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Interpreting and integrating multiple endemism metrics to identify hotspots for conservation priorities

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ABSTRACT

Endemic species represent an important component of biodiversity. They are functionally and evolutionarily distinct from cosmopolitan species, and are under greater threat of extinction. As a result, endemism hotspots are often used to examine the ecology of range size and to identify the most critical conservation priorities. However, many different definitions and scales have been used to quantify endemism for ecological and conservation research. Here, we review eight distinct, commonly-used metrics of endemism, examining their implications for ecological and conservation studies worldwide. We compare and contrast the spatial distribution and interpretations of the different endemism metrics by applying each of them to a case study of Mesoamerican mammals. We then evaluate the effect of different areal units on the trends in these metrics and their conservation efficacy Hotspots of each metric are identified and overlapped. These overlaps determine consensus endemism hotspots that integrate both the evolutionary history and richness of local endemics. In our case study, both the subdivision of the study region and the endemism metric used influenced the spatial distribution of endemism. Although different biologically-defined subdivisions resulted in similar trends in endemism, endemism hotspots using arbitrary-defined units differed substantially. All eight endemism metrics were positively correlated ($r \geq 0.27$), but highlight different hotspots across Mesoamerica. Only one subdivision was a hotspot for all four endemism categories. Despite their small area, these endemism hotspots protect a disproportionate number of species. These results underscore the importance of considering spatial effects and multiple aspects of endemism.

1. Introduction

The continued, accelerating growth of the human population has ushered the Earth into the Anthropocene, a new geologic age dominated by global-scale, human-caused effects on the environment and the arrival of a global mass extinction (Barnosky et al., 2011; Steffen et al., 2015). In the midst of unprecedented anthropogenic changes to the natural world, we will be unable to preserve all components of biological communities. Therefore, we must decide the characteristics of global biodiversity on which to focus our finite conservation efforts (Ducarme et al., 2013).

One possible such characteristic of biodiversity is endemism (Lamoreux et al., 2006). Endemic species are species, often small-ranged, that are unique to a given region (Myers et al., 2000). These species can represent evolutionary novelty and as such are often functionally and ecologically distinct from their non-endemic relatives (Sobral et al., 2016). For example, small-ranged hummingbirds (Trochilidae spp.) interact with unique flower species when compared with more widespread hummingbirds (Sonne et al., 2016). Endemic species might also provide ecosystem services that their widespread counterparts may be unable to, e.g., *Eucalyptus* trees endemic to Tasmania are less affected by native insect outbreaks than Australian trees with broader distributions (Gorman et al., 2014), and Hawaiian endemic birds disperse a greater diversity of native tree seeds than introduced bird species (Pejchar, 2015).

In their 4th Assessment Report, the Intergovernmental Panel on Climate Change highlighted the importance of endemic species as benchmarks for climate change effects (Fischlin et al., 2007). By virtue of their inherently restricted range sizes, endemic species are also disproportionately affected by climate change, habitat degradation, and

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other anthropogenic effects. Across more than 5000 mammals globally, range size is the most important predictor of extinction risk, particularly from habitat loss and urban development (Fritz et al., 2009). As a result, endemic and range-limited species often act as “indicator species” for their local biological communities. Coupled with their ecological and genetic novelty and their relative vulnerability, the importance of endemic species have made them top priorities for ecological and evolutionary research(Harrison and Noss, 2017). Endemic species also feature in a variety of conservation approaches at scales ranging from single species to landscapes (McDonald et al., 2018; Vargas et al., 2020). As a result, the study of endemism, its drivers, and its distribution on the landscape is an active field of research and is used globally in a variety of ways (Harrison and Noss, 2017; Smiley et al., 2020; Zuloaga et al., 2019).

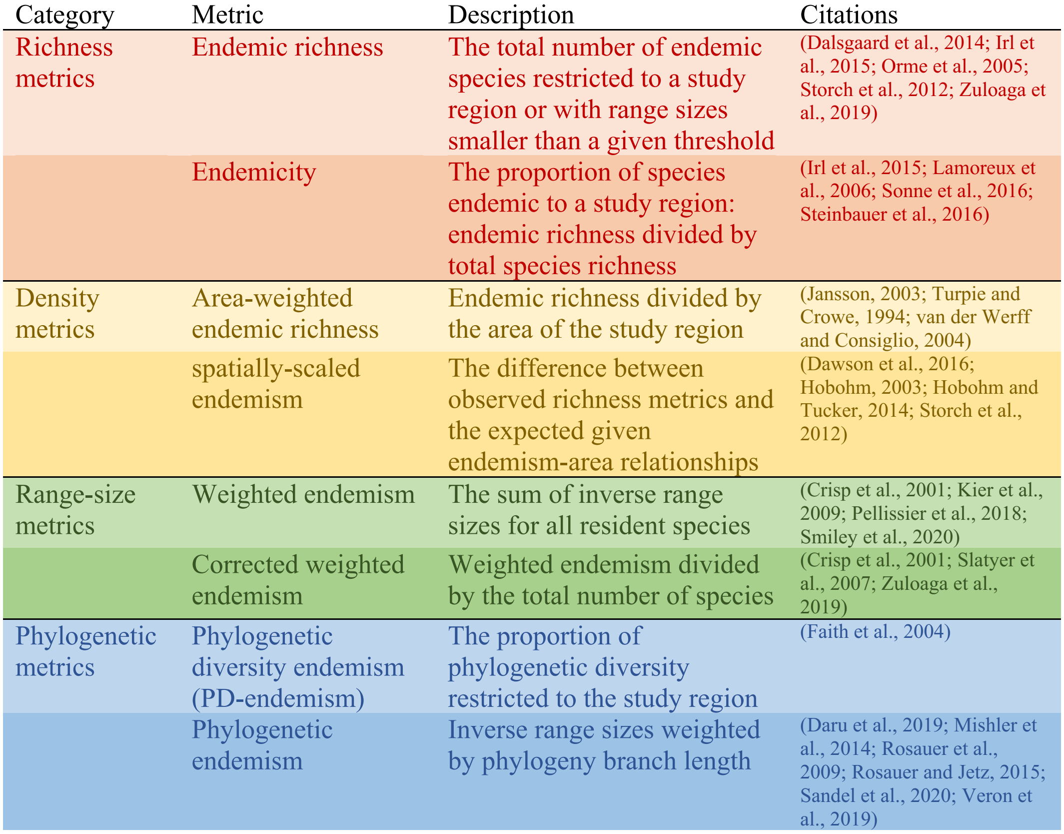
Identifying and describing endemism hotspots, or regions with exceptionally high rates of endemism, can help to understand the physical and biological drivers of endemism, prioritize certain broad-scale regions for conservation, and focus stakeholder efforts (Keppel et al., 2018; Myers et al., 2000; Wilson et al., 2006). Conserving endemism hotspots also protects higher overall biodiversity than expected by chance (Albuquerque and Beier, 2015; Lamoreux et al., 2006), even though endemism hotspots are not fully concordant with regions of high threat or diversity (Orme et al., 2005; Shrestha et al., 2019). Hotspot-based conservation has therefore been heralded as an effective (albeit oversimplified) strategy for global biodiversity conservation and is used by organizations ranging from global organizations like Conservation International and the World Wildlife Fund to regional ones such as the US Fish and Wildlife Service (Marchese, 2015).

Despite the ubiquity of endemism and endemism hotspots in ecological and conservation literature, we currently lack a scientific consensus on the quantitative definition of endemism (Hobohm and Tucker, 2014). Recently, the increase in high-quality, large-scale occurrence and range data has allowed researchers to examine questions relating to species distributions and range sizes easily and efficiently. As a result, many different metrics quantifying endemism have been developed, each with their own biological or conservation implications tailored to specific research questions spanning ecology, evolution, and conservation (Supplementary Table 1). Although the methods used to quantify endemism vary, the commonly-used endemism metrics generally provide information on one of four aspects of a biological community: 1) the number or proportion of endemic species within the community (*richness metrics*), 2) the density of endemic species within the community (*density metrics*), 3) the degree of range-restriction across taxa within the community (*range-size metrics*), and 4) the evolutionary distinctiveness of the community (*phylogenetic metrics*) (Table 1). The multiple, often contradictory definitions of endemism have caused some key questions to remain unresolved about the biology, geography, and conservation of endemic species (Dawson et al., 2016). Additionally, the differences among these metrics and how they are manifest in the realized distribution of endemism hotspots across geographic space have yet to be examined in any detail.

