REVISITING GLOBAL ENDEMISM PATTERNS OF TERRESTRIAL VERTEBRATES AND THEIR ENVIRONMENTAL PREDICTORS: PUTTING THE FOCUS ON SPECIES RANGE-RESTRICTIONS AT FINE SPATIAL GRAINS

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Abstract

Global endemism assessments at fine spatial grains can offer many information about the endemic species richness that inhabit an area, but unable to provide insights on to what extent species distribution ranges are restricted to that area. This inability to account for species range-restrictions prevents recognizing the level of species uniqueness to particular sites, which is necessary to both understand the processes involved in the maintenance of endemism patterns and effectively conserve worldwide biodiversity. To circumvent this problem, the research proposes to use an index capable of measuring the proportion of species restricted to small spatial units. Using species range maps of terrestrial vertebrates, it was assessed global endemism patterns based on species range-restrictions as a counter position to the common use of species richness. Furthermore, it has been evaluated the role that different environmental variables have as predictors of these patterns through simultaneous autoregressive regression. Results showed the highest reported congruence among vertebrate endemism patterns, which suggest the influence of similar processes that affect species range-restrictions through space. Environmental variables explained more than 68% of the total variance on vertebrate endemism, so it is discussed their role as factors that promote species range-restrictions by limiting organism geographic distributions.

Keywords*: Uniqueness; Irreplaceable; Species geographic range; Species conservation; Endemicity*

Introduction

The assessments of global endemism patterns allow identifying the spatial concentration of species with geographic ranges restricted to particular areas of the World [1]. These assessments are useful in quantifying levels of biological uniqueness in specific regions by providing information of species only found in the focal region [2-4]. Taking into account the literature on this issue, it is possible to note that information on biological uniqueness is only provided in studies developed at coarse spatial grains, such as countries, ecoregions or continents; where the number of species restricted to these large areas is relatively straightforward to be counted [5-9]. However, the ability of global endemism patterns to inform on biological uniqueness becomes more problematic when these assessments are developed at finer spatial grains.

Most of the studies on global endemism patterns at grain sizes of 100km², 10000km² or 40000km² [3, 10-12], were unable to inform to what extent the species distribution ranges were restricted to those areas [13]. This inability to account for levels of biological uniqueness was mainly caused by the use of a different definition of what an endemic species is. These studies considered as endemic those species whose distribution ranges were smaller than a threshold area arbitrarily determined by the researchers (e.g., 50000km² [2] or 250000km² [3]). Because the threshold areas used to define the endemic species were often larger than the grain sizes at

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which endemism patterns were assessed, these patterns reported on endemic species richness by unit of area [3].

The lack of information on biological uniqueness at fine grain sizes is problematic to understand the processes involved in the maintenance of global endemism patterns. This is because, the absence of this information obscure recognizing which factors are limiting species dispersion to other areas [14]. In addition, it is also problematic for the effective protection of species at small spatial scales, because ignoring biological uniqueness leads to miss the most used measure to prioritize areas for biodiversity conservation [4]. Even more, when global endemism was represented from endemicity measures that considered species spatial restrictions, it was reported the highest congruence among these patterns for different organism groups [6, 13].

A useful alternative to circumvent these problems is to use an index capable of measuring the proportion of species restricted to relatively small cells in a gridded map [15, 16]. This index, that is considered a measure of relative endemism [17], takes values between 0 and 1 and can be interpreted as the average per-species range-restriction to a cell. For example, a cell with index score of 0.8 means that, on average, 80% of the species occurring in a cell are restricted to that cell [18]. Contrary to the measure of endemic species richness by cells, this index does not consider a threshold to select for endemic species because it uses available information on species range-sizes. Endemism assessments based on this index have not yet been reported at global scales.

An important advantage of considering endemism patterns based on this index is to test most of the range limitation hypotheses. In this sense, several hypotheses were postulated to account for the role of environmental variables as factors that limit species distributions (see Table 1 for a list of current hypotheses). For example, the solar energy hypothesis, which posits that high temperature limits species geographic ranges because organisms can physiologically tolerate warmer climatic conditions [19]. According to the prediction of this hypothesis, it is expected to be greater endemism in warm than cold geographic areas [20]. Specifically, the role of the environment as determinants of global endemism patterns that consider species range-restrictions have not been comprehensively assessed at small spatial grains.

Table 1. General hypotheses postulated to relate environmental variables as factors that promote endemism patterns by limiting species distributions.

