

# ECOGRAPHY

## Research

### Museums and cradles of diversity are geographically coincident for narrowly distributed Neotropical snakes

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Factors driving the spatial configuration of centres of endemism have long been a topic of broad interest and debate. Due to different eco-evolutionary processes, these highly biodiverse areas may harbour different amounts of ancient and recently diverged organisms (paleo- and neo-endemism, respectively). Patterns of endemism still need to be measured at distinct phylogenetic levels for most clades and, consequently, little is known about the distribution, the age and the causes of such patterns. Here we tested for the presence of centres with high phylogenetic endemism (PE) in the highly diverse Neotropical snakes, testing the age of these patterns (paleo- or neo-endemism), and the presence of PE centres with distinct phylogenetic composition. We then tested whether PE is predicted by topography, by climate (seasonality, stability, buffering and relictualness), or biome size. We found that most areas of high PE for Neotropical snakes present a combination of both ancient and recently diverged diversity, which is distributed mostly in the Caribbean region, Central America, the Andes, the Atlantic Forest and on scattered highlands in central Brazil. Turnover of lineages is higher across Central America, resulting in more phylogenetically distinct PE centres compared to South America, which presents a more phylogenetically uniform snake

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fauna. Finally, we found that elevational range (topographic roughness) is the main predictor of PE, especially for paleo-endemism, whereas low paleo-endemism levels coincide with areas of high climatic seasonality. Our study highlights the importance of mountain systems to both ancient and recent narrowly distributed diversity. Mountains are both museums and cradles of snake diversity in the Neotropics, which has important implications for conservation in this region.

Keywords: CANAPE, paleo-endemism, phylogenetic diversity, phylogenetic endemism, phylogenetic turnover, Squamata reptiles

## Introduction

Areas with narrowly distributed organisms have always caught the attention of naturalists and are frequently used to interpret biogeographical history and to guide conservation prioritization (Rosen 1978, Kruckeberg and Rabinowitz 1985, Morrone 2018). Beyond geographical rarity, endemism can also be characterized by whether taxa are ancient or recently diverged (paleo- and neo-endemism, respectively – Stebbins 1974). Areas of paleo-endemism support the persistence of lineages extinct elsewhere (e.g. tuataras in New Zealand, Jones et al. 2009), and therefore potentially represent biodiversity museums (Nekola 1999). Conversely, areas of neo-endemism are inhabited by recently diverged lineages, such as the East African great lakes and the high-altitude Andean Páramos, both comprising species-rich radiations of cichlids and plants respectively, and therefore represent biodiversity cradles (Johnson et al. 1996, Madriñán et al. 2013). Besides these well-known examples, Earth's museums and cradles of narrowly distributed biodiversity still await to be precisely delimited (Rosauer and Jetz 2015).

Species richness, phylogenetic diversity, and the different species endemism metrics are traditionally used in the delimitation of biodiversity patterns (Faith 1992, Crisp et al. 2001). However, such metrics do not integrate information on geographical rarity and phylogenetic divergence among all taxa in a given region. This integration is better achieved by the phylogenetic endemism (PE – Rosauer et al. 2009), a metric that weights the branch lengths of each lineage by their respective geographic ranges. Additionally, different kinds of endemism can be distinguished with a method built upon PE, the Categorical Analysis of neo- and paleo-endemism (CANAPE, Mishler et al. 2014). Furthermore, the biodiversity patterns highlighted by PE and CANAPE allow the characterization of environmental conditions that enable evolutionary persistence and biotic diversification (Rosauer and Jetz 2015, Thornhill et al. 2017).

Several distinct topographical and climatic variables have been associated with high endemism levels (Steinbauer et al. 2016, Badgley et al. 2017). For example, strong environmental gradients provide opportunities for species to move in case of climate fluctuations (climatic buffering), potentially

reducing local extinctions (Ohlemüller et al. 2008). The presence and survival of paleo-endemics may be associated with long-term geographical isolation and climatic stability (Sandel et al. 2011, Irl et al. 2015, Antonelli 2017). In contrast, the presence of neo-endemics might be related to recent dispersal to new areas or the formation of new habitats (Antonelli 2015, Merckx et al. 2015). Although the evolutionary processes that promote the accumulation of paleo- and neo-endemics are distinct (e.g. local low extinction rates versus peripatric speciation), they are not necessarily mutually exclusive in geographical space (Mittelbach et al. 2007). For instance, current climatic conditions determine the distributions of terrestrial biomes, thus shaping the range sizes of their endemic lineages (Gallagher 2016) regardless of whether lineages have diverged as early as the Cretaceous or as recently as the Pleistocene. The role of evolutionary history in patterns of endemism remains to be tested, especially for most tropical areas and organisms, for which endemism patterns are not fully mapped or understood.

In the Neotropics, the diversity of terrestrial vertebrates reaches the highest levels throughout tropical forests of Central America, Amazonia, the Atlantic Forest and the Cerrado savannas (Roll et al. 2017). In contrast, species endemism and PE often do not coincide with species richness, with high PE in mammals occurring mostly on islands (e.g. the Caribbean Islands) and mountainous areas (e.g. the Andes and Pantepui) (Rosauer and Jetz 2015). However, it is difficult to assess if this pattern is a trend for other vertebrates that might present different responses to environmental correlates of range size and geographical turnover (Saladin et al. 2019). In Neotropical snakes, patterns of species richness were only recently described and follow the same trends as other terrestrial vertebrates (Roll et al. 2017, Guedes et al. 2018). The extreme diversity of Neotropical snakes is the result of a long and complex history of origin, colonization and diversification of distinct snake clades in the region (Head et al. 2009, Zaher et al. 2018, 2019), which have resulted in uneven patterns of diversity (Cadle and Greene 1993, Fenker et al. 2014); however, very little is known about the resulting patterns of endemism.