Another complicating factor in the study of endemism is that the apparent distribution of endemism across landscapes is highly influenced by the scale, resolution and extent of analyses (Daru et al., 2020; Dawson et al., 2016; García-Llamas et al., 2018). Often, the study region boundaries used for endemism studies (especially metrics that rely on discrete study region subdivisions like endemic richness) are arbitrary (e.g., political boundaries, grid cells) that have no real biological basis

Table 1

A summary of eight commonly-used endemism metrics, with a description of the metric and a list of papers that apply this metric to either conservation or ecological questions. See Supplementary Table 1 for a comprehensive list of papers examined for this review (Dalsgaard et al., 2014; Jansson, 2003; Mishler et al., 2014; Sandel et al., 2020; Turpie and Crowe, 1994).



Category	Metric	Description	Citations
Richness metrics	Endemic richness	The total number of endemic species restricted to a study region or with range sizes smaller than a given threshold	(Dalsgaard et al., 2014; Irl et al., 2015; Orme et al., 2005; Storch et al., 2012; Zuloaga et al., 2019)
	Endemicity	The proportion of species endemic to a study region: endemic richness divided by total species richness	(Irl et al., 2015; Lamoreux et al., 2006; Sonne et al., 2016; Steinbauer et al., 2016)
Density metrics	Area-weighted endemic richness	Endemic richness divided by the area of the study region	(Jansson, 2003; Turpie and Crowe, 1994; van der Werff and Consiglio, 2004)
	spatially-scaled endemism	The difference between observed richness metrics and the expected given endemism-area relationships	(Dawson et al., 2016; Hobohm, 2003; Hobohm and Tucker, 2014; Storch et al., 2012)
Range-size metrics	Weighted endemism	The sum of inverse range sizes for all resident species	(Crisp et al., 2001; Kier et al., 2009; Pellissier et al., 2018; Smiley et al., 2020)
	Corrected weighted endemism	Weighted endemism divided by the total number of species	(Crisp et al., 2001; Slatyer et al., 2007; Zuloaga et al., 2019)
Phylogenetic metrics	Phylogenetic diversity endemism (PD-endemism)	The proportion of phylogenetic diversity restricted to the study region	(Faith et al., 2004)
	Phylogenetic endemism	Inverse range sizes weighted by phylogeny branch length	(Daru et al., 2019; Mishler et al., 2014; Rosauer et al., 2009; Rosauer and Jetz, 2015; Sandel et al., 2020; Veron et al., 2019)

(Ferreira and Boldrini, 2011). Using discrete subdivisions often excludes species with distributions overlapping two of these arbitrary subdivisions, irrespective of the range-size, novelty, or vulnerability of those species. For example, the threatened Himalayan goral (*Naemorhedus goral*) has a very restricted range, but because its range stretches across four countries, it would be excluded from country-level endemism analyses. Furthermore, applying these metrics to discrete study region subdivisions of different shapes and sizes influences the apparent distribution of endemism across a landscape, a phenomenon called the Modifiable Areal Unit Problem (MAUP; Jelinski and Wu, 1996). The MAUP may lead to discrepancies between prioritized regions and the areas with the highest rates of endemism, especially if applied across arbitrary or non-biologically defined study regions (Ferreira and Boldrini, 2011). However, few studies have examined the MAUP in endemism (Daru et al., 2020; Ferreira and Boldrini, 2011; García-Llamas et al., 2018; Rahbek, 2005), especially across multiple endemism metrics. Because of these unresolved questions, the mechanisms behind the spatial distribution of endemic species are still unclear, and we lack a complete understanding of regions of high endemism (Hobohm, 2014; Orme et al., 2005).

Here we examine these questions using the current body of literature on the distribution of endemism hotspots. First, we compare and contrast eight commonly-used methods of quantifying endemism by reviewing recent literature examining the distribution of endemism hotspots (Supplementary Table 1), describing the benefits and challenges of applying each metric. We identify what each of the metrics contribute to our understanding of species range dynamics. We then review the biological interpretation and the conservation implications of endemism hotspots as they are influenced by the metric used, the scale of analysis, and the MAUP, using endemism in Mesoamerican mammals as a case study. Ours is the first comprehensive analysis examining how differences in definition influence continental-scale distributions of endemism. Finally, we explore the best practices and implications for using endemism for biogeographical studies and for conservation prioritization. We introduce a framework that provides a more holistic description of endemism trends and adds nuance to the research and conservation of endemism hotspots.

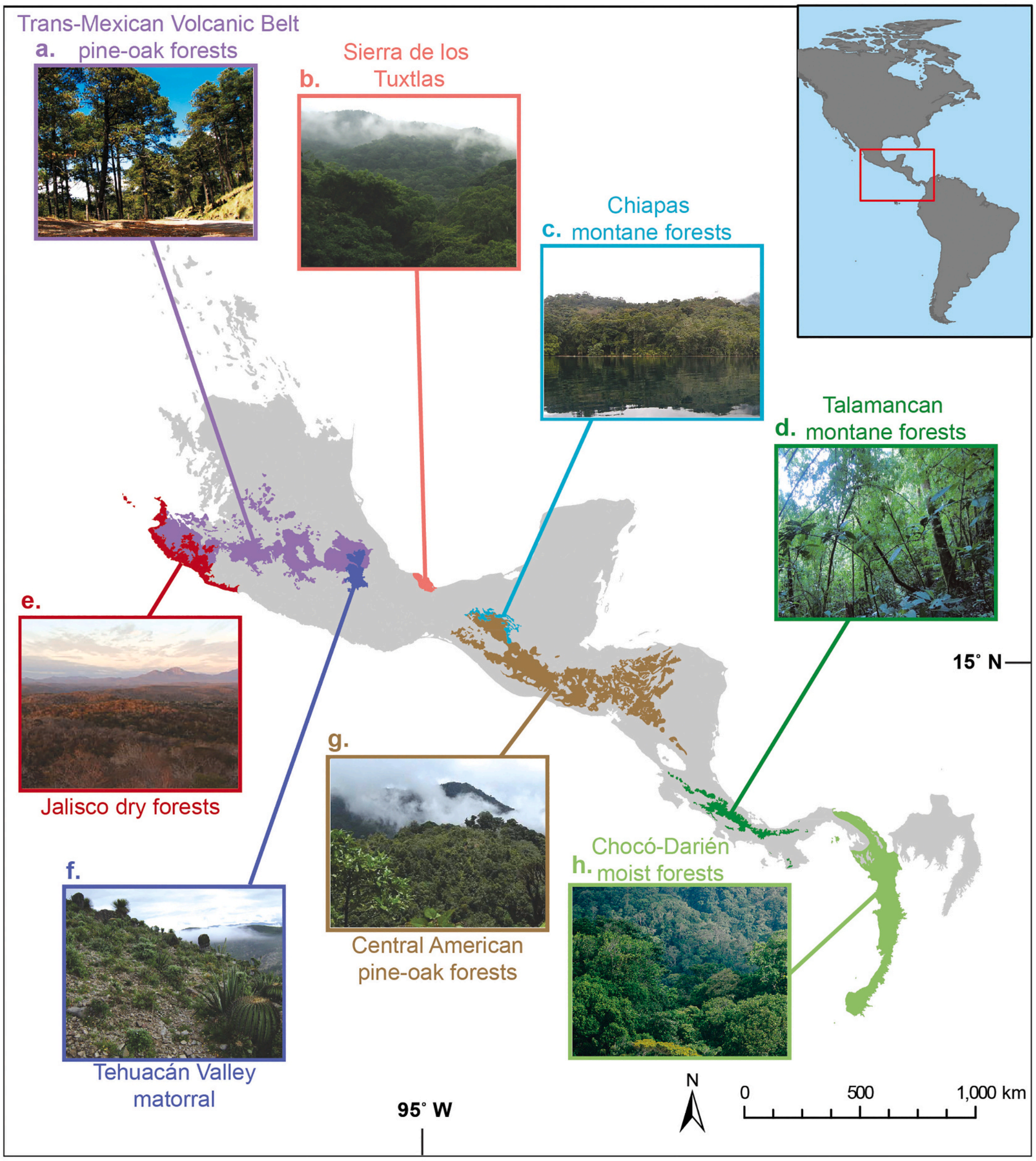


Fig. 1. A reference map of the study region, comprising 41 terrestrial ecoregions from Central Mexico through northern Colombia. Notable ecoregions referenced in this paper have been highlighted. Photo citations are listed in Appendix S7.

