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# The origin and nature of macroecological patterns in amphibians: old questions, novel approaches

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**Abstract.** The role of physiological parameters as determinants of macroscale patterns is still widely disputed. Using amphibians as a model, I revisited three fundamental themes in macroecology from a physiological perspective: the global diversity gradient, ecogeographical rules and the evolution of the climatic niche at physiological and macroecological scales. To do this, I used a variety of data types, performed a number of spatial and phylogenetic analyses and proposed novel applications for some methods. I also provided support for some well-established hypotheses regarding the physiological determinants of species diversity and trait variation across space, while revealing other lesser known patterns and the possible processes underlying species' distributions and niche evolution. I emphasize the need for a novel integration of theoretical and methodological approaches to improve the analysis of broad-scale ecological processes, in particular those related to the fundamental features (e.g. physiology) of species. I also highlight the strategic role of macroecology in this quest, especially in the face of ongoing environmental changes.

**Keywords.** Anurans, comparative phylogenetic methods, diversity gradient, ecogeographical rules, macroecology, macrophysiology, niche evolution, spatial analyses

Studies of broad-scale ecological patterns precede the conception of ecology as a discipline (Haeckel 1866). Many still-debated questions emerged in the 18<sup>th</sup> and 19<sup>th</sup> centuries, when naturalists documented and speculated on the patterns and drivers of the distribution of the variety of plants and animals around the world (Egerton 2012). Some of these ideas were then addressed more systematically in the early 20<sup>th</sup> century (e.g. Grinnell 1917, Arrhenius 1921, Willis 1922), culminating in the establishment of some conceptual cornerstones of broad-scale ecology (Hutchinson 1957, Preston 1960, MacArthur 1972), which underpin current macroecological thinking.

Macroecology (*sensu* Brown and Maurer 1989) first focused on the distribution of spatial and energetic resources among species on coarse spatial and temporal scales. The primary aim was to understand biological patterns on continental and global scales, and links with species richness and abundance. A consequence of this broad approach would be the formulation of natural laws and the unifying principles underlying the struc-

ture and function of natural systems (Blackburn and Gaston 2002). Macroecology soon linked up with other broad-scale ecological fields, such as biogeography, geostatistics, palaeoecology, and phylogenetic methods (Kent 2005). This permitted the generalization and integration of data and concepts that were often unconnected in their individual fields (Brown 1999, Blackburn and Gaston 2001, Beck et al. 2012), and favoured the application of a variety of approaches and techniques that bolstered the available applications and potential for investigation (e.g. Elith et al. 2006, Pausas and Verdú 2010, Rangel et al. 2010). More integrative analytical tools were also developed, allowing macroecologists to revisit classical ecological questions from a number of fresh perspectives. Examples include the integration of distinct approaches, such as geographical information systems, computational modelling, molecular phylogenies, palaeoenvironmental reconstructions and morphological and physiological data (e.g. Chown et al. 2004, Harrison and Cornell 2007, Diniz-Filho and Bini 2011).

Currently, macroecological studies aim to go well beyond the simple documentation of biodiversity patterns by also targeting their underlying processes. Indeed, a number of fundamental questions in macroecology remain elusive. This is in part due to the need for the development of novel, integrated analyses, even though the paucity of some fundamental data on parameters (e.g. relative abundance of species, genetic variability, biotic interactions and physiological traits) also imposes a fundamental limitation on analyses. I therefore applied a set of recently developed tools for spatial and phylogenetic analysis to assess some traditional ecological questions at coarse spatial scales. The thesis addresses three topics: 1) global patterns of species diversity, 2) ecogeographical rules and 3) the evolution of climatic niches. I use amphibians as a model, whose ectothermic characteristics and sensitivity to environmental variation make them suitable for testing questions related to the geographic distribution of traits and the evolution of climatic tolerance, which are particularly controversial. The specific focus is on the ecophysiological properties that determine the clade's tolerance of climatic variability, and should thus influence its macroecological patterns. The thesis has three chapters.

### **Spatial non-stationarity in species–environment relationships**

The first chapter (Gouveia et al. 2013a) addresses the effects of spatial non-stationarity (i.e. spatial structure in statistical relationships) on the relationship between species richness and three variables representing likely climatic drivers of species richness on a global scale. I drew on the ecophysiological attributes of the amphibians to formulate predictions that accommodate spatial non-stationarity. For this, I estimated the within-cell (2° resolution) species richness, based on the geographical ranges of all amphibians (IUCN 2009), and tested it against three global layers of environmental data representing factors purported to affect amphibian biology (e.g. Buckley and Jetz 2007): i) temperature and precipitation anomalies between the Last Glacial Maximum and the pre-

sent, as a measure of historical climate variability, used to test whether climatic variability has had a negative effect on species richness; ii) temperature and precipitation seasonality, representing current climatic variability (Hijmans et al. 2005), which is also assumed to be inversely related to species richness; and iii) actual evapotranspiration, as a proxy for environmental productivity (Willmott and Matsuura 2001), which is assumed to have a positive effect on species richness.