Hypothesis	Argument	Prediction	Reference	Hypothesis
Solar energy	Organisms physiologically can tolerate more warm climatic conditions	Greater endemism in warm than cold areas	Evans *et al.* (2005)	Solar energy
Solar energy stability	Organisms are not physiologically adapted to overcome more seasonality	Greater endemism in low than high temperature seasonality areas	Carrara and Vázquez (2010)	Solar energy stability
Productivity	Organisms can tolerate more conditions of high resources availability to consumption	Greater endemism in high than low productive areas	O'Brien (2006)	Productivity
Topographic heterogeneity	Organisms cannot circumvent geographic barriers	Greater endemism in heterogeneous than homogeneous areas	White (2016)	Topographic heterogeneity
Niche diversity	Organism specialization to a niche type in an area avoid evolve to different niches in other areas	Greater endemism in high than low niche availability areas	Rapoport (1982)	Niche diversity
River barriers	Organism cannot surpass water courses	Greater endemism in high than low river concentration areas	Rapoport (1982), Huston (1994)	River barriers
Islands	Organism cannot	Greater endemism in	Kier *et al.*	Islands

Hypothesis	Argument	Prediction	Reference	Hypothesis
	overcome the distance effect to other islands or to mainland	islands than in mainland	(2009)	

The aim of this study is to use the above-mentioned index to (a) assess global endemism patterns of terrestrial vertebrates that inform on levels of species range-restriction at fine spatial grain sizes, (b) evaluate the spatial congruence among these patterns and (c) analyze to what extent different environmental variables, hypothesized as factors that limit species dispersion, explain those patterns. Finally, the paper discuss the implications that these global endemism patterns have to be used in conservation biogeography.

Materials and Methods

Data source and endemism measure

For research it has been used digital maps of the terrestrial geographic ranges of vertebrate species, corresponding 6270 to amphibians, 3086 to reptiles, 5286 to mammals [21] and 10046 to birds [22] to represent species range-restriction patterns. To this end, the world has been divided (except for Antarctica) into 5445 equal-distanced cells of 2×2° with geographic projection and coordinate system measured in decimal degrees of latitude/longitude. It was used this scale because the bird range maps data at finer scales increases the probability of false occupancies, while using coarser scales decreases that probability [23]. Thus, to make results comparable it was used the same cell resolution for all vertebrate groups. To build the grids at this scale and rasterize the range maps of vertebrate species, it was utilized the freely available SAM software [24].

The endemism index (ER) was calculated for each cell as follows: first counting the number of cells in which each species of terrestrial vertebrates is distributed; second, calculating its inverse value (i.e., dividing one by the number of cells in which each species is distributed); third, adding up the inverse value of all species that occur in a cell; and fourth, dividing the obtained value in each cell by the species richness of that cell [17].

Environmental variables

Following K.L. Evans *et al.* [19], potential evapotranspiration (PET) it has been considered as a measure of solar energy. PET estimates were based on monthly averages of 60 years of weather data (1920-1980), gridded by K.H. Ahn and R. Tateishi [25] at 0.5× 0.5° resolution (<www.grid.unep.ch/data/download/gnv183.zip>). Annual averages of PET were used as a measure of total solar energy and the difference between monthly values of PET registered in July and January as an estimate of solar energy stability. The productivity measure used was the global Net Primary Productivity (NPP), which quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass [26]. Data on NPP was obtained from the NASA/EOS Project of the University of Montana (http://www.ntsg.umt.edu/project/ mod17#data-product) at 0.5×0.5° resolution. Topographic heterogeneity was measured as the difference between the highest and lowest superficial altitude (altitudinal range) found in a cell. Data on the altitude was obtained from a digital elevation model (www.worldclim.org/current) at 1.0×1.0km resolution [27]. Niche diversity was measured by counting the different types of land covers (niche numbers) in a cell, according to data posted on the website of the European Space Agency (http://bioval.jrc.ec.europa.eu/products /glc2000/glc2000.php) at 1.0×1.0km resolution [28].

River barriers were measured by counting the number of total rivers (river numbers) in a cell according to data obtained from National Centers for Environmental Information (www.ngdc.noaa.gov/mgg/shorelines/data/gshhg) [29]. To conclude, it was included a term that indicates if an area corresponds to an island (according to data available on Global Island Database, http://gid.unep-wcmc.org/).