2. Case study: Mesoamerica

We examine the differences between the eight commonly-used endemism metrics described in Table 1, together with the influence of the MAUP, by applying them to the distributions of mammalian endemics in Mesoamerica. Mesoamerica (i.e., central Mexico through Panama; Fig. 1) provides several benefits for studying endemism hotspots in both a biological and a conservation context. First, Mesoamerica is highly biodiverse, regardless of taxon. More than 20,000 plant species, 1000 bird species, and 500 mammal species are found within the region (Calderon et al., 2004). In fact, Mesoamerica is the second-most speciose biodiversity hotspot of the 25 originally defined by Myers et al. (2000). Mesoamerica also has high *endemism* regardless of how it is measured, possibly due to its unique geography as a topographically diverse, recently-formed isthmus conjoining two continental landmasses (DeClerck et al., 2010; Sarkar et al., 2009). Mesoamerica is located entirely within the tropics, which mitigates the potential effects of latitude on endemism calculations (Hillebrand, 2004). Despite its location in the tropics, the wide-ranging topography of Mesoamerica has led to five different biomes within the region. These habitats range from dry savannas to cloud forests and are highly heterogeneous, perhaps leading to increased habitat specialization (and therefore endemism) within the region (Bacon et al., 2016; Cárdenes-Sandí et al., 2019; DeClerck et al., 2010).

In addition to its biological and geographic relevance for endemism studies, Mesoamerica also provides a useful case study for conservation and management. The extraordinarily high biodiversity and endemism of Mesoamerica places it at a leading position in the receipt of global conservation efforts and studies. In contrast to many other tropical regions of comparable size (e.g., Brazil, Democratic Republic of the Congo, Indonesia), Mesoamerica comprises eight different countries, each with their own conservation aims and practices. Although Mesoamerica contains many large protected areas, the diversity of county-level policies and the wealth disparity across the eight countries have caused the efficacy of these protected areas to vary widely (Heino et al., 2015). For example, the protected areas in Belize, Costa Rica, Panama, and Mexico effectively guard against deforestation, but those in Guatemala and Honduras have higher rates of deforestation *within* protected areas than outside of them (Heino et al., 2015). In fact, Patuca National Park, a large protected area in Honduras, had the 4th highest rate of carbon emission of any IUCN-designated protected area between 2000 and 2012, primarily due to illegal logging (Collins and Mitchard, 2017).

To examine the trends in Mesoamerican endemism, we first describe the effect of the MAUP on the distribution of endemic richness across Mesoamerica. We define, interpret, and apply each of the eight common endemism metrics to Mesoamerican mammals, comparing the geographical distribution of hotspots resolved by each metric. Throughout, “study region” is defined as the entire area of interest (i.e., Mesoamerica), which can be subdivided into different discrete geographic subdivisions (e.g., countries, ecosystems, biomes). We used IUCN range maps (IUCN, 2020) to examine the differences between the metrics for mammals in Mesoamerica (Table 1).

3. Definitions of endemism

3.1. Richness metrics

Richness metrics examine and compare the number of species restricted to defined spatial areas. For example, the critically-endangered volcano rabbit (*Romerolagus diazi*) is found exclusively in central Mexico, and is therefore endemic to Mexico (Velázquez and Guerrero, 2019). Counting the number (endemic richness) or proportion (endemicity) of species that are similarly restricted to Mexico yields the richness-based metrics of Mexican endemism.

Endemic Richness (*E*) is the number of species (*E*) that have a global distribution restricted to a given, discrete subdivision of a study region. By describing the number of species that would be lost if the habitat of that subdivision were completely degraded, endemic richness can provide an assessment of each study region subdivision's role in maintaining global species richness(Myers et al., 2000; Orme et al., 2005). For ecological studies, if habitat types (or ecoregions) are used as the study region subdivisions, endemic richness can be interpreted as the number of habitat specialists (Ferreira and Boldrini, 2011).

Endemic richness is the most widely-used endemism metric in research on endemism hotspots and conservation today (Supplementary Table 1). For example, Parque Internacional La Amistad, on the border of Costa Rica and Panama, was inscribed into the UNESCO World Heritage List because of its “extraordinary levels of endemism across numerous taxonomic groups” with several amphibian species confined to the park boundaries (United Nations Educational, Scientific, and Cultural Organization (UNESCO), n.d.). The seminal biodiversity hotspots article by Myers et al. (2000), which uses endemic richness to classify global biodiversity hotspots by limiting hotspots to regions with >1500 endemic vascular plant species, is widely applied by the World Wildlife Fund and other organizations to determine regions of special importance. In fact, endemic richness predicts global protected area distribution better than overall biodiversity (Loucks et al., 2008).

A challenge of examining endemic richness is that, on global scales, it generally follows similar latitudinal trends as overall species richness. The broad relationship between latitude and range size, commonly called Rapoport's rule (Stevens, 1989), may be caused by the increasing annual climate variability towards the poles (Gutiérrez-Pesquera et al., 2016) and therefore broader thermal tolerances in temperate species (Cadena et al., 2012). Because of Rapoport's rule, local variations in endemic richness may become masked by trends in species richness, especially for studies spanning latitudes. The confounding effects of species richness may influence the description of endemism hotspots, biasing endemism-based conservation efforts towards regions that have more total species, regardless of the actual local rates of endemism.

Endemicity (*E/S*), the proportion of the total number of species within a community (*S*) that are endemic, factors out the influence of global richness trends (Irl et al., 2015). Instead of describing a study region subdivision's absolute contribution to global species richness (as measured with endemic richness), endemicity measures the relative contribution of the subdivision to local species richness. This metric indicates the percentage of the local species pool that may go extinct if all of the habitat within the subdivision were degraded. For local or regional-scale studies or studies that have little variation in species richness across subdivisions, trends in endemicity often closely mirror trends in endemic richness (see section 6). However, in global-scale studies with large variations in species richness or studies with very fine spatial resolutions, researchers should strongly consider using endemicity instead of endemic richness to determine regions of relatively high endemism (Irl et al., 2015; Sandel et al., 2011).

3.2. Density metrics

Endemic richness and endemicity can be effective for determining the overall contributions of defined study region subdivisions to biodiversity (Orme et al., 2005). However, when these subdivisions vary widely in size (e.g., if calculating endemic richness by country), biodiversity-area relationships must be taken into account. The well-documented species-area relationship states that larger regions are more biodiverse than smaller regions following a power law (Matthews et al., 2019; McGuinness, 1984). Larger regions also have greater numbers of restricted species (higher endemic richness). As a result, larger areas often appear disproportionately rich in endemic species and have a higher proportion of endemic species (endemicity) (Dawson et al., 2016; Hobohm and Tucker, 2014; Storch et al., 2012). Density-based metrics account for the relationship between endemism and the sizes of study region subdivisions (van der Werff and Consiglio, 2004).

Area-weighted Endemic Richness (*E/A*) is the simplest density-based metric to calculate and interpret, dividing the endemic richness of each study region subdivision by its area (A) (Hobohm and Tucker, 2014). Instead of describing the total or relative number of endemic species of the entire subdivision like richness metrics, area-weighted ER depicts the number of endemic species per unit area within each subdivision. Therefore, it can be used as an estimate of the marginal biodiversity cost of habitat loss within the region, in addition to the evolutionary "speed" in the region (Hobohm and Tucker, 2014).

