

Environmental factors related to biogeographical transition zones of areas of endemism of Neotropical mammals

Elkin Alexi Noguera-Urbano^{A,B} and Ignacio Ferro^{C,D}

^APosgrado en Ciencias Biológicas, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Ciudad Universitaria, Coyoacán, CP 04510, Mexico City, Mexico.

^BGrupo de Investigación en Biogeografía de la Conservación, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Ciudad Universitaria, Coyoacán, CP 04510, Mexico City, Mexico.

^CInstituto de Ecorregiones Andinas (INECOA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Jujuy (UNJu), Avenida Bolivia 1239, CP, 4600, San Salvador de Jujuy, Jujuy, Argentina.

^DCorresponding author. Email: ignacioferro@gmail.com

Abstract. Biogeographical transition zones are areas of a complex biotic mixture located at the borders between biogeographical units. Climatic, physical and ecological factors should play an important role in allowing coexistence of different biotic elements in the transition zone. Here, we explore the relationship between environmental factors and biogeographical transition zones, defined by Neotropical mammal distributions, by a model selection approach based on the Akaike information criterion and accounting for the spatial structure in the data. We detected three areas of high overlap between mammalian areas of endemism. Two of them corresponded to the well-established regional-level transition zones, namely Mexican (MTZ) and South American (SATZ) transition zones; the third was one located in south-eastern Brazil, approximately between the Paraná and Chacoan dominions that we call The Atlantic Forest integration zone (AF). Only one explicative variable was shared by the three transition zones (precipitation of the warmest quarter). However, shared variables with great explanatory power indicated two environmental aspects as facilitators for the coexistence of different biotic components in a given geographical area. The first one was the heterogeneity component, either topographic for the SATZ and MTZ or climatic for the AF. The second one was related non-extreme thermal conditions: precipitation of the warmest quarter, interpreted as a thermal buffer, shared by AF and SATZ, and isothermality shared by MTZ and SATZ.

Received 30 November 2016, accepted 24 July 2017, published online 31 January 2018

Introduction

The biogeographical regions are defined by the occurrence of taxa in a particular geographical area, and nowhere else, namely endemic taxa. When several endemic taxa share similar geographical distribution ranges, this is frequently considered to be a consequence of barriers (physical or ecological) that have historically isolated biota, promoting speciation and shaping their distribution through evolutionary time (Nelson and Platnick 1981; Haffer 1982; Cracraft 1985). Such sets of co-distributed endemic taxa, or sets of spatiotemporally integrated taxa that coexist in given areas (biotic components *sensu* Morrone 2009), define areas of endemism. Areas of endemism are the basic units of evolutionary biogeography (Parenti and Ebach 2009, Noguera-Urbano 2016) used to propose biogeographical categories (region, domain, province;

Escalante 2009). Biogeographical transition zones are areas of biotic mixture located at the borders of different biogeographical regions (Morrone 2006). Thus, the biogeographical transition zone occurs when two or more areas of endemism overlap each other (Naka 2011, Noguera-Urbano and Escalante 2015), leading to the blending of two distinct biotic components. The transition zone is a geographical area of overlap, replacement or partial segregation between these biotic components, either due to the attenuation of a pre-existing barrier or as an ongoing process of biotic limitation, such as progressive gradients of environmental conditions. Therefore, in a biogeographical transition zone, physical features, environmental conditions and ecological factors may all allow these biotas to mix but constrain their further diffusion into one another (Ferro and Morrone 2014).

Early zoogeographers recognised the Neotropical region on the basis of biotic singularity as a geographical area comprising South America, Central America, the southern half of Mexico and the Antilles, a scheme widely accepted by vertebrate zoogeographers (Cox 2001). Within South America, classical mammalian biogeographical regionalisation divides the continent into two subregions, namely, the north-eastern tropical lowlands (Guayano–Brazilian subregion) and the central Andean highlands and southern lowlands (Andean–Patagonian subregion; e.g. Wallace 1876; Sclater and Sclater 1899; Hershkovitz 1969). However, a more restrictive definition of the Neotropical region, proposed mainly by phytogeographers and invertebrate zoogeographers, considers the southern portion of South America as a different region, namely, The Andean region (see revision in Morrone 2014). This latter scheme defined the deepest transition of the biogeographical hierarchy in the American continent as follows: between the Holarctic kingdom and Holotropical kingdom in the Mexican transition zone (MTZ), and between Holotropical and Austral kingdom, in the South American transition zone (SATZ; Morrone 2015). Regardless of the hierarchical categorisation proposed by different authors (kingdom, region or subregion), this continental pattern of regionalisation has been repeatedly recovered by modern numerical techniques applied to vertebrate distributions (Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013; Noguera-Urbano and Escalante 2015; Escalante 2016).

Because transition zones occur between two or more biogeographical units, a desirable prerequisite for studying them is the definition of biogeographical units. In evolutionary biogeography, transition zones may be detected by conflicting results in cladistic biogeographical analyses (because a putative transition zone may be the sister area to different biogeographical areas) or by the presence of panbiogeographical nodes, namely areas where different generalised tracks converge (Morrone 2009). Although showing a mixture of biotic components, panbiogeographical nodes are unable to distinguish the geographical extent of transition zones. In contrast, hybridising areas of endemism on a general-area cladogram define transition zones with hard boundaries, thus neglecting the perception of spatial length and strength of transition zones (Ferro and Morrone 2014). Acknowledging that biotic component are spatio-temporal integrated sets of taxa and that may be either depicted as areas of endemism or as generalised tracks in panbiogeographical analysis (Morrone 2009), we used intersection of areas of endemism defined by mammal distributions to recognise transition zones in the present study. These areas of endemism were taken from a recently published analysis of Neotropical mammal endemism by Noguera-Urbano and Escalante (2015). On the basis of endemicity analysis, these authors identified areas of endemism that approximately coincided with classical biogeographical units. Also, they found two complex (transitional) areas and showed that these transitions matched with areas characterised by high topographic variability, namely, the Andes for SATZ and the Sierras Madres for MTZ. Nonetheless, the importance of environmental factors on the transitions zones remains unclear.

