Drosophila* are linked to species

distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences USA*, **109**: 16228–16233

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.

Lutterschmidt, W.I. & Hutchison, V.H. (1997a) The critical thermal maximum: data to support the onset of spasms as the definitive end point. *Canadian Journal of Zoology*, **75**, 1553–1560.

Lutterschmidt W.I. & Hutchison V.H. (1997b) The critical thermal maximum: history and critique. *Canadian Journal of Zoology*, **75**, 1561–1574.

Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T. & Yáñez-Arenas, C. (2013) Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, **9**, 1–5.

Olalla-Tárraga, M.Á., McInnes, L., Bini, L.M., Diniz-Filho, J.A.F., Fritz, S.A., Hawkins, B.A., *et al.*, (2011) Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *Journal of Biogeography*, **38**, 2237–2247.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends Ecology Evolution*, **23**, 149–158.

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

Ribeiro, P.L., Camacho, A. & Navas, C.A. (2012) Considerations for assessing maximum critical temperatures in small ectothermic animals: insights from leaf-cutting ants. *PloS one*, **7**, 1-7.

Roy, K., Hunt, G., Jablonski, D., Krug, A.Z. & Valentine, J.W. (2009) A macroevolutionary perspective on species range limits. *Proceedings of the Royal Society B – Biological Sciences*, **276**, 1485–1493.

Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.

Smith, A.B. (2012) The relative influence of temperature, moisture and their interaction on range limits of mammals over the past century. *Global Ecology and Biogeography*, **22**, 334–343.

Soberón J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.

Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**: 19644–19650.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2010) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B – Biological Sciences*, **278**, 1823–1830.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

682 Wiens, J.J. (2011) Re-evolution of lost mandibular teeth in frogs after more than 200
683 million years, and re-evaluating Dollo's law. *Evolution*, **65**, 1283–1296.

684 Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology, and species
685 richness. *Trends in Ecology and Evolution*, **19**, 639–644.

686 Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., *et*
687 *al.*, (2010) Niche conservatism as an emerging principle in ecology and conservation
688 biology. *Ecology Letters*, **13**, 1310–1324.

689 Willmott, C.J. & Matsuura K. (2001) *Terrestrial Water Budget Data Archive*: Monthly
690 Time Series (1950-1999). November, 2010, <<http://www.sage.wisc.edu>>.

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.

TABLES

Table 1. Phylogenetic Generalized Least Squares (PGLS) models between $CT_{\max}$ and macroecological niche traits. λ is the index that transforms the trait phylogeny to fit a 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

FIGURE CAPTIONS

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

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

714

715 **FIGURES**

716 **Figure 1**

717

SUPPLEMENTARY FIGURE LEGENDS

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

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

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

727 **Figure S1**

731 **Figure S2**