Although this metric provides a simple method to account for the size of each subdivision, because species richness and endemic richness increase with area as a power function instead of linearly, area-weighted ER tends to underestimate the endemism of larger regions in favor of smaller regions (Storch et al., 2012). Further, total species richness and endemic richness scale at different rates, influencing the relationship between *endemicity* and area (Storch et al., 2012). Because of the nonlinear relationships caused by aggregation effects and the MAUP, comparing multiple study regions using area-weighted ER is generally inadvisable (Hobohm and Tucker, 2014), and research that attempts to compare trends or determine drivers of endemism across a patchwork of differently-sized subdivisions should avoid the use of area-weighted ER.

Spatially-Scaled Endemism is an alternative density-based metric that acknowledges the non-linear relationships between species richness, endemic richness, and area. Developed originally by Bykov (1979) and expanded by Hobohm (2003), spatially-scaled endemism first models the expected relationship between endemism and area using a power function based on the combined area of all species ranges used in the study (Appendix S2),

$$\widehat{E} = x log_{10} A - b \tag{1}$$

where $\widehat{E}$ is the expected endemism, A is the area of the study region subdivision, and x and b are experimentally-derived constants (Appendix S2; Hobohm and Tucker, 2014). Then, the ratio between the actual and expected endemism for each study region subdivision is calculated: $(E/\widehat{E})$. This metric can be used with either endemic richness or endemicity to fit specific research questions by changing the modelled relationship. Spatially-scaled endemism gives an assessment of the relative endemism of a subdivision compared to the global or continental trend.

Similar to area-weighted ER, spatially-scaled endemism allows for an area-debiased estimate of the marginal effect of habitat degradation on biodiversity (Dawson et al., 2016). However, the calculated spatially-scaled endemism values are harder to interpret than area-weighted ER values, and cannot be compared across study regions unless global endemism-area relationships like those modelled by Storch et al. (2012) are used. Despite these issues, spatially-scaled endemism has the potential to be effective for identifying endemism hotspots and describing trends in endemism. Although it has yet to appear widely in ecological literature of vertebrates (Supplementary Table 1), recent biogeographical reviews recommend the use of spatially-scaled endemism over the richness metrics (Dawson et al., 2016).

3.3. Range-size metrics

Richness- and density-based endemism metrics all measure endemism as defined by a species being unique to a discrete region, whether the region is arbitrarily defined (e.g., grid cells), politically defined (e.g., country boundaries), or biologically defined (e.g., ecoregions). These metrics measure the number, proportion, or density of species found only within those regions, and as a result, they all suffer from the MAUP. However, another aspect of endemism important for both ecology and conservation is the actual area or extent of a species' range. For example, the short-tailed singing mouse (*Scotinomys teguina*) and Underwood's water mouse (*Rheomys underwoodi)* are both endemic to Mesoamerica. *S. teguina* is found across high-elevation Mesoamerica; however, *R. underwoodi* is restricted to the Talamancan range in western Panama and southern Costa Rica (Fig. 1d). All else being equal, the more range-restricted species could be a more important target for conservation actions, as it is at higher risk of extinction from habitat loss and climate change. For this reason, and because of the influence of areal unit on the analysis of endemism trends, many studies examining the distribution, drivers, and hotspots of endemism prefer to use the relative extent of a species' range instead of whether or not a species is entirely restricted to a certain discrete region (Guerin and Lowe, 2015; Kier and Barthlott, 2001; Veach et al., 2017). Range-size endemism metrics circumvent the need for an a priori defined areal unit, and as a result, are increasingly applied to both ecology and conservation questions.

Weighted Endemism is the most commonly- applied range-size metric. Weighted endemism is calculated as the sum of the inverse range size (through range maps or by summing occupied cells) of all study species at a given location (Guerin et al., 2015; Guerin and Lowe, 2015; Kier and Barthlott, 2001; Williams, 1998),

$$W = \sum_{i=1}^{S} \frac{1}{r_i} \tag{2}$$

where S is the total species richness at the location and r_i is the absolute range size or total number of pixels occupied by the i-th species (Guerin and Lowe, 2015). Species with extremely restricted ranges are therefore weighted more heavily than those with cosmopolitan distributions. The previously-described metrics evaluate the relative number or proportion of endemic species within a defined study region subdivision. However, weighted endemism measures how restricted the ranges of all the species resident to a single location are. The term "weighted endemism" is often used somewhat interchangeably with "range-size rarity" or similar names, although in many cases range-size rarity refers to the occupancy of a species within a limited study region, as opposed to the global species range (Guerin and Lowe, 2015; Williams, 1998).

Because it is not dependent on a particular study region or subdivision, weighted endemism is especially useful for global-scale analyses across many taxa (e.g., Kier et al., 2009; Pellissier et al., 2018). For example, Herkt et al. (2016) used weighted endemism to determine the spatial trends in bat endemism across Africa, and Zuloaga et al. (2019) applied weighted endemism while examining the predictive power of climate and topography on amphibian and mammal endemism. Although weighted endemism is still subject to aggregation effects (Daru et al., 2020), the lack of discrete study region subdivisions makes weighted endemism useful for evaluating hypotheses on the relationships between endemism and geographical covariates (Supplementary Table 1).

Inverse range sizes have also been used as a basis for conservation prioritization with significant success. In particular, prioritization schemes aiming to maximize the complementarity of selected sites (the proportion of total species in the study region that are protected) often builds upon range-size rarity or similar measures (Veach et al., 2017; Williams, 1998). For example, rarity is employed by the well-known Zonation program (Moilanen et al., 2005) in heuristic algorithms to rank spatial units by their marginal conservation importance (Moilanen et al., 2014). This method, in effect, integrates weighted endemism with prioritization schemes based on species richness in a way that preserves the most species in the amount of space. Proposed protected areas using algorithms such as these conserve a greater number of species than those that simply attempt to maximize species richness at *each* protected area for both terrestrial (Albuquerque and Beier, 2015; Veach et al., 2017) and marine (Astudillo-Scalia and de Albuquerque, 2020) systems.

Because weighted endemism sums all the inverse species ranges at a location, it is, like endemic richness, moderately correlated to the total species richness at the location (Slatyer et al., 2007). **Corrected Weighted Endemism (W/S)** decouples the trend between weighted endemism and species richness by dividing it by the species richness at each location (Crisp et al., 2001). Therefore, corrected weighted endemism gives values of the average inverse range-sizes of species at the location, resulting in a measure of range-restriction across the biological community. Corrected weighted endemism can be useful in studies examining the trends and drivers of small range size itself. However, corrected weighted endemism devalues regions that have more overall species, even if the number of range-restricted species is the same, as the species with broad ranges increase the average range size at the location (Slatyer et al., 2007). For example, a location containing only the range-restricted mouse *R. underwoodi would in fact have higher corrected weighted endemism than a location containing both R. underwoodi and the more broadly distributed S. teguina.* For the purpose of identification and research into the distribution and conservation of endemism hotspots, using corrected weighted endemism is therefore discouraged in favor of weighted endemism.

3.4. Phylogenetic metrics

Many different mechanisms can cause small range sizes in species, including speciation events (e.g., montane plants, Steinbauer et al., 2016), competition and dispersal constraints (e.g., tropical vertebrates, Cadena et al., 2012; Munguía et al., 2008), and recent range contractions (Gavin, 2015; Pellissier et al., 2018). By considering the evolutionary history of endemic hotspots, we can capture the novelty and distinctiveness of endemism across time and space (Rosauer et al., 2009), providing a more nuanced understanding of the communities and their significance.

Endemic Phylogenetic Diversity (herein called PD-endemism) was the first widespread method of incorporating phylogenetics into the study of endemism (Faith et al., 2004). This metric describes the proportion of phylogenetic diversity that is unique to a given, discrete study region subdivision,

$$PDE = \frac{\sum_{e=1}^{E} L_e}{\sum_{s=1}^{S} L_s} \tag{3}$$

where E is the endemic richness, S is the total species richness, and L_e and L_s are the phylogenetic branch lengths of the endemic species and all resident species, respectively (including the intermediate nodes on the phylogeny)(Faith et al., 2004). Similar to richness-based metrics like endemic richness, PD-endemism measures that subdivision's contribution to the global phylogenetic diversity, describing the amount of evolutionary history that would be lost if the region's habitat were entirely degraded. PD-endemism is a useful supplement to richness-based endemism metrics when examining the evolutionary importance of given study areas. However, like the richness metrics, PD-endemism is defined in terms of discrete subdivisions and is therefore influenced by the size and definition of each, suffering from the MAUP.