Here, we explored the relationship between biogeographical transition zones and environmental explanatory variables. Whereas the spatial pattern in species richness has been widely

related to climatic and environmental factors, the relationships between such factors and biogeographical transition zones have been poorly explored and not quantified. Because a transition zone implies that several species from two or more areas of endemism have reached their distributional-range limits, physical and climatic factors should play an important role, and, at least, may partially explain the phenomenon. Therefore, we hypothesise that if there is a general process shaping the pattern of transition zones, then it acts in a similar manner in different transition zones and involves the same variables.

Materials and methods

Detection of biogeographical transition zones

To detect biogeographical transition zones, we used recently published analysis by Noguera-Urbano and Escalante (2015) that identified areas of endemism on the basis of mammal distributions taken from IUCN range maps (IUCN 2012). These authors analysed a matrix of 1782 mammal species in a grid of 2° latitude–longitude of the American continent by endemicity analysis. We defined our study area as the area between 32°N and 32°S latitude, encompassing the whole Neotropical region. Within this studied area, we transformed 84 areas of endemism found by Noguera-Urbano and Escalante (2015) from vector format to raster at 0.5° latitude–longitude resolution. Then, the areas of endemism in raster format were summed to obtain a resulting raster of the areas of endemism overlap (AEO) in the Neotropical region. Therefore, we obtained a map of biogeographical transition zones based on the intersection between two or more areas of endemism defined by mammal distributions. To reduce the number of pixels involved in the analysis of the relationship between AEO and environmental variables, we focused on those zones with high AEO. Thus, we identified regions where the highest AEO occur, and then use a buffer of 300 km around those areas. All spatial processes were executed in QGIS, ver. 2.18 (QGIS Development Team, Open Source Geospatial Foundation Project, see <http://qgis.osgeo.org>, accessed 12 May 2015).

Explanatory variable selections

Explanatory variables were taken from the 19 bioclimatic layers, ver. 1.4 (Hijmans *et al.* 2005, see <http://biogeo.berkeley.edu/worldclim>, accessed 24 February 2015), at the resolution of 2.5 min (~5 km²) and a topographic variable layer (altitude) was obtained from the digital elevation model (DEM) at the same resolution. All explanatory-variable layers were resampled using cubic technique to 0.5 degrees, which was the final spatial resolution of this analysis (~5 km²). We evaluated multicollinearity among the 19 bioclimatic variables by the variance inflation factor (VIF; Zuur *et al.* 2010) and progressively eliminated variables until VIF was <2 for each variable (Pearson *r* of ~<0.5). Of the 19 bioclimatic variables, five (VIF of <2) were used for modelling biogeographical transition zones. The 14 variables removed after VIF analysis were used to build the climatic heterogeneity layer (see below). For the Mexican and the South American transition zones, the same five variables were retained for modelling (VIF of <2), and included isothermality (bio3), mean temperature of wettest quarter (bio8), precipitation seasonality (bio15), precipitation

of the warmest quarter (bio18), precipitation of the coldest quarter (bio19). For the Atlantic Forest integration zone, mean diurnal range in temperature (bio2) and mean annual precipitation (bio12) were retained together with bio3, bio8 and bio18. This resulted in eight explanatory variables (including eigenvector filters, topographic and climatic heterogeneity) included in each transition zone for the model-selection analysis.

Environmental factors and topographical variation emerge as primary predictors of mammal biogeographical patterns (Kerr and Packer 1997). Therefore, we included as predictors two other variables, namely, climatic and topographic heterogeneities. The climatic heterogeneity was calculated for each transition zone using the 14 variables removed after VIF analysis. First, we reduced dimensionality of the bioclimatic variables by principal-component analysis (PCA). The PCA facilitates to consider multiple climatic variables at the same time and summarises them into synthetic variables. We then calculated the climatic heterogeneity, weighting the first three principal components by the amount of variation (percentage of eigenvalues; Table S1, available as Supplementary material for this paper) explained across the map layer, and summed them to produce the final heterogeneity layer (see Brown 2014 for procedure details). Topographic heterogeneity was quantified as the standard deviation of the elevation calculated from each raster pixel and the 24 cells neighbouring the focal cell (5 cells by 5 cells). Statistical analyses were performed using SDMtoolbox (Brown 2014) and R (R Foundation for Statistical Computing, see <http://www.Rproject.org/>, accessed 25 October 2013).

Statistical modelling of transition zones

All selected variables were standardised into units of variance for further analysis. For modelling the biogeographical transition zones, we used an Akaike information criterion (AIC) model-selection approach, accounting for the spatial structure (autocorrelation) in the data by a technique known as spatial eigenvector mapping (SEVM) or eigenvector-based spatial filters (Diniz-Filho and Bini 2005). The spatial filters (eigenvectors), representing the structure of the data at different spatial scales, were obtained from the principal coordinate analysis of neighbour matrices from a truncated pairwise-distance relationship among cells. We selected the combination of filters that minimised the spatial autocorrelation in the model residuals by keeping Moran's I below 0.05 in the first distance class. Spatial eigenvector filters were incorporated as explanatory variables for all models (Diniz-Filho *et al.* 2008). The model-selection routine was performed in Spatial Analysis in Macroecology (SAM) software, ver 3.1 (Rangel *et al.* 2006, 2010, see <https://www.ecevol.ufg.br/sam/>, accessed 15 October 2014).

To evaluate the model that best explained each mammal biogeographical transition zone, we used the sample-corrected AIC (AICc) for each proposed model, selecting as the best models those with the minimum AICc. We evaluated models by calculating the difference between AICc of each model and the minimum AICc found for the set of models compared (Δ AICc). The relative contribution of each variable was estimated by the average of their coefficients across all models in which they were present, by the Akaike weight of each model w_i (Diniz-Filho *et al.* 2008).

Results

Detection of biogeographical transition zones

We detected three zones where areas of endemism were highly integrated (Fig. 1). One was located in Mesoamerica, approximately coinciding with the MTZ (Morrone 2014). Another one was located in the tropical Andes, coinciding with the Andean portion of the SATZ (*sensu* Morrone 2014). Finally, we detected a high mixture of areas of endemism located in south-eastern Brazil between the Paraná and the Chacoan dominion of the Neotropical region, that we call Atlantic Forest integration zone (Fig. 1).