Here we map PE in Neotropical snakes, classifying the different kinds of endemism using the CANAPE protocol for spatial phylogenetic analyses described in Mishler et al. (2014). Specifically, we address four main questions.

1) Where are the centres of PE for Neotropical snakes? We expect to find high endemism levels in islands and highlands, following the same trends of PE as in terrestrial mammals (Rosauer and Jetz 2015).

2) Where are the centres of paleo- and neo-endemism? Based on the presence of several relict taxa in Central America (e.g. *Loxocemidae*, *Loxocemus*) (Smith 2013) or in the Atlantic Forest (e.g. *Tropidophiidae*, *Tropidophis*) (Curcio et al. 2012), it is possible that these areas represent museums of snake diversity, thus potentially harbouring paleo-endemics. Areas with high species richness in the Andes and Amazonia might represent cradles of diversity (Rangel et al. 2018), thus potentially harbouring neo-endemics.

3) Do the PE centres have distinct phylogenetic community structure in different portions of the Neotropics? The uneven distribution of the major snake clades in local communities suggests phylogenetic differentiation of the Neotropical snake fauna (Cadle and Greene 1993, Moura et al. 2017). Alternatively, if biotic interchange was sufficiently high (Antonelli et al. 2018a) – e.g. especially after the faunal interchanges related to the Panama isthmus formation – very distant areas might contain phylogenetically similar faunas.

4) Which environmental characteristics are associated with high PE? We tested several known predictors of endemism, including topographic roughness, climate stability, climatic buffering and current climate (seasonality and biome sizes). We expect topographical-related variables to be the most important predictor of endemism, as suggested by regional species-level patterns of endemism (Nogueira et al. 2011, Guedes et al. 2014).

## Material and methods

### Spatial data

To address all four questions, we mapped the geographical distribution of Neotropical snake species using the most complete database of occurrence records available for the region (Guedes et al. 2018). This database includes a curated dataset constructed through taxonomic work and literature review as part of the ongoing project of the Atlas of Brazilian snakes (details in Guedes et al. 2018) supplemented by a taxonomically and geographically revised dataset downloaded from the global biodiversity information facility (GBIF) (updated to <<https://doi.org/10.15468/dl.qsynre>>). The final dataset comprises the records of 1087 species, which represents about 81% of the total number of species currently recognized for the Neotropics (Supplementary material Appendix 1). We followed the delimitation of the Neotropical region from Olson et al. (2001) excluding southern Florida, which harbours an exclusively Nearctic snake fauna, with the exception of exotic taxa recently introduced (Meshaka et al. 2004).

We used alpha hulls to delimit the geographical ranges of species with more than two records. Alpha hulls generate a geometrical representation of a range that closely matches the outermost presence records of each species, decreasing systematic biases associated with convex-hulls (Meyer et al. 2017). Alpha values were set as the minimal value resulting in one continuous range per species (Cox et al. 2016), except for species with naturally disjunct ranges, for which we allowed the formation of more than one alpha hull (details in Supplementary material Appendix 1). The remaining species with only one or two records were represented as points and lines, respectively. The distribution of each species was then mapped on a gridded cylindrical equal-area Behrmann projection, with a resolution equivalent to  $1 \times 1^\circ$  at the 30th degree of latitude (hereafter one-degree resolution). This resolution is the same used in previous studies of snake diversity and PE

in the region (Rosauer and Jetz 2015, Guedes et al. 2018), thus allowing direct comparisons. Additionally, to measure the sensitivity of our results to the chosen resolution, different grid sizes were tested (0.5° and 2° resolution). In order to verify whether the patterns observed for the Categorical Analysis of neo- and paleo-endemism (CANAPE) were robust enough to be recovered regardless of the mapping method, the same procedure was repeated considering point records only.

### Analyses

For the phylogenetic measures, we used the time-calibrated phylogeny of Squamata reptiles from Tonini et al. (2016), which we trimmed for the Neotropical snake species. This phylogeny also includes species with no molecular information available, which were randomly assigned at the genus level (54% of the total). To account for the variation related to the taxonomic assignment, we ran all analyses from a distribution of 100 separate phylogenies and used the median values in subsequent analyses. We tested the sensitivity of our results to this random taxonomic assignment by removing species within both: 1) the 20% highest variation in the tip ages across the sampled phylogenies (standard deviation values); and 2) species with the 20% smallest range sizes. We also repeated the analysis using only the backbone molecular phylogeny (Tonini et al. 2016). As genus ages and therefore the respective variation of species ages within each genus represent a very small proportion of the total amount of branch lengths, we predict that this variation will be less important to our results.