Statistical analyses

To describe the global endemism patterns based on species range-restrictions, it was used basic descriptive statistics; and to assess the congruence among these patterns, Spearman rank correlations. Then, to analyze the role of environmental variables as factors that determine those patterns, it has been used as in F.J.S. Whitton *et al.* [30] Ordinary Least Square (OLS) non spatial models and, if necessary, Simultaneous Autoregressive Regression (SAR) spatial models. It has been assessed the significance of environmental variables on measures of species range-restrictions using OLS, once models with only significant variables were specified, it was tested and analyzed for the spatial autocorrelation in model residuals by using Moran's (based on connectivity matrix according to Gabriel criterion) [31]. If residual models showed significant spatial autocorrelation implies that degrees of freedom are inflated and violate the assumption of independence in the distribution of errors [30]; thus, to control for the spatial autocorrelation it was assessed the fit of data to species range-restrictions with SAR error models (which assume that spatial structure occurs in the error term [24]). To avoid any influence that cell area sizes could have on endemism patterns, it has been used only those cells with more than 90% of land as response variable. It was added 1 to each endemism index to enable ln (natural logarithm) transformation [32]. All analyzes were performed with SAM software [24].

Results

Basic statistics on ER across vertebrates' groups showed strong differences. Amphibians, with an occupation of 74.25% of cells around the World, had a mean ER by a cell of 0.042 (interval confidence at 95% [CI95] = 0.040 – 0.044) with an observed range of ER between 0.002 – 1.000. This indicates that it is possible to find at least one cell in which all amphibian species occurring there have their ranges restricted to that cell. Reptiles, with a global occupation of 72.76% of cells, had a mean ER by a cell of 0.033 (CI95 = 0.031 – 0.035) with an observed range of ER between < 0.001 – 0.742. This indicates an absence of full restriction of reptile species ranges to one cell. The highest occupancy of cells on Earth was detected for mammals and birds (98.99% and 99.65%, respectively). However, the ER by a cell and the observed range of ER around the World were different between them: the mean ER for mammals was 0.015 (CI95 = 0.014 – 0.016) with an observed range of ER between < 0.001 – 1.000. This indicates that it is also possible to find at least one cell with complete restriction of mammal species. Instead, in birds the mean ER was 0.007 (CI95 = 0.007– 0.007) with an observed range of ER between < 0.001 – 0.336.

When ER patterns among terrestrial vertebrates' groups have been compared, it has been noticed a high spatial concordance among these patterns (Table 2) mainly in tropical areas (Fig. 1a-d).

Table 2. Spearman rank correlations among endemism patterns considering species range-restrictions across vertebrates' groups.

Vertebrate group	Amphibians	Reptiles	Mammals	Birds
Amphibians	1	0.802	0.870	0.858
Reptiles		1	0.762	0.710
Mammals			1	0.891
Birds				1

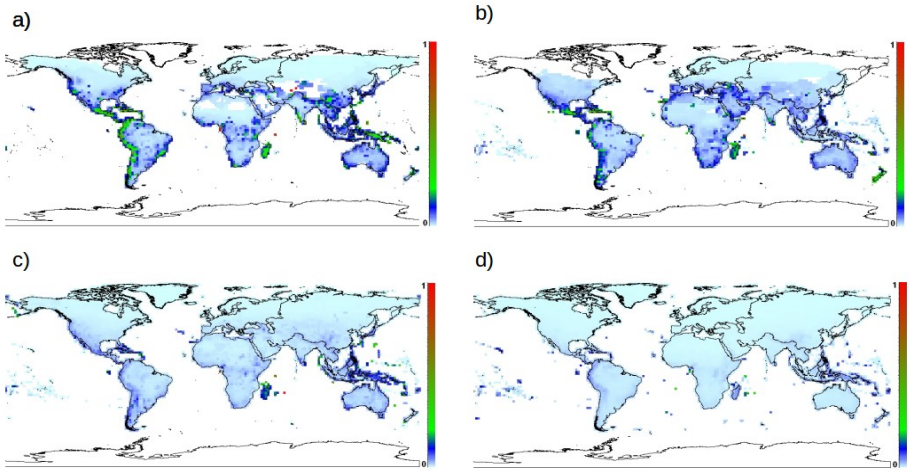


Fig. 1. Global endemism patterns considering species range-restrictions:
a. Amphibians; b. Reptil; c. Mammals; d. Birds.