Modelling biogeographical transition zone

Mexican transition zone

For the MTZ, of the 127 evaluated models, 6 were best models according to the AICc values, and can be considered equivalent according to their Δ AICc values of <2 (Burnham and Anderson 2002) (Table 1). All these models explained 94% of variation in this transition zone. Model length ranged from five to seven variables, but the best models were those with fewer variables. The two models with the lowest AICc were equal regarding the likelihood of being the best one (17%) according to w_i values, whereas the remaining models were below 8% according to w_i values. The following four variables were present in all selected models: precipitation of the warmest quarter (bio18); precipitation of the coldest quarter (bio19); isothermality (bio3); and topographic heterogeneity. The variable with the highest explanatory power, considering all models, was isothermality (bio 3) followed by topographic heterogeneity (see standardised coefficient in Table 2).

South American transition zone

Of the 127 possible models for the SATZ, four models with the lowest AICc were equivalent according to their Δ AICc (Table 1). Each model explained 89% of the variance in this biogeographical transition zone, including five to seven variables and different combinations across models. The model with the lowest AICc was the best one according to w_i values (21%). For the remaining three models, w_i values were below 12% (Table 1). Beyond eigenvector filters, which account for spatial structure in the data for every model (always present), of the seven alternative explanatory variables, the following four were present in all selected models: precipitation of warmest quarter (bio18); isothermality (bio3); topographic and climatic heterogeneity. The best model also included mean temperature of the wettest quarter (bio 8), which was present in three of the four best-ranked models. When considering the explanatory power of each variable across every model in which it was present, topographic heterogeneity was the variable with the largest standardised coefficient, followed by precipitation of the warmest quarter (bio18) and isothermality (bio3; Table 2).

Atlantic Forest integration zone

For this area, 14 models with Δ AICc < 2 were selected, each one explaining 96% of the variance (Table 1). The number of variables included in the selected models ranged from three to six, but best models included few variables. Only one variable

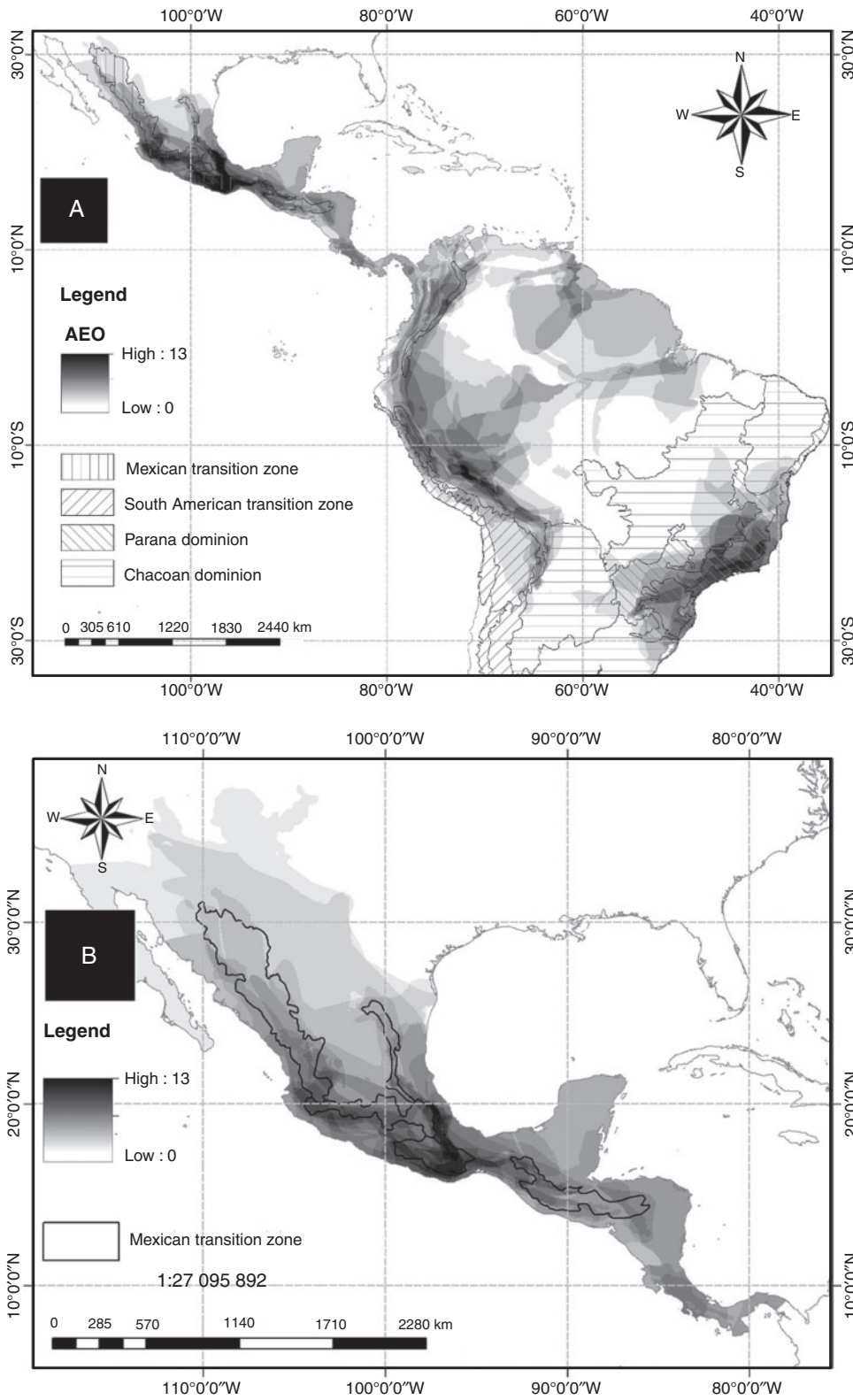


Fig. 1. Areas of endemism of the Neotropical mammals overlapping and the biogeographical transition zones defined in the present paper. A. Studied area, AEO (areas of endemism overlapping) and biogeographical units by Morrone (2014). B. Mexican transition zone. C. South American transition zone. D. Atlantic Forest integration zone. The scale indicates AEO from the lowest (light) to the highest (dark).