In contrast to PD-Endemism, which combined phylogenetics with richness endemism metrics, **Phylogenetic Endemism** combines phylogenetics with range-size metrics, in particular weighted endemism (Rosauer et al., 2009). Phylogenetic endemism weights each branch of the phylogeny containing all the species found within each subdivision by the range size of the related node,

$$\sum_{c=1}^{C} \frac{L_c}{r_c} \tag{4}$$

where C is the total number of nodes on the phylogeny containing all resident species, L_c is the branch length of the c-th node, and r_c is the combined range size of all descendants of the c-th node (Rosauer et al., 2009). This metric can be interpreted as an estimate of the phylogenetic and evolutionary "uniqueness" of a location.

Phylogenetic metrics (and phylogenetic endemism in particular) are increasingly applied successfully to ecological and conservation questions (Supplementary Table 1, Daru et al., 2019; Smiley et al., 2020; Veron et al., 2019). However, phylogenetic-based metrics are, naturally, highly dependent on the quality of the phylogeny used. If many species are unresolved in the phylogeny, error is introduced into both phylogenetic metrics. Unfortunately, the least-resolved species are often exactly the ones that influence these metrics the most by virtue of their rarity and small range sizes. One suggested method to mitigate this problem is to replicate the analyses over a large subset of bootstrapped trees (e.g., Rosauer and Jetz, 2015), which serves to estimate the uncertainty of the values at each location and to provide "consensus" values of phylogenetic endemism. Alternatively, maximum clade credibility trees can be developed from the posterior distribution of trees (Smiley et al., 2020). However, these methods are especially computationally-intensive, and for studies on relatively unresolved taxa, may not provide any additional clarification.

Spatial trends in phylogenetic metrics do not always match either phylogenetic diversity or other endemism definitions. Daru et al. (2019) calculated the overlap of regions with high phylogenetic endemism, phylogenetic diversity, and the endemic richness-based hotspots from Myers et al. (2000), finding some overlap in the tropics, but generally low concordance globally. This discordance highlights differences in the interpretations of the metrics. Whereas endemic richness measures the absolute numbers of species unique to a region, whether or not the species are closely related or genetically unique, phylogenetic endemism indicates the overall evolutionary novelty of each species pool. The spatial mismatch between phylogenetic metrics and richness-based metrics reaffirms that incorporating phylogenetics into endemism research can influence the geographical distribution of endemism and therefore its drivers and where conservation efforts are directed.

4. Consensus hotspots

Biological hotspots are usually calculated by delimiting regions with values higher than a given quantile threshold for a single metric. For example, Daru et al. (2019) defined hotspots as regions with phylogenetic endemism above the 97.5 percentile. Other studies have used the highest 10% or 15% of land area to delineate hotspots (de Albuquerque et al., 2015; Smiley et al., 2020). However, as described above, the different endemism metrics have different evolutionary and ecological implications, resulting in different uses for conservation. Furthermore, the hotspots of these metrics do not always align. Using a single endemism metric for these descriptions may therefore not adequately represent the distribution of endemism across regional or continental scales (Smiley et al., 2020). Therefore, understanding where they *do* align can further highlight areas of particular conservation importance (Lamoreux et al., 2006; Smiley et al., 2020). To that end, we suggest using "consensus hotspots", by evaluating each region of interest using multiple, less-correlated endemism metrics (for example, one of each of the four categories described in this review) and describing them based on the type and number of overlapping hotspots within each subdivision. This method parallels the one proposed by Smiley et al. (2020) for evaluating multiple dimensions of diversity (e.g., species richness, functional diversity, and phylogenetic diversity). By overlapping the hotspots created by different metrics, we can take advantage of the different reasons why endemism is important in both conservation and ecology. For example, the richness metrics describe specific ecoregions and their current biodiversity, whereas phylogenetic metrics focus on the evolutionary history of the community within the ecoregion. Like for ecological studies, the exact metrics chosen for conservation studies should depend on the research question and on the scale and structure of the data.

5. Case study: methods

5.1. Endemism metrics

We calculated all eight of the aforementioned endemism metrics for Mesoamerican mammals using expert range maps published by the

IUCN (IUCN, 2020). We used the full, global range of each species to perform all calculations. For richness and density metrics, we classified a species as “endemic” to a specific study region subdivision if 75% of the species' global range overlapped with the subdivision. We selected the threshold of 75% overlap to mitigate the effect of the well-known overestimation of species ranges in IUCN range maps (Hurlbert and Jetz, 2007) to prevent misidentification of endemic species as non-endemic (de Lima et al., 2020), and to compensate for the difference in precision between the ecoregion, country boundary, and IUCN datasets. A sensitivity analysis (Appendix S1, Fig. S1, S2, S3) demonstrates a significant decrease in the number of endemics at thresholds higher than 75%. We classified non-endemic species as “resident” to the ecoregion if its global IUCN range covered at least 5% of the ecoregion area.

For the range-size metrics and phylogenetic endemism, we used the global ranges to calculate the range size of each species, to calculate the true value of the sum of inverse range sizes, unconstrained by study region. To calculate the two phylogenetic metrics, we used the full phylogeny supertree from the PHYLACINE dataset (v. 1.2, Faurby et al., 2018). To ensure that the data were not influenced by any single replicate of the tree, we used 100 replicates of the supertree, aggregating the output values by taking the median of all the replicates at each subdivision (Faurby et al., 2018; Fig. S4). Appendix S3 shows the effect of aggregating bootstrapped replicates on phylogenetic endemism in Mesoamerican mammals. All calculations of each endemism metric and the comparison between them were conducted in R (v. 4.0; R Core Team, 2021), using the “raster” (Hijmans and van Etten, 2021) and “ape” (Paradis and Schliep, 2019) packages.

5.2. Modifiable areal unit problem

Because richness and density metrics (Table 1) require discrete study regions and subdivisions, they are influenced by the MAUP. Using IUCN range maps (IUCN, 2020) for Mesoamerican mammals, we examined the effect of the MAUP when using biologically-defined subdivisions as compared to arbitrary or politically-defined subdivisions on the apparent distribution of endemism. To do this, we calculated values of endemism across Mesoamerica using four different types of discrete study region subdivisions. First, we calculated endemism for each of the 41 terrestrial World Wildlife Fund (WWF) ecoregions found in Mesoamerica (Olson et al., 2001). WWF ecoregions divide the region into areas of similar dominant habitat (e.g., Talamancan montane forests, Fig. 1d). We repeated this analysis across a different biologically-defined ecoregion dataset, known as Bailey's ecoregions (Bailey, 1983). There are eight discrete ecoregions within Mesoamerica using this classification scheme. For arbitrary subdivisions, we divided the bounding box of the study region into a grid with a resolution of 3° (∼330 km). This grid size was chosen because it provided similar numbers of distinct units across Mesoamerica (52) and similar maximum endemic richness (11) as the biologically-defined subdivisions. Finally, we used country boundaries of the nine countries in the study region (eight Mesoamerican countries and northeast Colombia) as politically-defined subdivisions. To ensure that we used the same species pool for all analyses, we limited the country and arbitrary grid boundaries to the extent of the 41 chosen WWF ecoregions.

5.3. Hotspots

After calculating the endemism metrics and exploring the effect of different study region subdivision on their distributions, we measured how well hotspots of each metric conserve the species richness of Mesoamerica. We applied the Species Accumulation Index (SAI) popularized by Rodrigues and Brooks (2007) to compare the ability of each endemism metric to act a surrogate for conservation of all species in Mesoamerica, species endemic to the study region as a whole, and species endemic to a specific ecoregion. The SAI compares the species accumulation curves of each metric to those created by randomly sampling locations across the study region, and to either an optimal curve or a curve calculated as a reference (Ferrier and Watson, 1997; Rodrigues and Brooks, 2007). We used WWF ecoregions as the unit of analysis and accumulated quantiles of the Mesoamerican ecoregions (41 ecoregions total). For the random curves, we accumulated species from randomly selected ecoregions, iterating the process 100 times. To create the optimal species accumulation curve, we accumulated species from the richest ecoregions, iteratively removed the resident species from all remaining ecoregions, and continued accumulating richness from the remaining ecoregions in order of the remaining richness.