To address Question 1 – where are the centres of PE for Neotropical snakes? – we followed the CANAPE protocol for spatial phylogenetic analyses in Biodiverse 2.0 (Laffan et al. 2010, Mishler et al. 2014). First, two main measures of endemism were generated: phylogenetic endemism (PE – Rosauer et al. 2009) and relative phylogenetic endemism (RPE – Mishler et al. 2014). Phylogenetic endemism is the total branch length (from the time-calibrated phylogeny) of the lineages present at a grid cell divided by the range sizes of the respective lineages. Relative phylogenetic endemism is the ratio between PE measured from the original phylogeny in relation to the PE estimated from a phylogeny with equally distributed branch lengths (see more details in Mishler et al. 2014). When compared to a null distribution (see below), high RPE values represent grid cells with a predominance of longer branches than in the null phylogeny, indicating paleo-endemism. Likewise, low values of RPE indicate grid cell with neo-endemism.

To assess the statistical significance of PE and RPE, we followed the approach suggested by Mishler et al. (2014) in comparing the actual PE and RPE values of each grid cell to the 999 values of a null distribution. The null distribution was calculated by shuffling the terminals of the phylogeny while keeping constant the species richness of each grid cell and the range sizes of each lineage. P-values were estimated from a two-tailed distribution of values to identify areas with higher ( $> 0.975$ ) or lower ( $< 0.025$ ) PE or RPE than the null distribution.

To address Question 2 – where are the centres of paleo- and neo-endemism? – we used PE and RPE for classifying grid cells relative to the amount of paleo- and neo-endemics with CANAPE (Mishler et al. 2014). Grid cells with a higher or lower PE/RPE ratio than the null distribution indicate paleo- or neo-endemism, respectively. Grid cells with PE significantly higher than the null distribution but intermediate values of RPE indicate mixed-endemism (i.e. grid cells with high levels of both paleo- and neo-endemism). For simplicity, we also call grid cells below the 0.01 level of significance mixed-endemic, instead of using the term ‘super-endemism’ suggested in Mishler et al. (2014).

We tested the sensitivity of the CANAPE results to the total extent of our study area by the stepwise exclusion of: 1) the Caribbean Islands – since islands are naturally more isolated and might contain an unequal representation of lineages; 2) the Mesoamerican transition zones and Central American dominion (sensu Morrone 2014), ranging approximately from Mexico to the Costa Rican border with Nicaragua – because the northern parts of the Neotropics contain relatively more taxa with centres of diversity mainly located in the Nearctic or Palearctic regions, thus, with only a few species marginally entering the Neotropics; and 3) the South American ecoregions west of the Andes – trans-Andean South America, as the Andes are a geographical barrier for many Central American taxa to disperse further into South America, and vice versa (Cadle and Greene 1993). We then evaluated how these exclusions affected the patterns of endemism in South American ecoregions east of the Andes (cis-Andean South America).

To help in the interpretation of Questions 1 and 2, we tested whether PE and RPE patterns are similar to equivalent non-range weighted patterns, i.e. phylogenetic diversity (PD – Faith 1992) and relative phylogenetic diversity (RPD – Mishler et al. 2014). We measured these metrics against null models as described above. For comparison, we additionally measured species richness and species richness weighted by the inverse of the range size of each species in a grid cell – weighted endemism (Crisp et al. 2001, Guerin and Lowe 2015). All analyses were performed using Perl wrapper functions to run Biodiverse in the R environment modified from <[https://github.com/NunzioKnerr/biodiverse\\_pipeline](https://github.com/NunzioKnerr/biodiverse_pipeline)>.

To address Question 3 – do the PE centres have distinct phylogenetic community structure in different portions of the Neotropics? – we measured the turnover component of phylogenetic beta diversity among grid cells with the Simpson derived pairwise phylogenetic dissimilarity index (Leprieur et al. 2012). Grid cells were then clustered using unweighted arithmetic mean (UPGMA), which performs well in clustering dissimilarity matrices (Kreft and Jetz 2010).

### Correlations of endemism

To address Question 4 – which environmental characteristics are associated with high PE? – we initially calculated all environmental variables in a resolution equivalent to 0.1

degrees. We then aggregated the resulting values by median to the main resolution adopted in our study (one-degree). Bioclimatic variables were downloaded from CHELSA (Karger et al. 2016). A more detailed explanation on how each potential predictor of endemism was calculated is available in the Supplementary material Appendix 1. We calculated: 1) topographic roughness (or elevational range) of a grid cell – a surrogate for both habitat heterogeneity and geographical isolation (Ruggiero and Hawkins 2008); 2) climatic buffering – the availability of distinct climatic conditions within a short geographical distance (200 km as in Ohlemüller et al. 2008); 3) relictual climate – a measure of whether climatic conditions are very different from the surrounding areas (1000 km as in Ohlemüller et al. 2008); 4) distance to the border of a biome (sensu Olson et al. 2001) – to determine whether a grid cell contains, or is part of, small, isolated biome patches or if it is located in the middle of a large extension of biome; 5) precipitation and temperature seasonality – a measure of whether high seasonality selects lineages with larger ranges (due larger climatic niches, a potential result of higher climatic tolerances, Addo-Bediako et al. 2000); and 6) climate change velocity since the last glacial maximum (LGM; 21 000 yr ago) based on the mean annual temperature (Sandel et al. 2011) – as an estimation of climatic stability.

