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Title
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Permalink
https://escholarship.org/uc/item/6vd1m8qk

Journal
Frontiers of Biogeography, 9(2)

Author
Moura, Mario R

Publication Date
2017

DOI
10.21425/F59233210

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Thesis Abstract

Assessing the synergism among environmental gradients: Towards a better understanding of macroecological hypotheses

Mario Ribeiro Moura[1,2]

[1]Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Zoologia. Avenida Antônio Carlos, 6627, Pampulha. 31270-901. Belo Horizonte, MG, Brazil.

[2]Yale University, Department of Ecology and Evolutionary Biology. 165 Prospect St. 06511. New Haven, CT, USA.

mariormoura@gmail.com

Abstract. The role of environmental gradients as drivers of biological diversity has been the center of many discussions in ecology and evolution. Hypotheses proposed to explain broad-scale patterns of biological diversity have mechanistic bases that often overlap, at least partially. Consequently, it is often difficult to tease apart the potential effects of different hypotheses. Here I investigate the synergism among macroecological hypotheses commonly invoked to explain species diversity. More specifically, I address the role of ambient-energy, climatic stability, habitat heterogeneity, productivity, and topographic complexity in shaping broad-scale patterns of tropical vertebrates under three different aspects of biological diversity: species richness, species pools, and species composition. I show how differences in the degree of synergism among distinct types of environmental gradients can be used to improve our understanding of traditional macroecological hypotheses, highlighting the convergent findings across the three different aspects of biological diversity.

Keywords: ambient-energy, climatic stability, habitat heterogeneity, productivity, species richness, species composition, topography, vertebrates

Introduction

The impact of anthropogenic factors in changing the environmental conditions of the planet has reached unprecedented levels (Lewis and Maslin 2015). Humans have already modified as much as 50% of the terrestrial land cover (Reid et al. 2005). The intensification of human activities around the planet has increased global temperatures at least 1°C over the last century with consequences in the acceleration of global sea level rise and changes in climatological regimes (Hansen et al. 2006, Rahmstorf 2007). The biological diversity on Earth does not necessarily respond in similar ways to changes in different environmental conditions. Since climate, topography, and vegetation are naturally related to each other, changes in a given environmental gradient can influence how species respond to other types of gradients (Stein et al.

2014). Indeed, many ecological hypotheses invoked to explain patterns of animal diversity rely on synergistic associations among environmental gradients. For instance, the interplay between water-availability and energy-input is often associated with the productivity hypothesis, which assumes that the increase of energy flow through food chains ultimately affect species distribution (Wright 1983). Under the ambient-energy hypothesis, species distribution is constrained by physiological needs related to current climate or through the synergism between climate and topography (Ruggiero and Hawkins 2008). Moreover, changes in elevation are commonly associated to variation in vegetation, which forms the basis of the habitat heterogeneity hypothesis (Stein et al. 2014). Assessing the synergistic associations among environmental gradients can help elucidate potential

outcomes of global climate and land use changes on biodiversity.

Here, I investigate how the synergism among environmental gradients explains the variation in three different aspects of biological diversity: (i) species richness, (ii) species pools, and (iii) species composition. By species richness I refer to the sum of all species occurring in a given area or region. Species pools is used in a biogeographical context and defines the pool of species that potentially co-occur in assembling a given community (Carstensen et al. 2013). The changes in species composition can be translated as variation in community structure among a set of assemblages, also known as non-directional beta-diversity (Anderson et al. 2011). Each of those aspects of biological diversity is covered individually by Moura (2016), and here I seek integration. First, I explore preexisting biodiversity datasets (expert range maps) and recently developed environmental datasets to elucidate the role of climate, topography, and vegetation on species richness patterns of Neotropical vertebrates. Second, I explore contemporary and historical correlates of biogeographical species pools (henceforth, 'species pools'). It should be noticed that species pools defined using expert range maps may be geographically too broad and include species that would never co-occur in local communities (Carstensen et al. 2013). To alleviate this concern, I gather fine-scale information on local species composition of a major ectothermic clade, snakes, for the second largest rain forest of South America, the Atlantic Forest biodiversity hotspot. In doing so, I propose biogeographical subregions for an underinvestigated group and improve the potential applicability of my findings to the regional conservation planning of this biodiversity hotspot. Finally, third, I investigate how community species composition responds to environmental conditions. More specifically, I address the synergistic associations among topography, thermal, and water-related factors in structuring assemblages of tropical forest snakes under distinct climatological regimes. Overall, I address the influence of environmental gradients on (i) species richness, (ii) species pools, and (iii) species composition of one or more vertebrate group.