I first ran global ordinary least squares (OLS) models, and OLS that included spatial filters calculated through spatial eigenvector mapping (SEVM; Diniz-Filho and Bini 2005) to account for spatial autocorrelation. These global OLS and SEVM models were adopted as standards for comparison with the subsequent local analyses, which were based on geographically weighted regressions (GWR) for each species richness–climate relationship, accommodating spatial non-stationarity on a regional scale. I also ran a modified GWR (referred to as partial-GWR) to calculate partial coefficients, which provided the individual and shared effects of each predictor within each grid cell (see Gouveia et al. 2013a).

Despite the pervasive spatial non-stationarity in all species richness–climate relationships, the positive effects of productivity on species richness outweighed those of seasonality and historical variability in both global and regional models. Geographical variation in the dominance of productivity, relative to the other factors, was also evident, being stronger across most of Americas, the Palaeartic realm and Australia, where most of the extant species are found. Nevertheless, extensive overlap was found between pairs of predictors, indicating a substantial amount of collinearity between environmental factors. This means that the effects of each predictor could not be separated over large areas, although individual signals were sufficient to define the factors prevailing in most regions of the planet.

### **Unveiling the drivers of ecogeographical rules**

For the second chapter (Gouveia et al. 2013b), I combined information on the body size, geo-

graphic distribution and a phylogeny of Neotropical glassfrogs (Anura, Centrolenidae) to evaluate the adherence of the species to Bergmann's and Rapoport's rules—that is, the tendency for closely related lineages (e.g. species) to have larger body sizes or geographical ranges, respectively, at lower temperatures (across latitude and elevation, for example). I tested these hypotheses while compensating for spatial and phylogenetic autocorrelation in the data, and partitioned the latitudinal and altitudinal distribution of the species as an indirect measure of interspecific variability in thermal tolerance, in order to assess the main prediction of Bergmann's rule. I gathered data on body size, range size and altitudinal ranges for all 148 known glassfrog species (see Gouveia et al. 2013b).

I first mapped the species' distributions onto a 0.5°-resolution grid. I also constructed a complete phylogeny of the centrolenids based on a published classification (Guayasamin et al. 2009), into which I inserted missing species as polytomies, following generic and infrageneric grouping. In order to account for the phylogenetic autocorrelation in species' traits, I partitioned the body size data into phylogenetic and specific components through a phylogenetic eigenvector regression (PVR; Diniz-Filho et al. 1998). I then mapped body size and its phylogenetic and specific components for every species as a means of compensating for spatial autocorrelation. I adopted an 'assemblage-based approach', which uses individual grid cells as sampling units for the correlative analyses (see Diniz-Filho et al. 2009). I also decomposed the spatial distribution of the species' vertical and horizontal ranges (through a reduced major axis regression) into an estimate of the interspecific variability in tolerance. This procedure enabled me to test the 'heat balance hypothesis' (Olalla-Tárraga and Rodríguez 2007), which predicts a positive correlation between the body size of species (and the specific component of PVR) and its thermal tolerance (or a proxy thereof). I also tested three competing explanations of the body-size cline, namely temperature variability, aridity and productivity, all of which are supposed to affect body size positively

(Blackburn et al. 1999). Finally, I tested the adherence of the glassfrogs to Rapoport's rule, which predicts a negative correlation between range sizes and temperature. Both patterns were tested along latitudinal and altitudinal gradients.

I found that glassfrogs conform to Bergmann's rule along the altitudinal gradient (in particular in the Andean region). Larger-bodied species are also more tolerant to the cold, supporting the most recent proposal for the mechanism underlying Bergmann's rule, i.e. the heat balance hypothesis. The pattern is seen most clearly in the Andean region, with strong evidence of an historical association between the Andean uplift and the increase in body size. In contrast, no significant relationships were found between species range sizes and temperature.