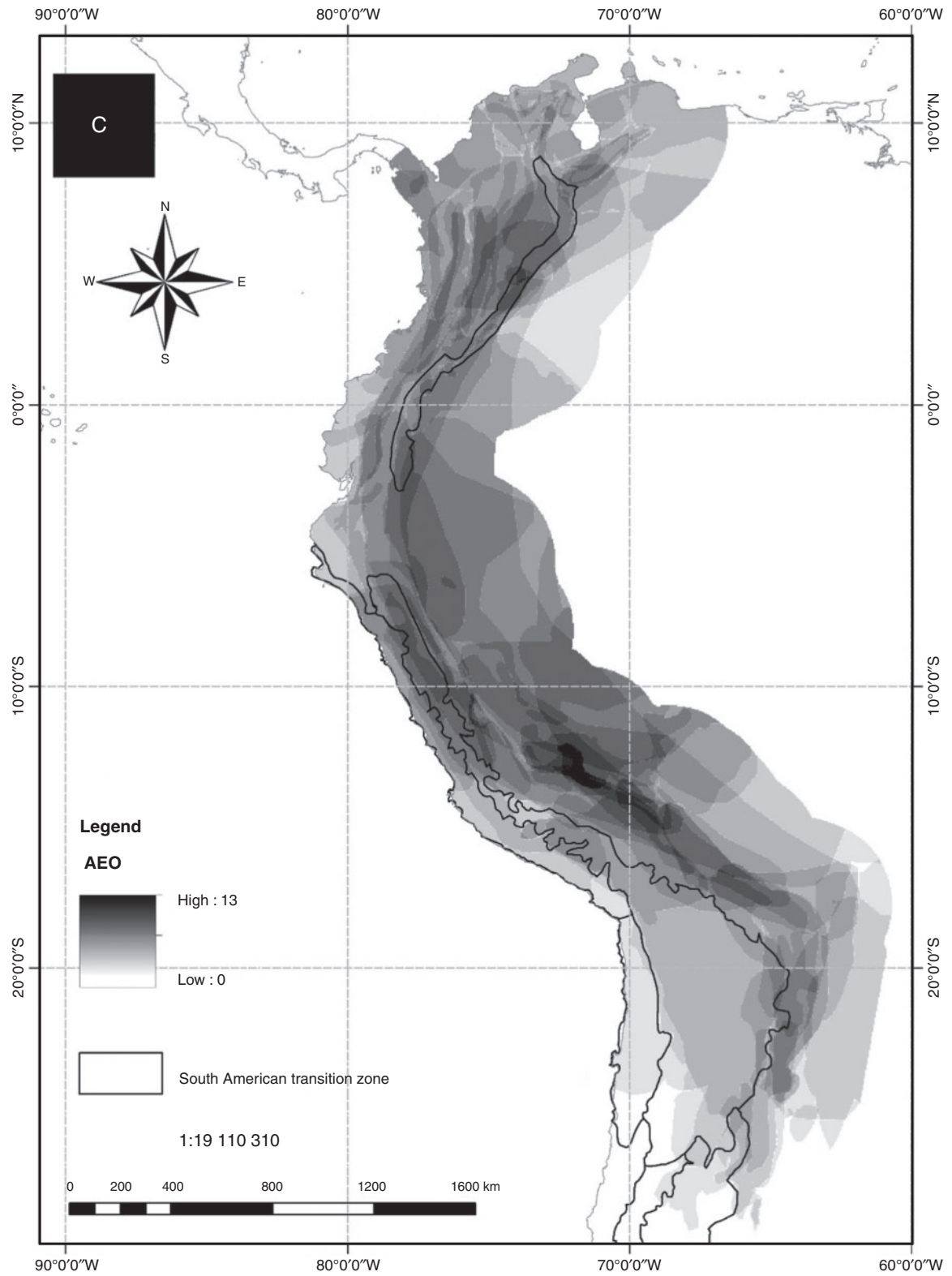


Fig. 1. (continued)

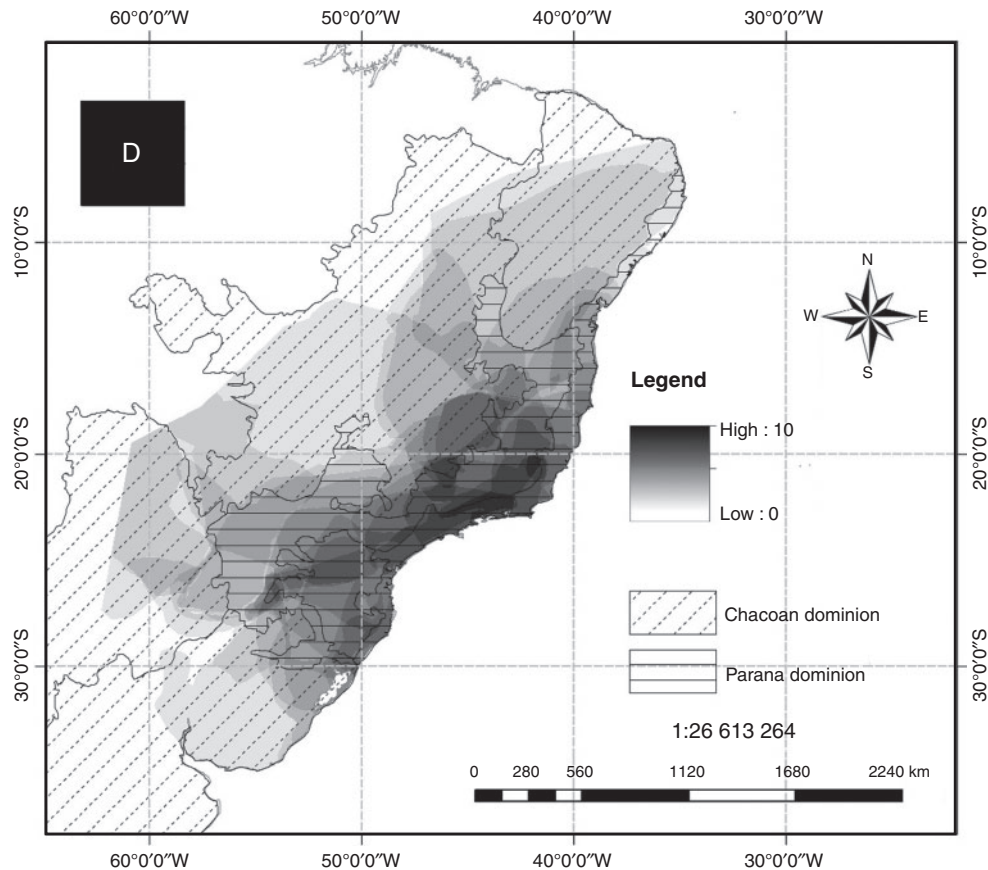


Fig. 1. (continued)

was present in all selected models, namely precipitation of the warmest quarter (bio18). The best explanatory variables according to standardised coefficient were precipitation of the warmest quarter (bio18) and climatic heterogeneity (Table 2).