Species richness and the synergistic associations among environmental gradients

Moura et al. (2016) addressed the relative influence of climate, topography, and vegetation as broad-scale drivers of species richness of amphibians, non-volant mammals, bats, and birds in the Neotropics. I address the synergism among these three general categories of environmental gradients and trace a parallel of the synergistic associations with three major macroecological hypotheses invoked to explain broad-scale gradients of species richness: ambient-energy, productivity, and habitat heterogeneity. I further make a quantitative comparison of such synergistic effects across groups with distinct dispersal ability and hypothesize that climatic factors would better explain the species richness of the most vagile groups whereas topographic factors would be more important to poorer dispersers.

I first obtained the species richness of each vertebrate group using a grid cell of 1º × 1º (ca. 110 × 110 km at the equator) based on expert range maps (BirdLifeInternational and NatureServe 2014, IUCN 2015). I extracted variables related to climate (mean annual temperature, annual precipitation, and annual ranges in temperature and precipitation) and topography (mean elevation, elevational range and roughness) from WorldClim (Hijmans et al. 2005), in addition to vegetation-related variables (land cover diversity, standard deviation and range of forest canopy height) from Latham et al. (2014) and Simard et al. (2011). I applied ordinary least square regressions (OLS) and variation partitioning (Borcard et al. 1992) to disentangle the contribution of each gradient type in explaining species richness of each vertebrate group. To account for the spatial structure in species richness, I used spatial eigenvector filtering analysis (spatial filters; Griffith and Peres-Neto 2006) to control for autocorrelation in OLS model residuals. Herein, the shared contribution between different environmental gradients (combinations of climate, topography, and vegetation gradients) in explaining the variation in species richness is regarded as a quantitative measure of the synergistic association among such environmental gradients (Prunier et al. 2015).
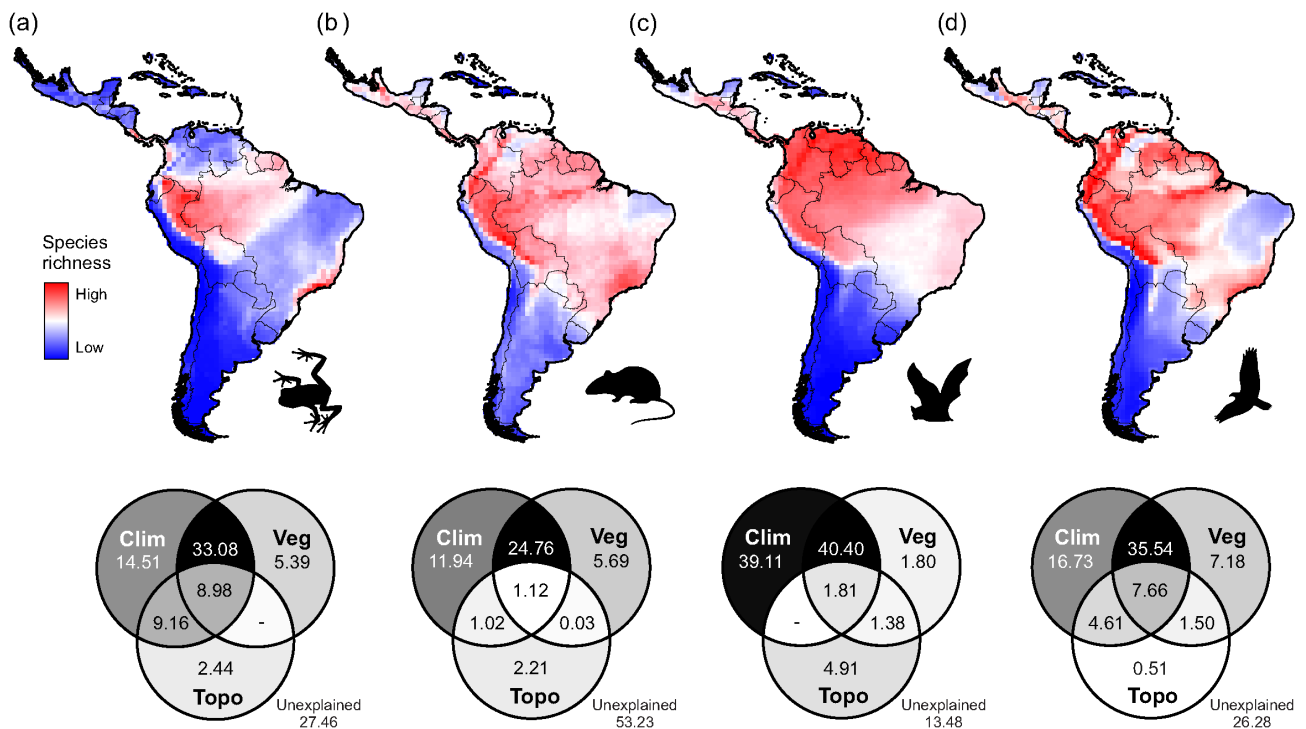
Figure 1. Patterns of Neotropical species richness for (a) amphibians, (b) non-volant mammals, (c) bats, and (d) birds. The Venn diagrams at the bottom show the variation partitioning of species richness according to gradients related to climate (Clim), topography (Topo), and vegetation (Veg). The light-dark colour gradient of the Venn diagrams represents the low-high variation explained by the predictor sets. For simplicity, the spatial predictor set is not shown in the Venn diagrams, but see Moura et al. (2016) for further details.