We also used the Zonation software (v 4.0, Moilanen et al., 2014) to generate complementarity-based priority ranks for Mesoamerica based on the IUCN mammal distributions (Appendix S6). The Zonation software uses heuristic algorithms to rank each pixel by its conservation priority, with a 1 being the highest priority. To effectively compare the results of Zonation with the ecoregion-level endemism metrics, we aggregated the rank values by calculating the mean rank value for each ecoregion before generating the species accumulation curves.

To demonstrate the consensus endemism hotspot method, we applied it to our case study of Mesoamerican mammals. Using one metric from each of the categories described in Table 1 (endemic richness, spatially-scaled endemicity, weighted endemism, and phylogenetic endemism), we defined hotspots for each metric as ecoregions with the highest 10% of values. We then classified consensus hotspots based on the number of definitions that present values in the top 10% for each ecoregion.

6. Endemism in Mesoamerica

6.1. Effect of subdivision type and MAUP on endemism trends

The distribution of endemism given the four different subdivision types demonstrates the influence of the MAUP on spatial trends in endemism (Fig. 2). For example, using endemic richness, the arbitrary (gridded) subdivisions (Fig. 2c) and the country boundaries (Fig. 2d) exhibited very different trends, with low spatial concordance between regions of high endemic richness. In contrast, the two ecoregion datasets (Fig. 2a and b) revealed similar trends in endemic richness, despite having different numbers of distinct subdivisions and therefore different counts of endemic species. This trend was exhibited regardless of the endemism metric calculated (Appendix S4). Following this comparison, we used WWF ecoregions for all subsequent analyses.

6.2. Comparisons of endemism metrics

We compared the geographical distribution of each endemism metric by calculating them for each terrestrial WWF ecoregion in Mesoamerica and running pairwise correlations between them (Fig. 3). Although all metrics had positive correlations to each other, the strength of the associations varied widely, from $r = 0.27$ between PD-endemism and corrected weighted endemism, to $r = 0.97$ between endemic richness and endemicity. The two richness metrics were highly correlated to each other, as were the two range-size metrics. Area-weighted endemic richness was more highly correlated to spatially-scaled endemism (the other density metric) than any other metric, although spatially-scaled endemism itself was more highly correlated to richness metrics. Finally, as expected, phylogenetic endemism (which normalizes the absolute species range sizes by the node branch length) was somewhat correlated to the two range-size metrics, whereas PD-Endemism (showing the phylogenetic diversity unique to a discrete study region subdivision) was more correlated to the richness-based metrics.

Across Mesoamerica, endemic richness and endemicity patterns were broadly similar, contrasting the results of Irl et al. (2015), which found decoupled patterns of endemic richness and endemicity in plants on the island of La Palma. However, because the WWF ecoregions in Mesoamerica have low endemic richness and broadly similar species richness

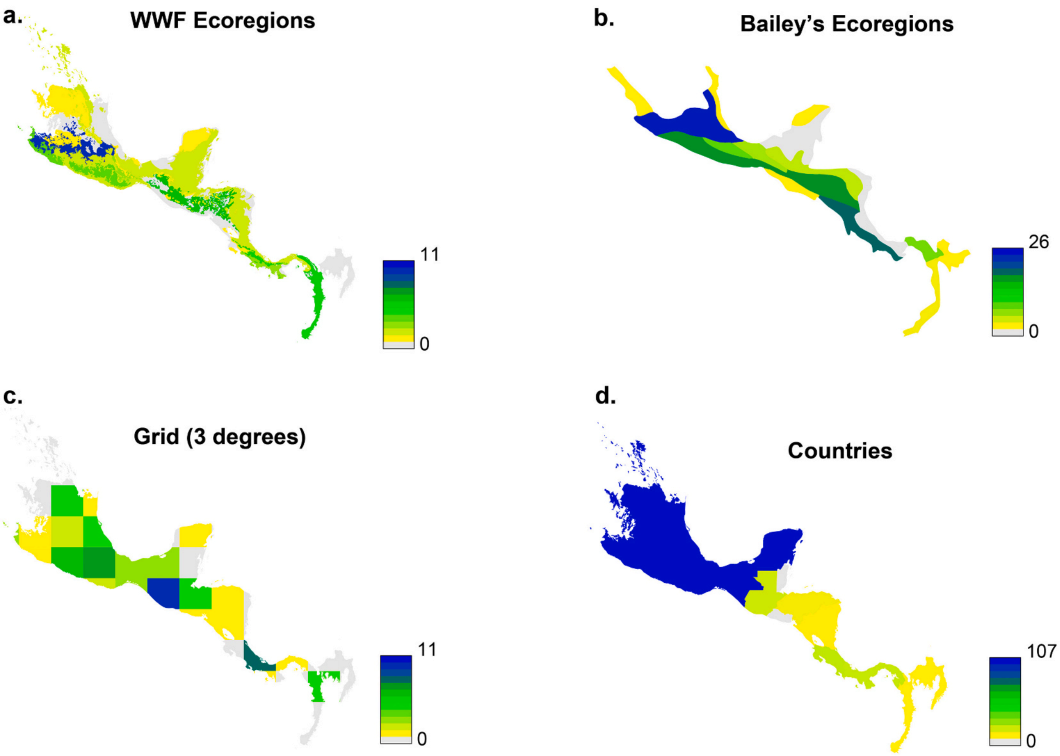


Fig. 2. Demonstration of the modifiable areal unit problem (MAUP) in trends of the endemic richness of Mesoamerican mammal species. The total number of species unique to each given areal unit was calculated for 4 different sets of units: a) World Wildlife Fund ecoregions (Olson et al., 2001), b) Bailey's ecoregions (Bailey, 1983), c) arbitrary grid cells with a 3 degree resolution, and d) country boundaries. While the trends in endemic richness between the 2 ecoregion datasets are relatively concordant, there are striking differences between those trends and the distribution of endemic richness using grid cells or country boundaries. Results for the other endemism metrics can be found in Appendix S4.

values, normalizing by species richness does not have a strong effect. The "Trans-Mexican Volcanic Belt pine-oak forests" (TMVB, Fig. 1a) ecoregion, with 11 endemic species, had both the highest endemic richness and endemicity. The TMVB contains some of the tallest mountains in Mexico and is a highly topographically diverse region, perhaps leading to reproductive isolation and subsequent speciation. Isolation appears to play a key role in other ecoregions with high values in endemic richness and endemicity. The "Central American pine-oak forests", the "Talamancan montane forests", and the "Jalisco dry forests" are similarly mountainous and topographically diverse (Fig. 1g, 1d, and 1e, respectively), and the extraordinary annual rainfall in the "Chocó-Darién moist forests" (Fig. 1h) may similarly act as a dispersal barrier (Fagua and Ramsey, 2019; García, 2006).

Although area-weighted endemic richness and spatially-scaled endemism both measure the relative densities of endemic species, the two density metrics are not as correlated as the two richness metrics. Whereas the trends in area-weighted endemic richness do not match those from the richness metrics, spatially-scaled endemism trends do (Fig. 3). Area-weighted endemic richness prioritizes small areas, and as a result the hotspots in Mesoamerican area-weighted endemic richness are all small ecoregions (e.g., the "Talamancan montane forests"; Fig. 1d). Area-weighted endemism shows a stronger preference for isolated regions, especially at the Isthmus of Tehuantepec (e.g., "Sierra de los Tuxtlas" and "Tehuacán Valley matorral"; Fig. 1b and 1f). The high proportion of southern Mexican ecoregions that are hotspots in area-weighted endemic richness may be due to the region's unique geography at the conjunction of two distinct geologic regimes (Dávila et al., 2002), the relatively stable climate in the region over the last 21,000 years (Sosa et al., 2020), or its complex geological history (Bryson et al., 2011). The hotspots in spatially-scaled endemism show similarities to both richness-based metrics (TMVB and Jalisco dry forests) and area-weighted endemic richness (Talamancan range forests).