Discussion

All the biogeographical divisions of earth imply the existence of transition zones between the divided units when contiguous. Biogeographical transitions are usually represented cartographically as sharp lines drawn on maps. However, rather than just static lines, transition zones involve areas containing gradients of biotic composition (Williams 1996; Ruggiero *et al.* 1998; Williams *et al.* 1999; Ruggiero and Ezcurra 2003). Such gradients in biotic composition should be mapped to identify places where major intergradations occur (Ferro and Morrone 2014). By measuring overlap between different mammalian areas of endemism we recovered three zones of substantial contact for the Neotropical region. Two of these zones coincide with the classical regional-level transition zones of the Neotropical region, namely the SATZ and the MTZ. However, whereas the location of MTZ defined by Morrone (2014) approximately coincided with our finding, the SATZ differed to some extent (Fig. 1). According to Morrone (2014), the SATZ in the tropical Andes includes the Paramos, and the western (dry) slopes of the Andes (Puna, Atacama, Prepuna and Monte biogeographical

provinces). Our findings agreed with those of Morrone (2014) in that the Paramos (northern Andes) are part of the SATZ, but differed in the central Andes, where the transition zone was located at the eastern (humid) slopes of the Andes. The third prominent area identified in the present paper, the Atlantic Forest integration zone, is located between the Chacoan dominion and the Paraná dominion. This area has not been previously recognised as a strong continental transition zone and would require a formal definition. However, recent continental analysis of species turnover showed a high rate of replacement in this area for birds (Melo *et al.* 2009) and rodents (Maestri and Patterson 2016). Additionally, Costa (2003) reported incongruence of branching patterns among areas using cladistic approach for small mammal taxa occurring throughout Atlantic Forest, Amazon forests, Cerrado and Caatinga regions. Furthermore, the Atlantic Forest (Paraná Dominion) and Brazilian Cerrado (Chacoan Dominion) have been repeatedly recognised as a hotspot of endemism and biodiversity (Myers *et al.* 2000; Mittermeier *et al.* 2004, 2011). Thus, all this evidence suggests an existence of a prominent biogeographical transition zone in this region.

A commonality among the areas of biotic component mixture reported in the present paper is the presence of mountain areas associated with each one, including the central Andes in South America, the Sierras Madre in Mesoamerica and the Serra do Mar in eastern Brazil. This is important because

Table 1. Parameter estimates for best Neotropical transition-zone models selected according to Akaike weights (AICc w_i)

Bioclimatic variables (bio): 2, mean diurnal range in temperature; 3, isothermality; 8, mean temperature of wettest quarter; 12, mean annual precipitation; 15, precipitation seasonality; 18, precipitation of warmest quarter; 19, precipitation of coldest quarter. CH, climatic heterogeneity; TH, topographic heterogeneity; EF, eigenvector filter; Cond.Num., conditional number; AICc, corrected Akaike's information criterion; delta AICc, difference between AICc and the minimum AIC found for the set of models compared

Transition zone	Best model	Variable	r^2	Cond.Num.	AICc	Delta AICc	AICc w_i
Mexican transition zone	Mod #71	3, 8, 18, 19, TH, EF	0.937	3.449	2124.31	0	0.172
	Mod #74	3, 18, 19, TH, EF	0.937	3.449	2124.322	0.013	0.171
	Mod #8	3, 8, 15, 18, 19, TH, EF	0.937	3.526	2125.7	1.39	0.086
	Mod #70	3, 8, 18, 19, CH, TH, EF	0.937	3.504	2125.761	1.451	0.083
	Mod #73	3, 18, 19, CH, TH, EF	0.937	3.501	2125.811	1.501	0.081
	Mod #11	3, 15, 18, 19, TH, EF	0.937	3.522	2126.064	1.755	0.072
South American transition zone	Mod #85	3, 8, 18, CH, TH, EF	0.89	2.993	865.036	0	0.21
	Mod #22	3, 8, 15, 18, CH, TH, EF	0.89	3.3	866.099	1.063	0.12
	Mod #88	3, 18, CH, TH, EF	0.889	2.794	866.168	1.132	0.12
	Mod #70	3, 8, 18, 19, CH, TH, EF	0.89	3.222	867.029	1.994	0.078
Atlantic Forest integration zone	Mod #79	2, 18, CH, EF	0.959	2.075	1977.847	0	0.049
	Mod #16	2, 12, 18, CH, EF	0.96	2.761	1977.857	0.01	0.049
	Mod #3	2, 12, 18, EF	0.959	2.63	1978.624	0.777	0.034
	Mod #66	2, 18, EF	0.959	1.914	1978.717	0.87	0.032
	Mod #94	18, CH, EF	0.959	1.962	1978.749	0.902	0.031
	Mod #13	2, 8, 12, 18, CH, EF	0.96	3.088	1979.158	1.311	0.026
	Mod #9	2, 3, 12, 18, CH, EF	0.96	2.84	1979.331	1.484	0.024
	Mod #17	2, 12, 18, CH, TH, EF	0.96	3.01	1979.404	1.557	0.023
	Mod #18	2, 12, 18, TH, EF	0.959	2.822	1979.436	1.589	0.022
	Mod #31	12, 18, CH, EF	0.959	2.573	1979.597	1.75	0.021
	Mod #80	2, 6, 18, TH, EF	0.959	2.361	1979.598	1.751	0.021
	Mod #72	2, 3, 18, CH, EF	0.959	2.2	1979.615	1.768	0.02
	Mod #12	2, 8, 12, 18, EF	0.959	2.947	1979.641	1.794	0.02
	Mod #76	2, 5, 18, CH, EF	0.959	2.203	1979.764	1.918	0.019

differences in elevation entails strong environmental changes that certainly affect the distribution of organisms, imposing biotic limitation and promoting differentiation among biota. Indeed, β diversity as a measure of the difference in species composition has proved to be useful for detection of transition zones between biogeographical regions (Williams 1996; Ruggiero *et al.* 1998; Ferro 2013, Ferro *et al.* 2017). An assessment of environmental drivers for β -diversity at continental scales has shown that topographic heterogeneity is the best predictor for turnover patterns of birds and mammals in the American continent (Melo *et al.* 2009, Maestri and Patterson 2016). Additionally, even within ecoregions, variability in elevation is a good predictor for β diversity in birds (Veech and Crist 2007).