Overall, vertebrate richness was mostly driven by the synergism between climate and vegetation, reinforcing the role of productivity in explaining broad-scale patterns of vertebrate richness (Fig. 1). Climate was more important to good dispersers, particularly bats. The species richness of amphibians and non-volant mammals (relatively poor dispersers in comparison to bats and birds) presented a stronger spatial structure, corroborating the importance of limited dispersal in explaining cohesive structure of species richness gradients in less vagile groups (Padial et al. 2014). Even so, the dispersal ability showed a limited influence on vertebrate' responses to different gradients, probably due to the use of vertebrate groups with distinct morpho-physiology. Interestingly, topography and vegetation presented a weak synergistic association, suggesting caution in using topographic complexity as a surrogate of habitat (vegetation) heterogeneity, at least at the scale of this study (i.e. grid cells of 1º × 1º latitude-longitude).

Historical and contemporary drivers of species pools

Moura et al. (2017a) explored the geographical organization in one of the most neglected vertebrate groups, the reptiles. In contrast to other terrestrial vertebrates, the representation of reptile species in online datasets is scarce. Thus, I compiled a literature-based dataset on 3606 species occurrence records of snakes distributed across 218 local assemblages in the Atlantic Forest hotspot (Fig. 2). Then I ask which ecological and historical factors explain the species pools of snakes as estimated from compositional dissimilarity between assemblages.