Calculating the range-size metrics in Mesoamerican mammals shows marked differences in hotspot distribution to the previously described endemism metrics. Although the two range-size metrics are highly correlated (a testament to the consistent species richness values across Mesoamerican WWF ecoregions), they do not correlate well to any of the other metrics. The "Central American pine-oak forests" ecoregion (Fig. 1g), containing seven endemic species, has high weighted and corrected weighted endemism. However, other hotspots of weighted endemism have low endemic richness — the "Chiapas montane forests" (Fig. 1c) and "Sierra de los Tuxtlas" (Fig. 1b) ecoregions have only one endemic species apiece. This result indicates that, even if species found in the weighted and corrected weighted endemism hotspots are not *exclusive* to those habitats, range-sizes across the respective hotspots appear to be relatively restricted, perhaps occurring in only small sections of other ecoregions.

The two phylogenetic metrics differ in how they are calculated and interpreted, and as such they show different trends across Mesoamerica. PD-Endemism, describing the total phylogenetic novelty restricted to discrete subdivisions, closely matched endemic richness ($r = 0.89$). The TMVB (Fig. 1a) had by far the highest PD-Endemism, likely due to the three monotypic mammal species (*Romerolagus diazi*, *Zygogeomys trichopus*, and *Neotomidon alstoni*) that are found only within that ecoregion. In contrast, phylogenetic endemism, which uses the absolute range sizes of each lineage, matches range-size metrics more closely. Regions of high phylogenetic endemism appear to be concentrated around southern Mexico, Guatemala, and Honduras, with the "Chiapas montane forests" (Fig. 1c) and the "Central American Atlantic moist forests" having the highest phylogenetic endemism values. The location of this region on the boundary of three distinct tectonic plates and repeated separation of highland regions from valleys may have led to isolation and subsequent diversification (Rovito et al., 2012). For a more detailed discussion of the results of endemism metrics in Mesoamerica

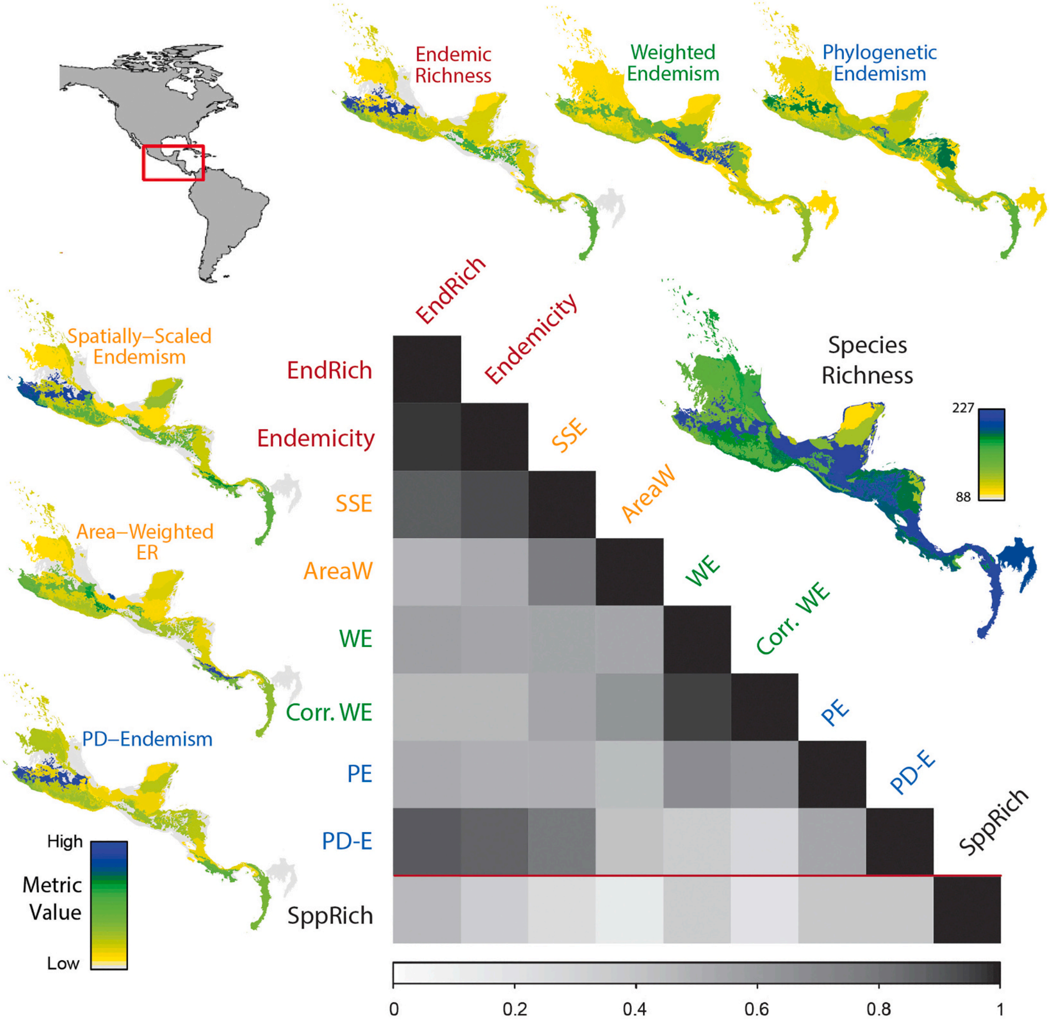


Fig. 3. A comparison of the 8 endemism metrics as applied to Mesoamerican mammal species across WWF ecoregions. A correlation matrix for all metrics in addition to species richness is provided, with darker values indicating stronger correlation. EndRich = endemic richness, SSE = spatially-scaled endemism, WE = weighted endemism, PE = phylogenetic endemism, PD-E = PD-endemism, SppRich = species richness. All correlations were positive ($r > 0$). Maps for endemicity and corrected weighted endemism are not displayed because of their high similarity to endemic richness and weighted endemism, respectively.

and their implications for conservation in that region, see the Supplementary discussion (Appendix S5).

It is possible that the large number of cryptic rodents and bats in Mesoamerica may have skewed our analyses towards those clades. Applying a lineage-based approach to endemism (e.g., Procheş et al., 2015), considering the ranges of entire mammal clades, instead of a species-based approach might decrease this skew towards cryptic and recently-evolved taxa. However, lineage-based approaches also, by definition, devalue a key element of endemism (recent speciation events), and for conservation strategies that rely on a species concepts, using the actual species may in fact be more informative than using evolutionary lineages.

6.3. Hotspots

As expected, hotspots applying richness and density metrics conserved greater total species richness than expected by chance, while those applying range-size metrics and phylogenetic endemism (both of which do not directly relate to species richness) conserved roughly the same number of species as would be expected by chance (Fig. 4, Appendix S6). However, for Mesoamerican endemic richness and ecoregion-level endemic richness, all metrics performed significantly above average, and outperformed the aggregated values provided by Zonation (Appendix S6).

We applied the consensus hotspot technique described above (Smiley et al., 2020) to the WWF ecoregions of Mesoamerica (Olson et al., 2001), assessing mammalian endemism. Only one ecoregion (TMVB) out of the 41 terrestrial ecoregions in Mesoamerica is in the top 10% of all four chosen definitions, further highlighting the differences between the definitions and what they measure. When compared to any one of the hotspots maps generated by taking a single metric, the consensus hotspot map shows different distributions and trends of mammalian endemism (Fig. 5). It highlights multiple centers of endemism across the Mesoamerican sub-continent, mainly corresponding to montane vegetation or regions with topographic heterogeneity. The TMVB ecoregion is clearly resolved using the consensus hotspot definition, as are the Central American pine-oak forests, the Talamancan montane forests, and the Chocó-Darién moist forests ecoregions. However, this new definition adds extra sensitivity to hotspots analysis, demonstrating that some ecoregions that surround the classic hotspots (e.g., Chiapas montane forests, Jalisco dry forests) may also hold high rates of certain aspects of endemism.