We then calculated the standardized effect size scores of PE and RPE (Molina-Venegas et al. 2017). This score is the actual PE or RPE in a grid cell minus the mean value of the null PE distribution (from the 999 randomizations for each phylogeny) divided by the standard deviation of the null PE distribution. This procedure allowed us to incorporate information on how much these values deviate from the null distribution as well as to minimize the effects of the number of terminals of the phylogeny occurring in a grid cell, which generally affects PE scores (Rosauer and Jetz 2015).

To test relationships among PE and RPE with the mentioned predictors of endemism, we regressed their respective standardized effect size scores in each grid cell using generalized linear models (GLM) and spatial autoregressive (SAR) models with spatially autocorrelated errors (SAR<sub>err</sub>) to account for spatial autocorrelation (Kissling and Carl 2008). We inferred the degree of spatial autocorrelation through correlograms of the residuals of both SAR<sub>err</sub> and GLM models using the R package ‘spdep’ (Bivand et al. 2011). First, the number of neighbours for the SAR<sub>err</sub> models was selected in order to minimize the corrected Akaike information criterion (AICc). Then, we tested models for all combinations of variables, excepting those that included both climate change velocity and topographic roughness, which are highly correlated ( $r = -0.8$ ), and selected the best model (lower AICc). We also considered any additional model with  $\Delta AICc$  smaller than two as an equally supported model. The values of all environmental predictors were standardized so that the resulting model coefficients indicated the relative contributions of each variable to explain PE or RPE.

## Results

Phylogenetic endemism in Neotropical snakes is significantly high in the entire Central America and in the Andes, in scattered grid cells in the Atlantic Forest, Cerrado and Caatinga, and significantly low in lowland Amazonia (Question 1; Fig. 1a). For RPE, only a few scattered grid cells across the Neotropics were significantly high, indicating that paleo-endemism is not concentrated in any major region (Fig. 1b). In contrast, there is a concentration of grid cells with low

RPE in the central and in the southern Andes (especially at the western slopes).

There is a spatial mismatch between the non-range weighted patterns (PD and RPD – Fig. 1c–d) and the narrowly distributed patterns (PE and RPE – Fig. 1a–b). The only exceptions apply to a small number of grid cells in the Caribbean Islands and Central America with significantly high PE, RPE, PD and RPD. An additional area in the Guiana Shield presents significantly high PD and RPD, indicating the distribution of ancient widely distributed