All selected models included shared variables with strong explanatory power. Particularly, for the SATZ and the MTZ, the following three of the four selected variables for each best model were shared: topographic heterogeneity, isothermality and precipitation of the warmest quarter (Table 1). For the Atlantic Forest integration zone, the following two variables were consistently selected: precipitation of the warmest quarter, also selected for models in the other two transitions zones recognised in the present paper, and climatic heterogeneity, also selected for all best models of the SATZ. The presence of a similar set of variables with strong explanatory power in different transition zones suggests the existence of a general process shaping this phenomenon, but the difference in the explanatory power of these variables in different models also indicates some singularities for each region.

Topographic heterogeneity quantifies the variation among pixel values of an elevation layer. This variable yielded the greatest explanatory power for the SATZ, where the elevation gradient is notoriously abrupt (more than 3500 m in a few dozen linear kilometres), and it was the second most important one, considering its explanatory power, for the MTZ. As discussed above, differences in altitude and the correlated temperature variations are surrogates for habitat differentiation and are related to biological diversity. However, heterogeneous topography can also play a role in the intermingle of biotic components, favoured by non-extreme climatic conditions. As a consequence of topographic heterogeneity, microclimatic conditions frequently vary within small geographical areas. For instance, solar radiation depends on slope orientation, moist capture is higher on ridges, whereas adjacent valleys are frequently dryer (Sarmiento 1986). These microclimatic conditions generate a network of vegetation patches with an associated distinctive fauna (Ferro and Barquez 2009). Thus, the interacting influences of climate, topography and soil on a mounting side may be important determinants of species distributional range-limit integration at a local scale. Although mountain ranges are present in the Atlantic forest integration zone, the topographic heterogeneity was not a relevant variable in this region, being present only in 4 of 14 selected modes (Table 1) and with a low explanatory power (Table 2). This was probably due to the short elevation gradient, with only isolated peaks being higher than 2000 m (Safford 1999). However, the topography, together with the decreased rainfall away from the

Table 2. Summary of the parameter estimates for variables averaged across 127 spatial ordinary least squares (OLS) for Neotropical transition zones. Numbers indicate bioclimatic variables (bio; see Table 1). CH, climatic heterogeneity; TH, topographic heterogeneity; PF, predicted by filter; coeff., coefficient; s.d. coeff., standardised coefficients; s.e., standard error and *t*, *t*-values associated to standardised coefficients

Transition zone	Variable	Importance	Coeff.	s.d. coeff.	s.e.	<i>t</i>	95% lower	95% upper
Mexican transition zone	Constant	–	–0.8	0	0.209	–3.822	–1.21	–0.39
	3	0.999	0.014	0.053	0.003	4.113	0.007	0.02
	8	0.543	0.001	0.013	0.001	2.816	0.001	0.001
	15	0.314	0.001	–0.005	0.001	–1.726	–0.001	0.001
	18	0.801	0.001	0.025	0.001	2.726	0.001	0.001
	19	0.878	0.001	–0.026	0.001	–2.725	0.001	0.001
	CH	0.337	–0.003	–0.008	0.001	–2.412	–0.005	0.001
	TH	1	0.875	0.045	0.202	4.327	0.479	1.271
	EF	1	0.936	0.905	0.014	67.292	0.909	0.964
South American transition zone	Constant	–	0.001	0	0.009	0.001	–0.018	0.018
	3	0.91	0.031	0.031	0.011	2.863	0.01	0.053
	8	0.709	–0.025	–0.025	0.009	–2.697	–0.043	–0.007
	15	0.374	–0.013	–0.013	0.005	–2.423	–0.023	–0.002
	18	0.99	0.041	0.041	0.012	3.376	0.017	0.065
	19	0.289	0.001	0.001	0.004	0.005	–0.008	0.008
	CH	0.748	–0.025	–0.025	0.009	–2.722	–0.043	–0.007
	TH	0.987	0.05	0.05	0.016	3.102	0.018	0.081
	EF	1	0.954	0.898	0.013	72.771	0.928	0.979
Atlantic Forest integration zone	Constant	–	0.12	0	0.153	0.785	–0.18	0.42
	2	0.602	–0.001	–0.009	0.001	–2.756	–0.003	0.001
	3	0.353	–0.001	–0.005	0.001	–2.393	–0.003	0.001
	8	0.318	0.001	–0.004	0.001	–1.903	0.001	0.001
	12	0.486	0.001	–0.009	0.001	–2.607	0.001	0.001
	18	0.844	0.001	0.017	0.001	2.54	0.001	0.001
	CH	0.603	0.004	0.01	0.001	2.775	0.001	0.007
	TH	0.366	0.173	0.006	0.07	2.47	0.036	0.311
	EF	1	0.989	0.969	0.007	133.264	0.974	1.004

coasts, creates a complex mosaic of vegetation types (rain forest, *Araucaria* forests, seasonal deciduous and semideciduous forest, and the Cerrado), accounted for in our analysis by climatic heterogeneity, which certainly affects mammals distributions and has affected their evolution in this region (Costa and Leite 2012, Machado *et al.* 2013, Leite *et al.* 2016).

Another observed recurrent explanatory variable is isothermality (bio 3), which was the variable with greatest explanatory power for the MTZ (mean = 60%). This variable quantifies thermal variability as a quotient between diurnal temperature oscillations relative to the annual temperature range. The higher the value, the more similar the diurnal and annual temperature ranges are. Thus, in isothermal regions, temperature remains fairly constant year-round, with the seasonal variation in temperature regime being similar to the day–night variation. Because biogeographical transition zones are areas where marginal distributional ranges of species overlap, populations inhabiting the transition zones are at, or near, their limits of physiological tolerance. Therefore, high isothermal regions would prevent extreme cooling or heating events, favouring the persistence of species belonging to different biotic components with different historical settings. In fact, high rates of mortality in marginal populations occur after extreme environmental events (Gaston 2009 and reference therein).