### **Transferability and evolution of climatic niches at multiple scales**

In the third chapter (Gouveia et al. 2014), I tested the hypothesis that the climatic niche at a physiological level is more closely related, in terms of its variability and evolutionary rates, to a positional measure of the niche than to its boundaries on a macroecological scale. The analysis was based on the larval critical thermal maxima, or  $CT_{max}$ , of 47 species of Neotropical and Palaearctic anurans (Duarte et al. 2012), a set of macroscale climatic variables for the known species' ranges—geographic maximum temperature ( $T_{max}$ ) and variability ( $T_{var}$ )—and the position and breadth of the niches within the climatic hyperspace of each species. These latter were calculated through the 'outlying mean index' multivariate technique (Doledec et al. 2000), which describes a hypervolume of the species' niche based on the input variables. The resulting parameters include a niche breadth (the hypervolume), the niche overlap among species, and the position relative to a theoretical, average niche (the niche marginality). I then tested the relationships between physiological and macroecological features of the climatic niche with non-phylogenetic (OLS) and phylogenetic (Freckleton et al. 2002) regressions. Finally, I compared the evolutionary rates of physiological and macroecological niche components

across the phylogeny using a phylogenetic signal representation curve approach (Diniz-Filho et al. 2012).

Physiological limitations (i.e.  $CT_{max}$ ) predict the position of the niche better than other macroecological parameters. In addition, the  $CT_{max}$  and macroecological niche position present similar rates of evolutionary change, i.e. they evolve faster than Brownian motion, contrary to  $T_{max}$  and  $T_{var}$ , which evolve more slowly, or niche breadth, which evolves at random. The implications of these findings are striking: the physiological limits of a species may be completely unrelated to the limits of its geographical range, which implies that inferences on the evolution of niche limits may be erroneous if they are based on the climatic limits of geographic ranges.

### Convergent findings

Each of these three studies demonstrates how macroscale biodiversity—such as species diversity and biogeography, and the evolution of climatic niches—are related to basic biological processes, such as the physiology of the organisms. There were also common themes. For example, the first and second studies both demonstrated the effects of the duration and magnitude of macroclimatic changes on patterns of adaptability and clade diversity across environmental gradients. Similarly, the second and third studies showed that the size of a species' geographic range is not necessarily determined by its tolerance of environmental conditions on a large spatial scale, but rather by factors such as biotic interactions and limitations to dispersal, which can affect the distribution of a given species group, to a greater or lesser extent. Perhaps more importantly, the studies found that the evolutionary rates of niche characteristics that are calculated based on the limits of the climatic space may differ considerably from evolutionary rates based on the centroid of the climatic space. This has important implications for the evaluation of the evolutionary patterns of climatic niches.

The results raise some important questions for macroecology in general, and in particular in relation to problems of inference and the detectability of ecological patterns, which are crucial for

progress in each area of study (diversity gradients, ecogeographical rules and niche evolution). For example, the first chapter emphasizes that inferences on the global drivers of diversity gradients are strongly structured on regional to continental scales, implying a major compromise between generality and precision in the construction and interpretation of ecological models (Gouveia et al. 2013a). The third chapter pointed out that the evolutionary rates of niche traits derived from either the central position or the boundaries of a species' distribution in terms of climatic space can be quite divergent, leading to divergent inferences on the evolutionary model of the climatic niche of a species. This problem is especially relevant in that it may mislead conclusions on the evolution or conservatism of species' niches—a major current topic in macroecology (Gouveia et al. 2014). The second chapter indicates that the conformity of a clade to a given ecogeographical rule may depend on an environmental gradient steep enough to prevent the asymmetry in biological traits being counteracted by other factors (e.g. dispersal). This finding is relevant considering our incomplete understanding of the ecological and evolutionary forces underlying geographical gradients in biological and ecological traits (Blackburn et al. 1999; Gouveia et al. 2013b).

### Conclusions

Many central questions in macroecology rely on conjectures about the influence of fundamental parameters (e.g. biophysical and biochemical characteristics) of the individual (Chown et al. 2004, Gaston et al. 2009). However, most of these parameters are unavailable at a macroecological level (Gaston et al. 2009). In this thesis, I conducted specific analyses that aimed to provide insights into the integration of phenomena at fundamental levels and their consequences on a macroscale. This approach required the integration of various techniques derived from macroecology, biogeography, spatial analysis, comparative phylogenetic methods and ecophysiology. The data were derived from either direct measures of the fundamental features of each species (e.g. thermal tolerance in the third chapter) or from infer-

ences (in the second chapter) and theoretical assumptions (in the first chapter), based on the known physiological characteristics of each species. While more reliable data and additional analytical approaches are clearly needed, I conclude that a reliable assessment of a number of fundamental ecological questions can be provided by combining existing tools and approaches. Ongoing environmental changes reinforce the need to understand these processes at all levels of organization. In this sense, physiological traits were shown to play an essential role in the determination of species' limits and requirements, and consequently in their patterns of abundance, distribution and diversity (Gaston et al. 2009). Overall, my primary recommendation is to encourage the combination of distinct methods and approaches (e.g. from local to global, from current to deeper evolutionary time scales) in order to reliably address the many fundamental and still unanswered questions in macroecology, in particular those related to the ability of species and assemblages to cope with the changing environment.