The highest ER scores for amphibians were located in islands of the Bight of Biafra and Seychelles, and continentally in areas shared by China, Uzbequistan, Afganistan, Tajikistan, and Kirgistan. For reptiles, the highest ER scores were located in islands such as Canarias, Seychelles, Socotra, Puerto Rico, Dominican Republic, Clarion, southwest of New Zealand and in southeast of Egypt. For mammals, the highest ER scores were located in Bight of Biafra, Port Mathurin and Seychelles. Finally, for birds the highest ER scores were located in islands such as Seychelles, Port Mathurin, Mauricio, Santo Tome and Principe and Santa Elena.

Because OLS regression analyses results showed residuals spatially correlated in all terrestrial vertebrate groups, we conducted SAR to discard the effect of space as a factor that inflated the probability of type I error in variables significance [33]. Spatial regression outcomes (Table 3) demonstrated that topographic heterogeneity, solar energy and net primary productivity significantly influenced amphibians' endemism. These three variables together explained a 70 % of variance (SAR: N = 2819, F = 649.39, P < 0.001). Almost concordant with previous results, reptiles' endemism was influenced by topographic heterogeneity, solar energy and river barriers. These three variables together explained a 68 % of variance (SAR: N = 2556, F = 361.68, P < 0.001). In mammals, solar energy, topographic heterogeneity, net primary productivity and islands explained an 82 % of variance (SAR: N = 3095, F = 514.964, P < 0.001) on endemism patterns. In birds, the most influential variables were solar energy and topographic heterogeneity, which explained an 88 % of variance (SAR: N = 3095, F = 1326.70, P < 0.001).

Table 3. Spatial regression (SAR) results for environmental predictors of global endemism patterns considering species range-restrictions across vertebrate groups (see Data and Methods).

Vertebrate groups	Environmental variables	SAR standardized coefficient	*t*	*P*-value	Moran's *I*	Moran's *I* *P*-value

Amphibians	Altitudinal range	0.498	18.902	<0.001	-0.032	0.110
	PET	0.338	4.991	<0.001		
	NPP	0.146	3.631	<0.001		
Reptiles	Altitudinal range	0.367	13.927	<0.001	-0.001	0.974
	PET	0.285	4.414	<0.001		
	Number of rivers	0.054	3.256	<0.001		
Mammals	PET	0.490	9.25	<0.001	0.020	0.255
	Altitudinal range	0.282	13.814	<0.001		
	NPP	0.222	6.685	<0.001		
	Islands	0.113	5.142	<0.001		
Birds	PET	0.437	10.367	<0.001	-0.018	0.327
	Altitudinal range	0.289	18.471	<0.001		

Discussion

For the first time, this study reported, global endemism patterns of terrestrial vertebrates, which account for species range-restrictions at relatively fine spatial grain sizes. Previous works developed at the same scale and considering similar spatial grain sizes, failed to provide this information because they used a threshold area to define an endemic species. Therefore, they were able to identify endemic species richness patterns where each species had the same importance regardless of if their distribution ranges were confined to one, two or more units of analysis [13]. Instead, from ER pattern it was possible to observe the percentages in that species were restricted to a cell, which undoubtedly constitutes a primary quantification of species uniqueness to an area. Particularly, having information about species uniqueness on space is strongly important because allow recognizing specific areas where genetic, physiological, ecological and behavioral characteristics of species are not elsewhere [34].

When spatial distributions of endemism were compared among terrestrial vertebrates, they showed a common pattern of high scores of ER between the tropics. This common pattern promoted a high spatial congruence of ER among groups. Compared with other similar research, this spatial congruence constitutes the highest reported for terrestrial vertebrates at global scales [6, 10-11]. This finding, as that of J.F. Lamoreux *et al.* [6], suggests that the same processes may limit species geographic ranges across vertebrate groups.

Spatial regression results showed a high predictive power of environmental variables on endemism patterns of vertebrates. Three of the tested hypotheses found statistical support in more than one vertebrate group: the topographic heterogeneity and solar energy hypotheses for all groups, and the productivity hypothesis for both amphibians and mammals. Likely, the common influence of these environmental variables was responsible for the high spatial congruence observed among endemism patterns. We should then ask how these environmental variables are limiting vertebrate species distribution ranges?

Topographic heterogeneity can limit species geographic ranges through two paths [35]. The first path, the ecological, posits that topographic heterogeneity promotes species specialization by increasing the number of ecological niches in an area. This specialization to specific niches precludes species from exploiting other niches in different areas [20, 36].

According to the results reported in this work, this path is not supported by the data because of the absence of statistical significance between ER and the number of niches available in an area.