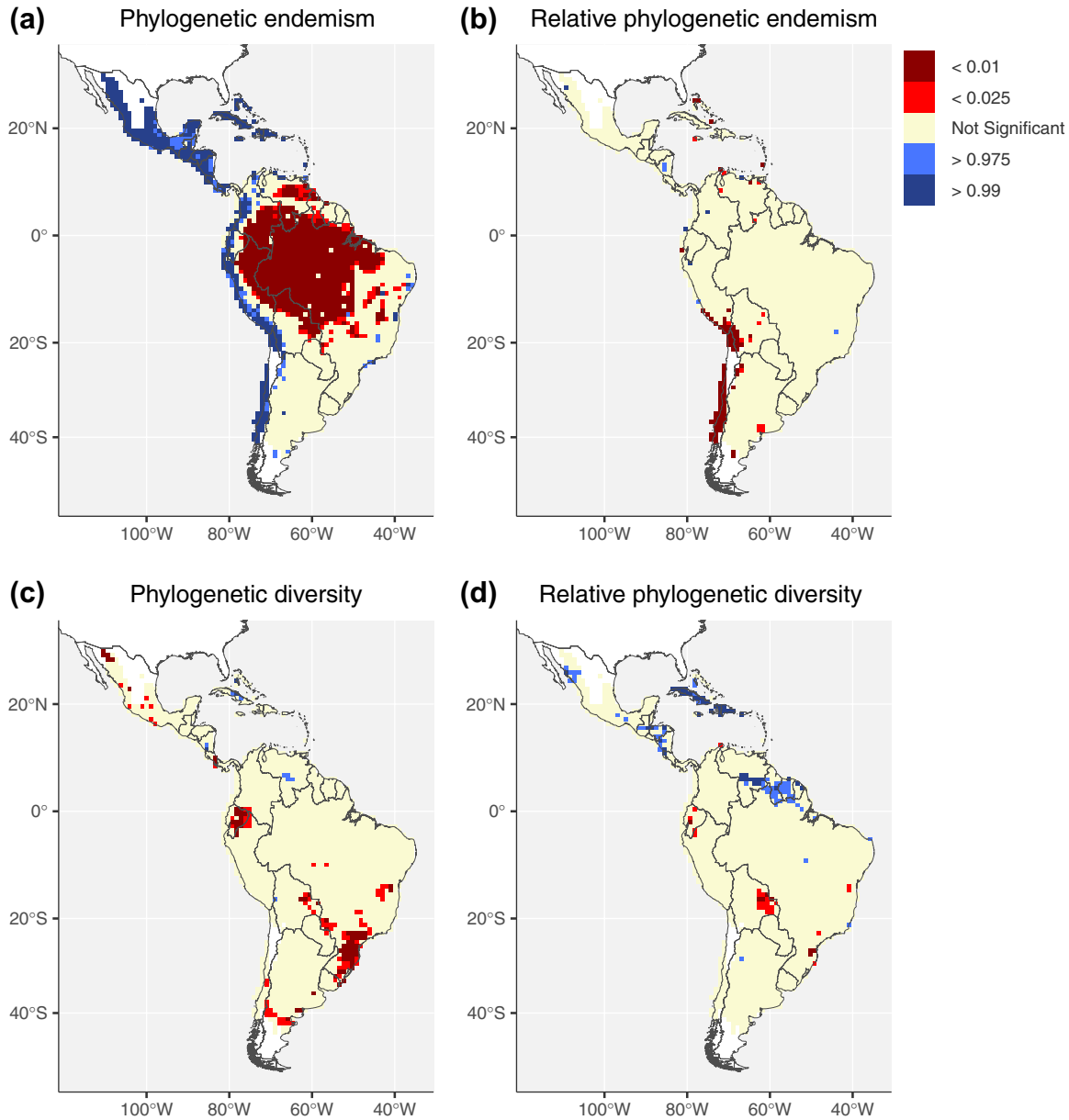


Figure 1. (a–b) Distribution of phylogenetic endemism (PE) and relative phylogenetic endemism (RPE) for Neotropical snakes ( $n = 1087$  species). (c–d) For comparison, similar plots using equivalent non range-weighted metrics: phylogenetic diversity (PD) and relative phylogenetic diversity (RPD). Grid cells with both high PE and high RPE indicate paleo-endemism. High PE and low RPE indicate neo-endemism (Fig. 2). Grid cells with both high PD and RPD indicate a significantly high concentration of ancient PD. In general, range-weighted patterns are very distinct from non-range weighted diversity.

diversity. Such spatial mismatch between widely and narrowly distributed diversity is also indicated by species richness and weighted endemism (Supplementary material Appendix 1 Fig. A1a–d).

CANAPE classified most grid cells with significantly high PE (Fig. 1a) and non-significant RPE (Fig. 1b) as mixed-endemism (Fig. 2a), i.e. significantly high neo- and paleo-endemism (Question 2). Most of the neo- (92 grid cells), paleo- (10 grid cells) and mixed-endemism grid cells (483 in a total of 2150) are located in (or close to) mountainous areas in Central America and in the Andes (Fig. 2d). The CANAPE

analysis restricted to the cis-Andean South America results in an increased extension of mixed-endemism grid cells, especially in the southern portion of the Atlantic Forest, Patagonia and the eastern Andean slopes (Fig. 2b and sensitivity tests below). The CANAPE grid cells are clustered into three main regions according to their phylogenetic similarity (Question 3): 1 – the Caribbean, 2 – the northern portions of Central America and 3 – all remaining grid cells in Central and South America (Fig. 2c). Additionally, the turnover of lineages is considerably smaller within South America than in Central America (Fig. 2c).