For this, I used unconstrained ordination techniques coupled with interpolation methods to produce a spatially cohesive representation of the snake compositional dissimilarity over the Atlantic Forest. I applied non-hierarchical clustering techniques to classify the compositional dissimilarity into a number of species pools (categorical variable with multi-levels) established a priori. I used
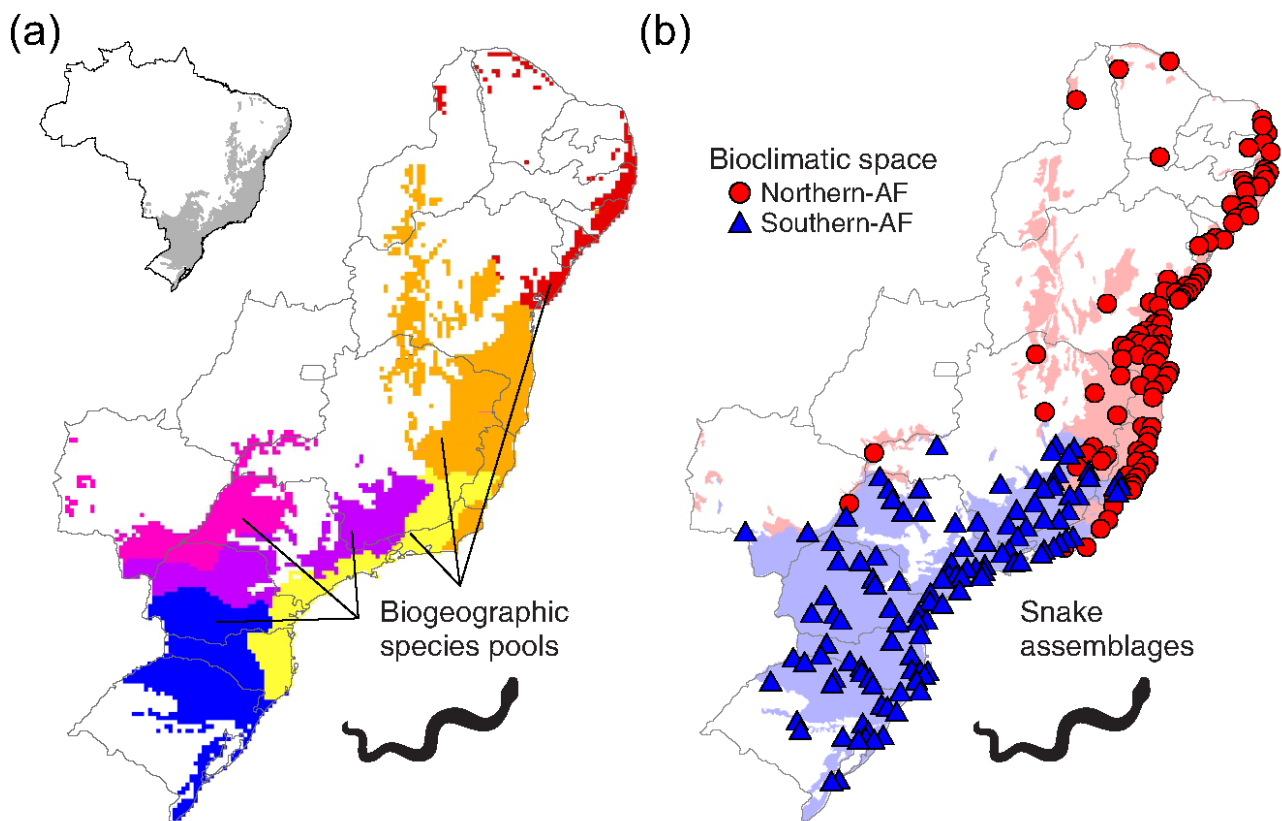
Figure 2. (a) Regionalization of Atlantic Forest (AF) snakes into six biogeographical species pools and (b) the distribution of snake assemblages according to climatological regimes of northern-AF and southern-AF. Gray lines in (a) and (b) denote borders of the Brazilian states while the inset map shows the boundaries of AF in Brazil.

multinomial logistic models in concert with deviance partitioning techniques to explore the contributions of climatic stability, productivity, topographic complexity, and historical variation in climate in explaining the species pools of snakes.

Overall, I detected six biogeographical species pools (BSP) for snakes in the Atlantic Forest (Fig. 2a). The three coastal snake BSP were largely congruent with BSP and areas of endemism of other vertebrates, such as amphibians (Vasconcelos et al. 2014), mammals (Costa et al. 2000) and birds (Silva et al. 2004). The variability in BSP was explained mostly by the climatic stability and productivity. Interestingly, topographic complexity was effective in explaining snake BSP only if historical variation in climate was dropped from the models, suggesting that topographic gradients along this tropical forest actually reflect a historical legacy of Quaternary climate change. The substantial influence of Quaternary climate on the contemporaneous species pools reinforces the view that poor dispersers might be less able to track suitable climatic conditions over time (Araújo et al. 2008), suggesting a high susceptibility of this ectothermic group to changing climate.

Environmental drivers of species composition

In tropical regions, ectotherms need to rely on thermoregulatory behaviour to achieve cooler temperatures and avoid overheating (Huey et al. 2009). The ability of ectotherms to buffer thermoregulatory constraints is highly affected by their hydration status (Kearney et al. 2013). Thus, ectotherms experiencing concurrent warm and dry conditions might be less able to cope with extreme heat than those occurring at warm and humid conditions. Moura (2017b), investigated the equilibrium of snake assemblages with environmental conditions in tropical forests with different climatological regimes. Unlike other tropical forests, the variation in climatic stability in the Atlantic Forest (AF) is such that modern patterns of humid air circulation show two distinct climatological

regimes within this tropical forest, with dry summers in its northern part and rainy summers in the south (Grimm 2003). This scenario creates a singular opportunity to investigate the influence of climatological regimes on species composition of tropical forest ectotherms. I hypothesize that tropical snake assemblages in regions with rainy summers would present greater equilibrium with environment than those assemblages experiencing dry summers. Moreover, if thermoregulatory needs are a major mechanism determining ectotherms' responses to environmental conditions, the synergism between thermal and water-related conditions would emerge as the main factor explaining the differences between ectothermic assemblages' responses in northern- and Southern-AF.