The geological path, posits that topographic heterogeneity promotes the appearance of strong geographic barriers that species cannot surpass [35, 37]. At first glance, this path has some support considering that amphibians and reptiles, the vertebrates with the lowest capacity of mobility [38], were the groups most influenced by this variable (Table 3). However, topographic heterogeneity also showed a significant effect on mammals and birds' endemism, which indicates that physical barriers can affect vertebrates with higher dispersion capabilities [39]. A plausible explanation for these outcomes is that, as topographic heterogeneity is a variable that indicates strong altitudinal differences in an area, mammals and bird's species may evolve narrow thermal tolerances within specific altitudinal bands which limit their dispersion to other bands [36, 40].

Solar energy has been suggested as a factor that limits species ranges by affecting organisms' physiology [19, 41]. This is because low solar inputs have negative effects in warm- and cold-blooded species metabolism and growth rates [34], which in turn promotes low population abundances and high extinction risk [42]. Thus, when solar energy is insufficient to maintain viable populations, species see limited distribution ranges [19, 43]. There is evidence that species distributional limits coincide with climatic shifts [19], supporting that solar energy can influence endemism patterns.

Net primary productivity may also limit amphibians and mammals' geographic distribution as solar energy does. That is, by influencing metabolism, growth rates, population abundances and extinction risk [42, 44-45]. K.L. Evans *et al.* [19] suggested that net primary productivity can be interpreted as a surrogate of the climatic water-energy balance, or as a measure of plant resources available to consume. Probably, productivity may limit amphibians ranges via water-energy balance because its ecophysiology is strongly constrained by water and temperature, enabling its energetic costs survive in low productive environments [32, 46]. Contrarily, productivity may limit mammal ranges via resource consumption because they require high levels of intake to maintain constant body temperature [44].

In mammals and reptiles two variables affected ER patterns given support to island and river barrier hypotheses, respectively. The role of islands as centers of endemism is well-recognized, although its importance has been underestimated in previous studies. This is because they analyzed its effect on endemism patterns using endemic species richness as response variable; thus, as islands often have less richness than mainland, its significance was often not detected [47]. In this work, from considering endemism in based on species range restriction and not species richness, the role of islands as a factor that limits species geographic ranges can be recognized. So, it is clear that the distance to other islands or to mainland constitutes a strong barrier for the dispersion of mammal species [48].

But, if islands promote endemism, why other vertebrates' groups do not show statistical significance with this variable? Probably, the explanation is different for the amphibian and reptiles than for birds. For the former two groups, is because they show high levels of range-restriction both in islands and mainland. Thus, the statistical significance of this variable cannot be distinguished. For the last group, is because they have an extraordinary power of dispersion, so that island distances effect can be easily surpassed.

River barriers have been suggested as factors that promote endemism by limiting species geographic ranges for different organisms [14, 20]. However, in this work this variable was only significant for reptiles [49]. Rivers cannot be considered barriers for amphibians but probably corridors because they live in an interface between terrestrial and aquatic

environments [50], and for mammals and birds because they show high power of dispersion [20].

Conclusions

The findings reported in this study can be considered to have strong implications for biodiversity conservation. The possibility of representing ER at relatively fine grains offers an informative, better comparable estimator of species vulnerability through space, because species geographic ranges represent a straightforward predictor of extinction risk [43, 51]. For example, the cells where amphibians and mammals show full restriction (ER = 1), have the greatest likelihood to extinction because species inhabiting that cell are unique of those cells [4, 52] and thus, must be considered as priority sites to protect worldwide biodiversity [53]. In this sense, the use of this index to set conservation priorities can help to increase the protection of species with restricted geographic ranges, since it was demonstrated that the pervasive use of endemic species richness to identify biodiversity hotspots tend to miss most of endemic taxa [13, 54].

Furthermore, the high spatial congruence on endemism patterns across the terrestrial vertebrates found in this research makes it possible to consider any of these patterns as an effective surrogate to protect species of other groups [6]. The significance of the same group of environmental variables explaining these patterns suggests a strong role as factors that in the actuality are limiting species ranges [14]. In this regard, the results pinpointed that climate change arise as main threat to endemic species survival because its probable effects may promote more species geographic ranges contractions and thus, an increase in their extinction risk [55]. Has to be accepted that the index used in this work has some critics [56], and that demands information about species' geographic ranges [13]. However, it was considered that its use can help in understanding the processes involved in the maintenance of global endemism patterns and to delineate precise conservation practices.

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