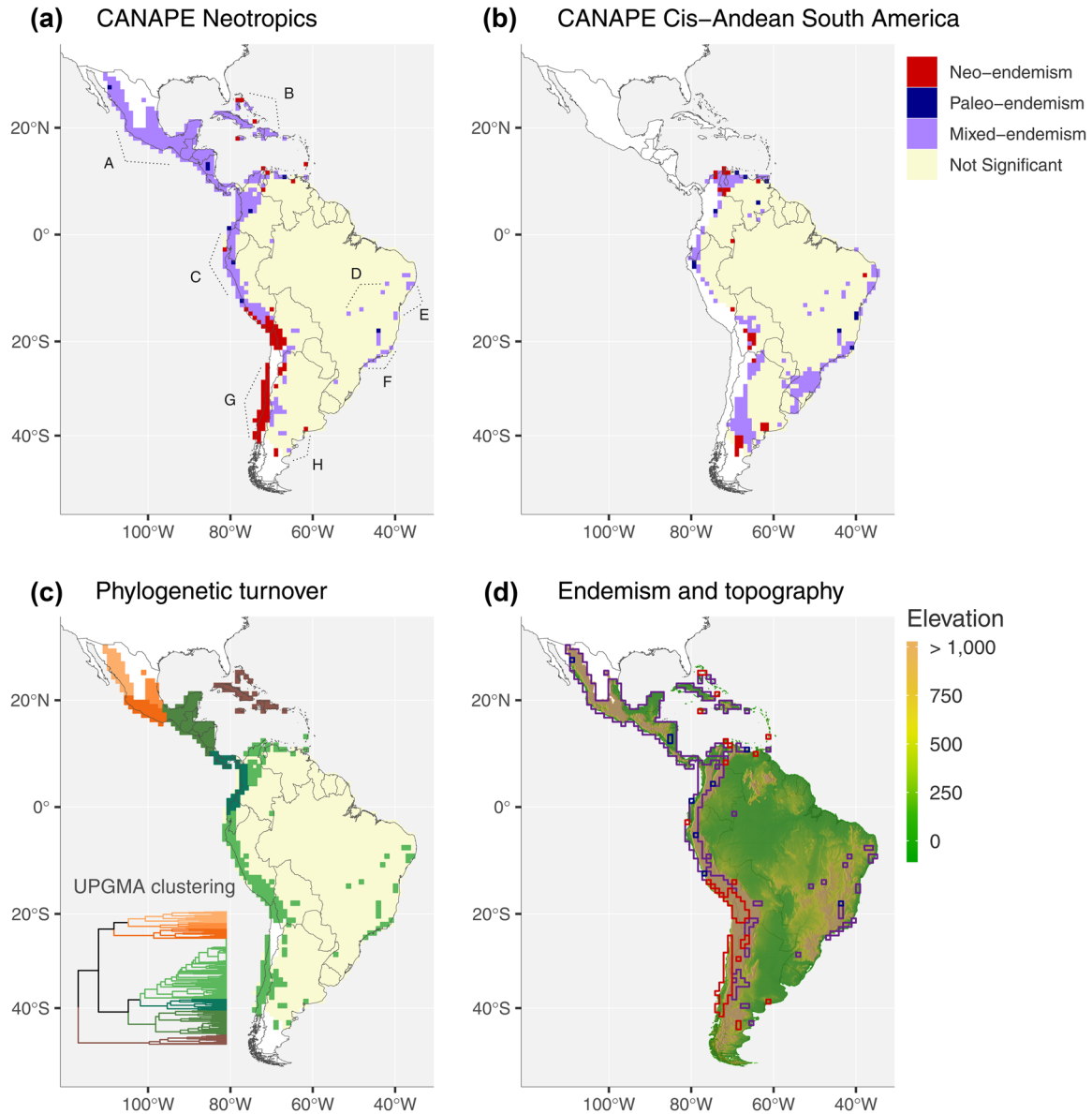


Figure 2. (a) Categorical analysis of neo- and paleo-endemism (CANAPE) for Neotropical snakes. (b) CANAPE restricted to the cis-Andean South America. (c) Phylogenetic dissimilarity (turnover component) of high PE grid cells. Brown, orange and green shades indicate the first three UPGMA clusters. Each terminal in the dendrogram represents a grid cell. (d) Areas with high endemism detected in CANAPE are located mostly on mountains or plateaus. A – Central America, B – the Caribbean, C – northern Andes, D – Cerrado and Caatinga Highlands, E – Northern Atlantic Forest, F – Southern Atlantic Forest, G – southern Andes, H – Patagonia.

The CANAPE results are robust to the removal of species with both small ranges and high age variation across the distribution of phylogenies (Supplementary material Appendix 1 Fig. A2). Even after removing all species without molecular data, the CANAPE results keep the general pattern of mixed-endemism for most grid cells of high PE (Supplementary material Appendix 1 Fig. A2d). Overall, our results are also robust to the grid sizes, always capturing the overall pattern of high mixed-endemism in Central America and in the northern Andes (Supplementary material Appendix 1 Fig. A3, A4). The sequential removal of portions of the study area has only a small effect on the patterns of endemism in the cis-Andean South America, except when this area is analysed alone (Supplementary material Appendix 1 Fig. A5).

The spatial autoregressive error models indicate that topographic roughness is the most important correlate of both PE ( $R^2=0.44$ ) and RPE ( $R^2=0.64$ ) (Question 4 – Table 1). Additional models are within the threshold of  $\Delta AICc=2$ , all of them indicating topographic roughness as the main predictor of PE and RPE (Supplementary material Appendix 1 Table A1). All the additional models also include climatic buffering and low precipitation seasonality as additional predictors of PE, and low precipitation and temperature seasonality for high RPE. Topographic roughness remained the strongest coefficient to explain PE and RPE across the half and two-degrees resolution (Supplementary material Appendix 1 Table A2). Besides the high correlation between topographic roughness and climate change velocity, none of the models within the  $\Delta AICc$  threshold included the last variable (Supplementary material Appendix 1 Table A2). Correlograms indicate that the  $SAR_{err}$  models removed the spatial autocorrelation in the variables in comparison with linear models (Supplementary material Appendix 1 Table A3,

Fig. A6). Therefore, we discuss our results based on the  $SAR_{err}$  models only.

## Discussion

### Diversity patterns and types of endemism

The geographical distribution of phylogenetic endemism (PE) in Neotropical snakes matches an emerging general trend found in mammals (Rosauer and Jetz 2015, López-Aguirre et al. 2018) – that of high PE values prevailing across Central America, the Caribbean Islands, the Andes and the Atlantic Forest (Question 1 – Fig. 2a). Coincident patterns of endemism among such distinct groups of organisms in terms of thermophysiology (ectotherms versus endotherms) or dispersal abilities (bats versus snakes and non-flying mammals) are suggestive of a common evolutionary process producing geographically and historically unique biotas (Jetz et al. 2004, Hughes et al. 2013). Most significantly, high PE for Neotropical snakes predominantly comprises a mix of both ancient and young narrowly distributed diversity (i.e. a mixed-endemism pattern – Question 2). This result indicates that rare, relictual components of diversity are co-occurring with a more recently evolved narrowly distributed diversity (Harrison 2013, Thornhill et al. 2017).

Centres of neo-endemism potentially indicate places where peripheral isolation and recent diversification tend to occur (Mishler et al. 2014). The neo-endemism in grid cells along the western slopes of the southern Andes represents the main deviation from the mixed-endemism trend in Neotropical snakes (Fig. 2a). Additionally, neo-endemism is not a phenomenon seen in plants in the western Andean slopes (Scherson et al. 2017), and for bats, this area is actually a centre of paleo-endemism (López-Aguirre et al. 2018). This indicates that the neo-endemism for snakes in the southern Andes is related to the unique biogeographical history of the group in this region rather than by environmental predictors of endemism alone. For instance, neo-endemism in snakes in this area is explained by the presence of only two endemic species that belong to relatively species-rich genera (Dipsadidae: *Philodryas* and *Tachymenis*) (Cadle 1985, Núñez 1992). Interestingly, the eastern Andean slopes and the Patagonia region at the same latitudes present both mixed- and neo-endemic grid cells (Fig. 2b). These southernmost parts of South America were strongly affected by several glaciation cycles since the Late Miocene (~7 Ma) (Rabassa et al. 2005). These events triggered the extinction of several snake lineages in Patagonia (indicated by the fossil record in the Miocene, Albino 2011) and probably prevented the colonization of the western Andean slopes by additional snake lineages.