I used unconstrained ordination and clustering analyses to classify the bioclimatic space within the AF into two climatological units that represent forests with dry summers and rainy winters (northern-AF) and forests with rainy summers and dry winters (southern-AF, Fig. 2b). I used a dissimilarity matrix across assemblages, based on Simpson Index, to represent snake beta-diversity for the whole AF, northern-AF, and southern-AF. I obtained environmental variables from WorldClim (Hijmans et al. 2005) and group them into predictor sets related to thermal (temperature of the warmest quarter, temperature seasonality), water (precipitation of the warmest quarter, precipitation seasonality), and topographic (elevational range and roughness) conditions. To account for spatially structured processes, I used distance-based Moran's eigenvector map analysis (Legendre et al. 2015) to build a set of spatial predictors (spatial filters). I used multiresponse permutational tests (McArdle and Anderson 2001) in concert with variation partitioning to disentangle the influence of these distinct predictor sets in explaining snake beta-diversity in the whole AF, northern-AF and southern-AF.

The structure of snake assemblages was more affected by environmental conditions in forests with rainy summers/dry winters than in forests with dry summers/rainy winters. As expected, the synergism between thermal and water-related conditions emerged as key cause behind this difference. The total contribution of spatial filters was similar for snake assemblages from both northern- and southern-AF, regardless of the climatological regimes. These findings points out that the balance in thermo-hydric conditions might affect ectothermic assemblages' response to environment. The use of climatic measures averaged over the year increases the probability of misleading in the inference of underlying processes that maintain ectothermic populations. Overall, this study highlights that even within tropical forests, significant differences in climatological regimes can determine the sensitivity of ectotherm assemblages to climate change.

Conclusions

Broad-scale patterns of species richness, species pools, and species composition are affected by environmental gradients. Of particular interest are the synergistic associations between distinct types of environmental gradients, particularly those representing climatic stability, solar energy-input and water-availability. Although these climatic gradients are commonly used to represent the 'current climate', it is worth noting that mechanistic bases underlying variability and availability in particular climatic conditions are not the same (Fine 2015). On the one hand, water-availability and energy-input are often associated with the productivity hypothesis, which is translated as the increase of energy flow through food chains leading to an increase of populations, and thereby reduction of extinction rates (Wright 1983). On the other hand, the climatic stability hypothesis relies on the decrease of extinction rates under stable conditions, which, given enough time, may promote specialization and increase speciation rates (Pianka 1966, Evans et al. 2005). In splitting the role of current climate in separate measures of water-energy availability and climatic variability, I found greater influence of contemporary climatic stability in explaining variation in the species pools and species composition, which is in line with factors determining terrestrial and marine global patterns of species richness (Fine 2015).

I have also explored an additional interpretation to the role of water-availability and energy-

input in structuring ecological communities. Measures of energy, such as potential evapotranspiration, mean annual temperature, and solar radiation, have been traditionally used to investigate the ambient-energy hypothesis in which physiological requirements ultimately determine an organism distribution (Hawkins et al. 2003), shaping therefore the patterns of species richness, species pools, and/or species composition. Alternatively, in using measures of water-energy (e.g., actual evapotranspiration, net primary productivity, or even mean annual temperature in concert with annual precipitation), the hypothesis under investigation changes to productivity, whose assumption relies on the conversion of water-energy in food resources by plants and the subsequent increase of energy flow through food chains (Wright 1983). The findings herein reported shift the view of the productivity hypothesis in showing that the simultaneous influence of solar energy-input and water-related conditions may also determine thermoregulatory constraints for ectotherms. By thermoregulatory constraints I refer not only to the influence of solar energy-input but also to the importance of water-availability to buffer unfavorable conditions in climate, principally in the tropics where the rule is staying cool (Kearney et al. 2009). Consequently, the mechanistic base of the productivity hypothesis (energy flow through trophic cascades) would not entirely hold for tropical ectotherms.

In conclusion, several ecological and evolutionary hypotheses have been proposed to explain patterns of biological diversity (see Fine, 2015 for a recent review). Although originally thought to explain to species richness patterns, the underlying mechanisms of many of these hypotheses are applicable to the level of species distribution. It is not unexpected therefore to find convergent results on the role of environmental gradients in shaping broad-scale patterns of species richness, species pools, and species composition. It can be difficult to isolate the potential effects of underlying mechanisms of different hypotheses; however, I encourage future research to explore the synergism among environmental gradients as a way to improve our understanding of several non-

mutually exclusive hypotheses in ecology and evolution.

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