The third pervasive variable is precipitation of the warmest quarter (bio 18), which was present in the best models for the three transition zones here identified (mean MTZ = 635 mm,

SATZ = 919 mm, AF = 570 mm). High temperatures and water availability have been repeatedly mentioned as direct key climatic determinants of species richness across the world (see revision in Hawkins *et al.* 2003). However, although obviously related to water supply, this variable can be interpreted as a temperature buffer, preventing heat stress in the framework of transition zones. Mammals, as endotherms, can better tolerate low temperatures than high temperatures by daily torpor or increased food consumption to maintain energy balance. Indeed, high temperatures and the resulting heat stress have large effects on most aspects of reproductive function in mammals (Heldmaier *et al.* 2004). The evaporative cooling effect of rainfall during the warmest period of the year can enhance the thermoregulatory demand of mammals, reducing the deleterious effects of heat stress (Hansen 2009). Thus, rainfall in the warmest quarter probably facilitates the coexistence of a set of mammal species with different distributional ranges, and presumably with different thermal requirements, in a given geographical area.

Our results have demonstrated the existence of a similar set of related environmental variables for all the transition zones, with the variables being almost the same for the MTZ and SATZ, but different for the Atlantic Forest integration zone. Despite their differences, some commonalities could be found. The most apparent one was the heterogeneity component, being topographic for the SATZ and MTZ but climatic for the Atlantic Forest. The precipitation of the warmest quarter, which is the variable with the greatest explanatory power for the Atlantic

Forest integration zone, and the second-greatest for the SATZ, is interpreted as thermal buffer. Whereas precipitation variable had low explanatory power for the MTZ, the variable with the highest explanatory power for this zone was isothermality, which is related to thermal stability throughout the year. Therefore, we found some support for our hypothesis of the existence of general processes shaping biogeographical transition zones. However, the contribution of these variables to all models was small, suggesting that additional factors may enhance our understanding of the processes in biogeographical transition zones. Particularly, historical factors such as orogeny, river dynamics, history of glacial cycles, sea-level changes, climatic changes favouring the formation of refuges, and ecological factors such as guild composition and niche differentiation among biotic components would return a more complete picture of the integration of biotic components in biogeographical transition zones (Leite *et al.* 2016; Ficetola *et al.* 2017). Nonetheless, as a first approach to assess the climatic and environmental properties of biogeographical transition zones, our findings suggest a general trend in predictors as transition-promoting factors related to heterogeneity (topographic and climatic) and non-extreme thermal conditions (precipitation of the warmest quarter and isothermality). So as to confirm or reject the generality of our results, further investigation should evaluate transition zones at different spatial and hierarchical scales, as well as from different regions around the world.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

Thanks go to the editors of this special issue. This work was developed during the visit of EANU to the 'Programa de Investigaciones de Biodiversidad Argentina' (PIDBA) – Universidad Nacional de Tucumán and 'Instituto de Eco-regiones Andinas' (INECOA) – 'Consejo Nacional de Investigaciones Científicas y Técnicas' (CONICET) – Universidad Nacional de Jujuy-Argentina. E. A. Noguera-Urbano thanks all people at both institutions for their hospitality during his visit. Special thanks go to the 'Becas Mixtas 2016 MZO 2017 Movilidad en el extranjero (291062); to Programa de Apoyos a Estudiantes de Posgrado (PAEP), Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México (UNAM); and the Consejo Nacional de Ciencia y Tecnología of México' (CONACyT) (Doctoral scholarship 262582) for financial support.

References

- Brown JL (2014) SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution* **5**, 694–700. doi:10.1111/2041-210X.12200
- Burnham KP, Anderson DR (2002) 'Model Selection and Multimodel Inference. A Practical Information-Theoretical Approach.' (Springer: New York, NY, USA)
- Costa LP (2003) The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography* **30**, 71–86. doi:10.1046/j.1365-2699.2003.00792.x
- Costa LP, Leite YLR (2012) Historical fragmentation shaping vertebrate diversification in the Atlantic forest biodiversity hotspot. In 'Bones, Clones, and Biomes: the History and Geography of Recent Neotropical Mammals'. (Eds BD Patterson, LP Costa) pp. 283–306. (University of Chicago Press: Chicago, IL, USA)
- Cox CB (2001) The biogeographic regions reconsidered. *Journal of Biogeography* **28**, 511–523. doi:10.1046/j.1365-2699.2001.00566.x
- Cracraft J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs* **36**, 49–84. doi:10.2307/40168278
- Diniz-Filho JAF, Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography* **14**, 177–185. doi:10.1111/j.1466-822X.2005.00147.x
- Diniz-Filho JAF, Rangel TFLVB, Bini LM (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography* **17**, 479–488. doi:10.1111/j.1466-8238.2008.00395.x
- Escalante T (2009) Un ensayo sobre regionalización biogeográfica. *Revista Mexicana de Biodiversidad* **80**, 551–560.
- Escalante T (2016) A natural regionalization of the world based on primary biogeographic homology of terrestrial mammals. *Biological Journal of the Linnean Society. Linnean Society of London* **120**, 349–362. https://doi.org/10.1111/bij.12898
- Ferro I (2013) Rodent endemism, turnover and biogeographical transitions on elevation gradients in the northwestern Argentinian Andes. *Mammalian Biology* **78**, 322–331. doi:10.1016/j.mambio.2013.02.005
- Ferro LI, Barquez RM (2009) Species richness of nonvolant small mammals along elevational gradients in northwestern Argentina. *Biotropica* **41**, 759–767. doi:10.1111/j.1744-7429.2009.00522.x
- Ferro I, Morrone JJ (2014) Biogeographic transition zones: a search for conceptual synthesis. *Biological Journal of the Linnean Society. Linnean Society of London* **113**, 1–12. doi:10.1111/bij.12333
- Ferro I, Morrone JJ, Navarro-Sigüenza AG (2017) Biogeographical transitions in the Sierra Madre Oriental, Mexico, shown by chorological and evolutionary biogeographical affinities of passerine birds (Aves: Passeriformes). *Journal of Biogeography* **44**(9), 2145–2160. doi:10.1111/jbi.13015
- Ficetola GF, Mazel F, Thuiller W (2017) Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution* **1**, 0089. doi:10.1038/s41559-017-0089
- Gaston KJ (2009) Geographic range limits: achieving synthesis. *Proceedings. Biological Sciences* **276**, 1395–1406. doi:10.1098/rspb.2008.1480
- Haffer J (1982) General aspects of the refuge theory. In 'Biological Diversity in the Tropics'. (Ed. GT Prance) pp. 6–24. (Columbia University Press: New York, NY, USA)
- Hansen PJ (2009) Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society of London – B. Biological Sciences* **364**, 3341–3350. doi:10.1098/rstb.2009.0131
- Hawkins BA, Field RH, Cornell V, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–3117. doi:10.1890/03-8006
- Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory Physiology & Neurobiology* **141**, 317–329. doi:10.1016/j.resp.2004.03.014
- Hershkovitz P (1969) The evolution of mammals on southern continents. VI. The recent mammals of the Neotropical region. A zoogeographic and ecological review. *The Quarterly Review of Biology* **44**, 1–70. doi:10.1086/405975
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978. doi:10.1002/joc.1276
- Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jönsson KA, Nogués-Bravo D, Wang Z, Whittaker RJ, Fjeldså RJ, Rahbek C (2013) An update of Wallace's