The very low number of paleo-endemic grid cells, which are distributed predominantly amongst extensive mixed-endemism centres seems to indicate that mixed-endemism is the main regional trend. Even the presence of relict snake taxa in Central America has not driven distinct levels of paleo-endemism in relation to neo-endemism in the

Table 1. Best spatial autoregressive error models ( $SAR_{err}$ ) for the relationships among the standardized effect size scores of phylogenetic endemism (PE), relative phylogenetic endemism (RPE) and the respective environmental correlates (only variables selected in the respective best models). Topographic roughness was the best predictor of both high PE and RPE, whereas climatic seasonality was negatively correlated to both measures. Asterisks indicate: \*  $p<0.05$ , \*\*  $p<0.01$ , \*\*\*  $p<0.001$ . Gelkerke pseudo R-squared ( $p-R^2$ ). Corrected Akaike information criterion (AICc).

|       | Variables                 | Coefficients      | $p-R^2$ | AICc |
|-------|---------------------------|-------------------|---------|------|
| PE ~  | Topographic roughness     | 0.198 (0.04)***   | 0.44    | 4430 |
|       | Climatic buffering        | 0.153 (0.061)*    |         |      |
|       | Precipitation seasonality | -0.143 (0.045)**  |         |      |
|       | Distance to biome border  | -0.157 (0.049)**  |         |      |
| RPE ~ | Topographic roughness     | 0.262 (0.032)***  | 0.64    | 3528 |
|       | Precipitation seasonality | -0.217 (0.044)*** |         |      |
|       | Temperature seasonality   | -0.181 (0.066)**  |         |      |

region. Instead, northern Amazonia along the Guiana Shield emerges as an additional area with an over-representation of long branches (high PD and RPD), but which are not geographically rare (although with mixed-endemism grid cells in the cis-Andean analyses – Fig. 2b). The high PD and RPD is probably the result of biological communities being formed as the result of multiple colonisations of distantly related lineages (Tucker and Cadotte 2013), from competitive exclusion among closely related taxa, or from an area functioning as a biogeographical museum of non-narrowly distributed diversity (Chown and Gaston 2000). Mechanistic models of speciation/extinction and biogeographical reconstructions of ancestral ranges could be explored in future studies to test these alternative hypotheses.

The contrasting pattern between lowland Amazonia (low PE) and the Andes (high PE) was also reported at the species level for plants, with geographic clustering of rare species in highlands versus the opposite pattern across the lowlands (Zizka et al. 2018). This contrast between highlands and lowlands was also identified for squamate reptiles in the Cerrado and the Caatinga domains in Brazil (Nogueira et al. 2011, Guedes et al. 2014, Azevedo et al. 2016). Additionally, Amazonia contains the largest extension of a biome in the Neotropics (Olson et al. 2001, Ab'Sáber 2003), implying that some of its endemic lineages have wider ranges compared to endemic species in other biomes (especially if most rivers are not important barriers to dispersal, Santorelli et al. 2018, Oliveira et al. 2019); which is also supported by the negative correlation between PE and distance to the biome border (Table 1). Although our method of computing species distributions based on alpha-hull polygons may have overestimated the ranges of some species (Graham and Hijmans 2006), thus exaggerating low PE patterns, the interpretation of our results is robust to the different mapping strategies and grid resolutions (Supplementary material Appendix 1 Fig. A3, A4). Low sampling in Amazonia (Guedes et al. 2018) might account for part of the low PE, but there are still a large number of species occurring across disjunct areas; thus resulting in large ranges when estimated by alpha hulls. Cryptic diversity might play a particular role in the weak endemism of Amazonia, and additional taxonomic reviews and phylogeographic studies may reveal additional species complexes in the region (Prudente and Passos 2010, Passos et al. 2016, 2018) as well in as other parts of the Neotropics (Domingos et al. 2017). Thus, our results set the ground for additional studies on hypotheses concerning the impact of cryptic diversity on PE patterns in the Neotropics.

### Phylogenetic regionalization

The regionalization of the high PE areas in Neotropical snakes (Question 3) offers a perspective on how processes generating endemism may differ across the region. For instance, the long-term oceanic isolation and the relatively smaller areas of islands heavily influence patterns of dispersal and extinction (Kier et al. 2009). Such characteristics of islands might explain why the Caribbean clustered separately from the rest

of the Neotropics in terms of phylogenetic composition – for example, the Caribbean Islands harbour a radiation of tropidophiid snakes, while these snakes are relictual in the rest of the Neotropics (Curcio et al. 2012). In contrast, high PE in grid cells in the northernmost parts of the Neotropics (orange shades in Fig. 2c) are related to the presence of many snake taxa of which the main centres of diversity are in the Nearctic region, appearing as rare branches in the Neotropics (Pinou et al. 2004, Roll et al. 2017). High PE grid cells from southern Mexico to the entire South American continent (green shades in Fig. 2c) harbour a phylogenetically similar snake fauna, a result of the interchange of animal and plant lineages since the Miocene (Bacon et al. 2015). In a broader zoogeographical perspective, this area is also coincident with the northernmost limits of the Neotropical region found for birds, mammals and amphibians (Kreft and Jetz 2013). Finally, grid cells of high endemism as geographically separated as the northern Andes and the Atlantic Forest in South America are more similar to one another than geographically close grid cells in Central America. This reinforces the patterns of high connectivity among different regions within South America (Antonelli et al. 2018a).