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### References

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, 9, 95–99.

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., et al. (2012) What's on the horizon for macroecology? *Ecography*, 35, 673–683.

Blackburn, T.M. & Gaston, K.J. (2002) Macroecology is distinct from biogeography. *Nature*, 418, 723.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, 5, 165–174.

Brown, J.H. (1999) Macroecology: progress and prospect. *Oikos*, 87, 3–14.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, 243, 1145–1150.

Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B*, 274, 1167–73.

Chown, S.L., Gaston, K.J. & Robinson, D. (2004) Macrophysiology: large-scale patterns in physiological. *Functional Ecology*, 18, 159–167.

Diniz-Filho, J.A.F. & Bini, L.M. (2011) Geographical patterns in biodiversity: towards an integration of concepts and methods from genes to species diversity. *Natureza e Conservação*, 9, 179–187.

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., Martí, D.A., Richter-Boix, A. & Gonzalez-Voyer, A. (2012) Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Global Change Biology*, 18, 412–421.

Egerton, F.N. (2012) *Roots of ecology: antiquity to Haeckel*. University of California Press, Berkeley.

Elith, J., Graham, C.H., Anderson, R.P., et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.

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.

Gaston, K.J., Chown, S.L., Calosi, P., et al. (2009) Macrophysiology: a conceptual reunification. *The American Naturalist*, 174, 595–612.

Gouveia, S.F., Hortal, J., Cassemiro, F.A.S., Rangel, T.F. & Diniz-Filho, J.A.F. (2013a) Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography*, 36, 104–113.

Gouveia, S.F., Dobrovolski, R., Lemes, P., Cassemiro, F.A.S. & Diniz-Filho, J.A.F. (2013b) Environmental steepness, tolerance gradient, and ecogeographical rules in glassfrogs (Anura: Centrolenidae). *Biological Journal of the Linnean Society*, 108, 773–783.

Gouveia, S.F., Hortal, J., Tejedo, M., Duarte, H., Cassemiro, F.A.S., Navas, C.A. & Diniz-Filho, J.A.F. (2014) Climatic niche at physiological and macroecological scales: thermal tolerance–geographic range interface and niche dimensionality. *Global Ecology and Biogeography*, 23, doi: 10.1111/geb.12114.

Grinnell, J. (1917) The niche-relationships of the California Thrasher. *Auk*, 34, 427–433.

Guayasamin, J.M., Castroviejo-fisher, S., Trueb, L., Ayarzagüena, J., Rada, M. & Vilà, C. (2009) Phylogenetic systematics of Glassfrogs (Amphibia: Centrolenidae) and their sister taxon *Allophryne ruthveni*. *Zootaxa*, 2100, 1–97.

Haeckel, E. (1866) *Generelle Morphologie der Organismen, Erster Band*. Druck und Verlag von Georg Reimer,

- Berlin.
- Harrison, S.P. & Cornell, H.V. (2007) Introduction: merging evolutionary and ecological approaches to understanding geographic gradients in species richness. *The American Naturalist*, 170, S1–S4.
- 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.
- Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.
- IUCN 2009. Global Amphibian Assessment. Conservation International and NatureServe. Available at [www.globalamphibians.org](http://www.globalamphibians.org) (accessed November 2010).
- Kent, M. (2005) Biogeography and macroecology. *Progress in Physical Geography*, 29, 256–264.
- MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. New York: Harper and Row.
- Olalla-Tárraga, M.Á. & Rodríguez, M.Á. (2007) Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography*, 16, 606–617.
- Pausas, J.G. & Verdú, M. (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, 60, 614–625.
- Preston, F.W. (1960) Time and space and the variation of species. *Ecology* 41, 612–627.
- Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography*, 33, 46–50.
- Willis, J.C. (1922) *Age and area*. Cambridge University Press, Cambridge, UK.
- Willmott, C.J. & Matsuura, K. (2001) Terrestrial water budget data archive: monthly time series (1950–1999). University of Delaware, Newark, DE. Available at <http://www.sage.wisc.edu/atlas/maps.php?datasetid=58&includerelatedlinks=1&dataset=58> (accessed March 2012).

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