- zoogeographic regions of the world. *Science* **339**, 74–78. doi:10.1126/science.1228282
- IUCN (2012) Red list of threatened species, 2012.1. (IUCN: Cambridge, UK) Available at <http://www.iucnredlist.org/technical-documents/spatial-data> [Verified 5 May 2013]
- Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* **385**, 252–254. doi:10.1038/385252a0
- Kreft H, Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography* **37**, 2029–2053. doi:10.1111/j.1365-2699.2010.02375.x
- Leite YLR, Costa LP, Loss AC, Rocha RG, Batalha-Filho H, Bastos AC, Quaresma VS, Fagundes V, Paresque R, Passamani M, Pardini G (2016) Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 1008–1013. doi:10.1073/pnas.1513062113
- Machado SF, Gregorin R, Mouallem PSB (2013) Small mammals in high altitude phytophysiognomies in southeastern Brazil: are heterogeneous habitats more diverse? *Biodiversity and Conservation* **22**, 1769–1782. doi:10.1007/s10531-013-0511-7
- Maestri R, Patterson BD (2016) Patterns of species richness and turnover for the South American rodent fauna. *PLoS One* **11**, e0151895. doi:10.1371/journal.pone.0151895
- Melo AS, Rangel TFLVB, Diniz-Filho JAF (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* **32**, 226–236. doi:10.1111/j.1600-0587.2008.05502.x
- Mittermeier RA, Robles Gil P, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, daFonseca GAB (2004) 'Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions.' (CEMEX: Mexico City, Mexico)
- Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: the critical role of hotspots. In 'Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas'. (Eds FE Zachos, JC Habel) pp. 3–22. (Springer-Verlag: Berlin, Germany)
- Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology* **51**, 467–494. doi:10.1146/annurev.ento.50.071803.130447
- Morrone JJ (2009) 'Evolutionary Biogeography: an Integrative Approach with Case Studies.' (Columbia University Press: New York, NY, USA)
- Morrone JJ (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa* **3782**, 1–110. doi:10.11646/zootaxa.3782.1.1
- Morrone JJ (2015) Biogeographical regionalisation of the world: a reappraisal. *Australian Systematic Botany* **28**, 81–90. doi:10.1071/SB14042
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. doi:10.1038/35002501
- Naka LN (2011) Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. *Journal of Biogeography* **38**, 681–696. doi:10.1111/j.1365-2699.2010.02443.x
- Nelson G, Platnick NI (1981) 'Systematics and Biogeography: Cladistics and Vicariance.' (Columbia University Press: New York, NY, USA)
- Noguera-Urbano EA (2016) Areas of endemism: travelling through space and the unexplored dimension. *Systematics and Biodiversity* **14**, 131–139. doi:10.1080/14772000.2015.1135196
- Noguera-Urbano EA, Escalante T (2015) Áreas de endemismo de los mamíferos (Mammalia) neotropicales. *Acta Biologica Colombiana* **20**, 47–65. doi:10.15446/abc.v20n3.46179
- Parenti LR, Ebach MC (2009) 'Comparative Biogeography: Discovering and Classifying Biogeographical Patterns of a Dynamic Earth.' (University of California Press: Berkeley, CA, USA)
- Procheş Ş, Ramdhani S (2012) The world's zoogeographical regions confirmed by cross-taxon analyses. *Bioscience* **62**, 260–270. doi:10.1525/bio.2012.62.3.7
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography* **15**, 321–327. doi:10.1111/j.1466-822X.2006.00237.x
- Rangel TFLVB, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography* **33**, 46–50. doi:10.1111/j.1600-0587.2009.06299.x
- Ruggiero A, Ezcurra C (2003) Regiones y transiciones biogeográficas: complementariedad de los análisis en biogeografía histórica y ecológica. In 'Una perspectiva Latinoamericana de la Biogeografía'. (Eds JJ Morrone, J Llorente) pp. 141–154. (Las prensas de Ciencias, UNAM: Mexico City, Mexico)
- Ruggiero A, Lawton JH, Blackburn TM (1998) The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography* **25**, 1093–1103. doi:10.1046/j.1365-2699.1998.00253.x
- Safford HD (1999) Brazilian paramos. I. An introduction to the physical environment and vegetation of the *campos de altitude*. *Journal of Biogeography* **26**, 693–712. doi:10.1046/j.1365-2699.1999.00313.x
- Sarmiento G (1986) Ecological features of climate in high tropical mountains. In 'High Altitude Tropical Biogeography'. (Eds F Vuilleumier, M Monasterio) pp. 11–45. (Oxford University Press: Oxford, MA, USA)
- Sclater WL, Sclater PL (1899) 'The Geography of Mammals.' (Kegan Paul, Trench, Trübner & Company: London, UK)
- Veech JA, Crist TO (2007) Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology and Biogeography* **16**, 650–656. doi:10.1111/j.1466-8238.2007.00315.x
- Wallace AR (1876) 'The Geographical Distribution of Animals. Vol. I & II.' (Harper and Brothers: New York, NY, USA)
- Williams PH (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings. Biological Sciences* **263**, 579–588. doi:10.1098/rspb.1996.0087
- Williams PH, de Klerk HM, Crowe TM (1999) Interpreting biogeographical boundaries among afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography* **26**, 459–474. doi:10.1046/j.1365-2699.1999.00294.x
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3–14. doi:10.1111/j.2041-210X.2009.00001.x

Handling editor: Tania Escalante