### Environmental correlates of phylogenetic endemism

The predominance of mixed-endemism in our results suggests that similar environmental configurations lead to the accumulation of both paleo- and neo-endemics – for example, climatic stability enables the persistence of ancient diversity but can also promote the morphological differentiation of diverging lineages (Fjeldså and Lovett 1997). Consistent with this trend, mixed-endemism grid cells in the Brazilian Atlantic Forest (Fig. 2a) are coincident with some of the more stable portions of this domain – climate refugia (Costa et al. 2018), especially when considering the cis-Andean analysis (Fig. 2b).

High spatial heterogeneity on small scales may also account for the presence of distinct conditions needed for the accumulation of both paleo- and neo-endemics (Zuloaga et al. 2019). In this way, topographic roughness, a well-recognized correlate of low extinction rates for reptiles and a proxy for habitat heterogeneity (Araújo et al. 2008), was the most important predictor of PE in our study. As shown in the case of the Andes, topographic roughness is associated with a continuous history of geological changes (Jetz and Rahbek 2002, Antonelli et al. 2018b). Such topographical changes occur on a deeper timescale than the available climate variables and may explain the even higher correlation between topographic roughness and high RPE (paleo-endemism). Our findings also support the idea that low extinction rates are related to higher climatic buffering in mountainous regions (Table 1), also an indirect measure of environmental heterogeneity (Ohlemüller et al. 2008). The combined effects of topography and climate on PE patterns are not only a Neotropical phenomenon but were also recorded for a variety of groups of organisms in different continents (Rosauer and Jetz 2015, Rosauer et al. 2015, Barratt et al. 2017). Therefore, our results add support to the idea that the interactions of topography and climate are related

to the formation of museums and cradles of biodiversity along mountainous regions (Question 4; Rangel et al. 2018).

The relation of high PE and RPE in Neotropical snakes to current climatic variables such as low precipitation seasonality or the distribution of terrestrial biomes (Table 1) suggests some influence of niche-related processes in generating patterns of endemism (e.g. selection of lineages with narrower niches in less seasonal environments, Slatyer et al. 2013). As niche breadth and dispersal abilities are sometimes phylogenetically conserved (Wiens and Graham 2005), it is possible that even if the environmental conditions are similar, grid cells with phylogenetically distinct communities may display distinct patterns of endemism (Zuloaga et al. 2019). In line with this, the high spatial autocorrelation in the residuals of the GLM models indicates that PE is also linked to more local factors, which could be related to the local history of diversification (Rosauer and Jetz 2015). For example, although the increase of high PE grid cells in the cis-Andean analysis (Fig. 2b) might be the result of pruning taxa that are more widely distributed outside this area, it could also suggest a dynamic of higher dispersal (resulting in larger ranges) of snake lineages in this area. Therefore, our results set the ground for potential studies focusing on particular clades of snakes (with the increase of available molecular data) or in particular regions (e.g. within Amazonia, with the increase of distribution data and taxonomic knowledge). Thus, it will be possible to test whether PE in Neotropical snakes is the result of an emerging trend or the average of disparate individual biogeographical histories.

## Conclusions

In relation to the long-standing discussion on whether mountainous areas of the Neotropics act as museums or cradles of diversity (Fjeldså et al. 2012), our results indicate that for narrowly-distributed Neotropical snakes the answer is both. Topography and certain climate-related characteristics are responsible for the maintenance of both ancient and recent diversity. The areas of high PE found here add conservation value to the already recognized centres of high species richness for snakes in the Neotropics, such as Amazonia (Guedes et al. 2018), and those undergoing extreme habitat loss, such as the Cerrado savannas (de Mello et al. 2015). Some areas already identified as biodiversity hotspots, such as the Atlantic Forest (Myers et al. 2000), are also recovered as centres of mixed-endemism and, therefore, of high conservation value both for their current diversity patterns and for their respective underlying evolutionary and ecological potential (Crandall et al. 2000). Our results highlight the importance of accounting for different biodiversity metrics for a comprehensive characterization of centres of biodiversity.

## Data availability statement

The presence records database used in this study is available in Guedes et al. (2018). Alpha hull polygons are available from the Dryad Digital Repository: <<https://doi.org/10.5061/>

[dryad.3tx95x6bf](https://doi.org/10.5061/dryad.3tx95x6bf)> (Azevedo et al. 2019). The sample of phylogenies used in the analyses is available in Tonini et al. (2016). Scripts used here are available on <[https://github.com/Josh212325/PE\\_Neotropical\\_snakes](https://github.com/Josh212325/PE_Neotropical_snakes)>.

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Supplementary material (available online as Appendix ecog-04815 at <[www.ecography.org/appendix/ecog-04815](http://www.ecography.org/appendix/ecog-04815)>). Appendix 1.