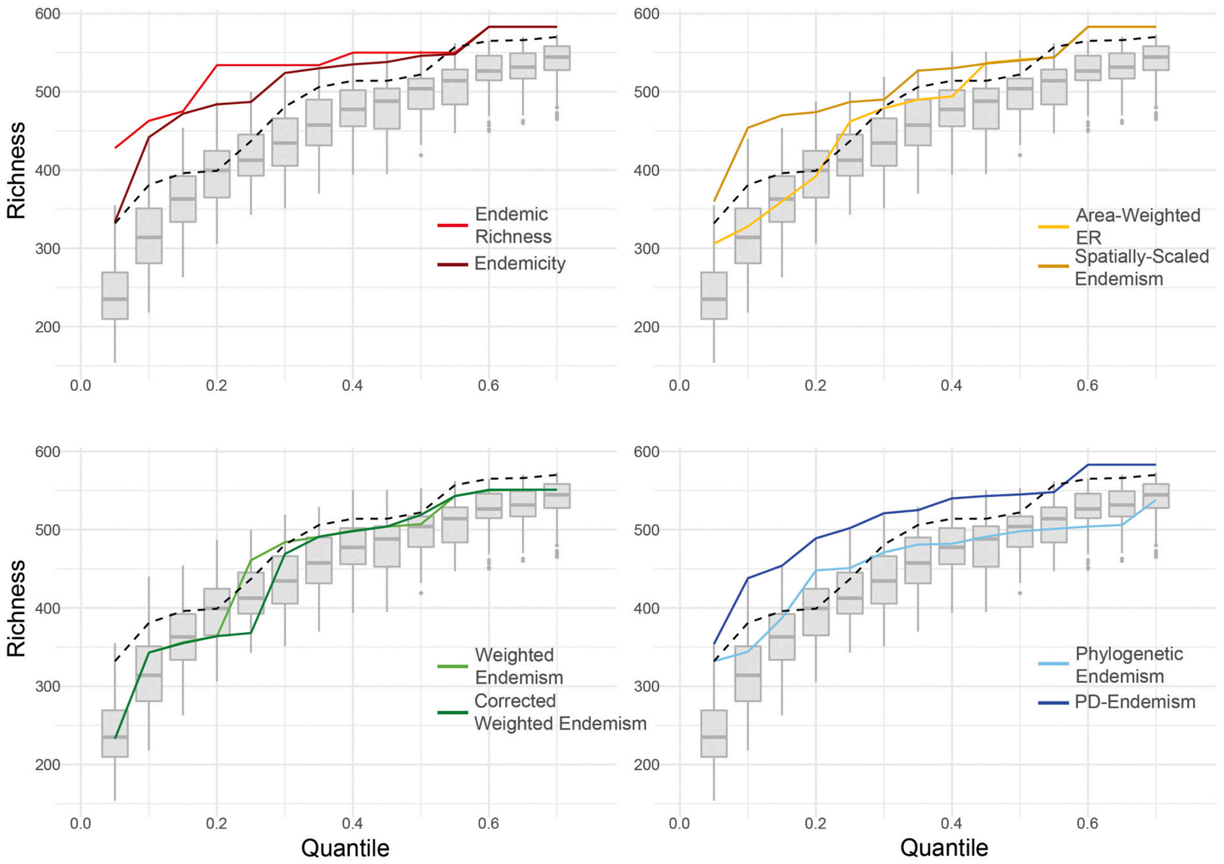


Fig. 4. Species accumulation curves for ecoregion-level endemism metrics and complementarity. These graphs show the number of species protected for a given quantile of the 41 terrestrial WWF ecoregions in Mesoamerica. The grey boxplots indicate the distribution of species protected by randomly sampling the given number of ecoregions and the dashed line indicates the number of species protected using conservation priority ranks calculated by Zonation (aggregated by taking the mean priority rank for each ecoregion). At greater than 70% of the ecoregions protected (quantile >0.7), the total species richness protected was $>95\%$ of the total number of species resident to Mesoamerica. Similar graphs accumulating Mesoamerican endemics and ecoregion-level endemics may be found in the supplement (Appendix S6).

7. Recommendations for studying endemism

7.1. *Mitigating the MAUP*

When calculating endemism metrics across Mesoamerica, the size and shape of the subdivisions significantly affected the discovery and interpretation of regions with high endemism (Fig. 2). For example, the arbitrary grid subdivisions revealed southern Mexico and Guatemala as the primary hotspot within Mesoamerica, whereas both of the ecoregion sets determined the highest endemic richness to be much farther north, across the TMVB. This discrepancy manifested despite the use of exactly the same extent of analysis and species pool, highlighting the importance of considering subdivision types when developing research questions and management practices. The similarities between the two biologically-defined subdivisions and their discordance with trends using more arbitrary units supports the suggestions of Ferreira and Boldrini (2011), that endemism is a biological concept that should be evaluated using biologically-relevant units.

Although the aggregation bias inherent to research based on discrete areal units can never be entirely removed, the relative similarity between the two ecoregion-based analyses suggest that using biologically defined subdivisions (e.g., biomes, ecoregions, soil types) may help to mitigate some of the areal unit effects (Ferreira and Boldrini, 2011; García-Llamas et al., 2018). Furthermore, applying biologically-relevant subdivisions to these metrics allows for more precise interpretation of the requisite habitat for each endemic species (e.g., “endemic to Neotropical cloud forests” instead of endemic to “Mexico”).

7.2. *Integrating endemism metrics*

This review demonstrates that different endemism metrics measure different aspects of a community, and the different commonly-used endemism metrics exhibit distinct spatial organizations across Mesoamerica. Furthermore, the different metrics each measure very different aspects of endemism, and their interpretations can, knowingly or not, change the outcomes of both conservation and ecological research. For example, in the case study highlighted in this review, endemic richness and endemicity show similar broad trends (Fig. 3). However, in study systems where the species richness of each study region subdivision differs significantly, the two metrics may indicate entirely different evolutionary or ecological processes. Similarly, if there is large variation in the size of the subdivisions (e.g., ecoregions) within the study region, there will be significant differences between the trends in richness metrics (e.g., endemic richness) and density metrics (e.g., spatially-scaled endemism). Choosing a particular endemism metric must be done with the objectives of the study, the biological interpretation, and the target audience in mind. Figure 6 summarizes the situations in which given endemism metrics may be the most appropriate, their interpretations, and possible confounding factors to consider when applying the given metric. Multiple factors work in tandem to influence species ranges, diversification, and specialization, although their relative contributions to endemism itself is still unknown. By treating endemism as a multi-faceted trait of a species or community, the origins and drivers of high endemism across the globe can more effectively parsed.

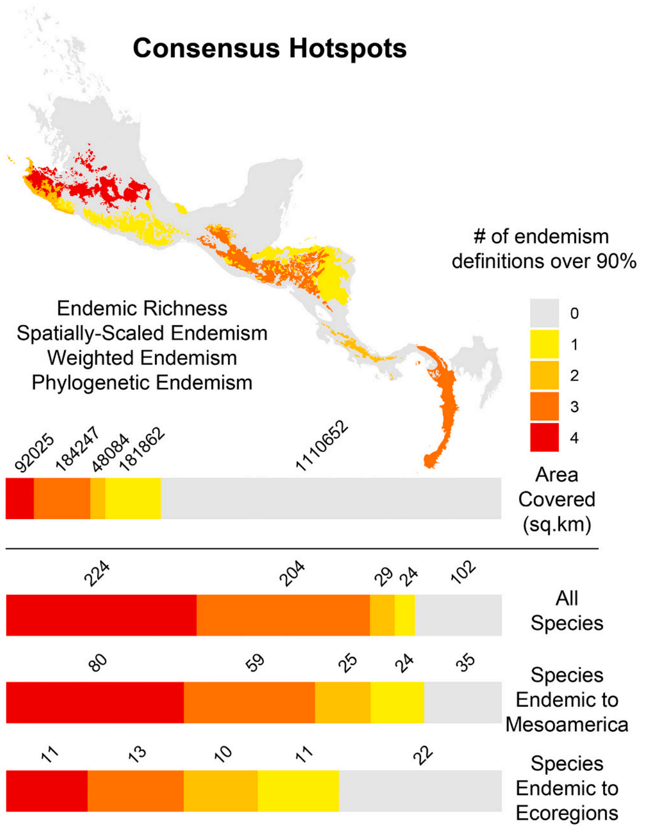
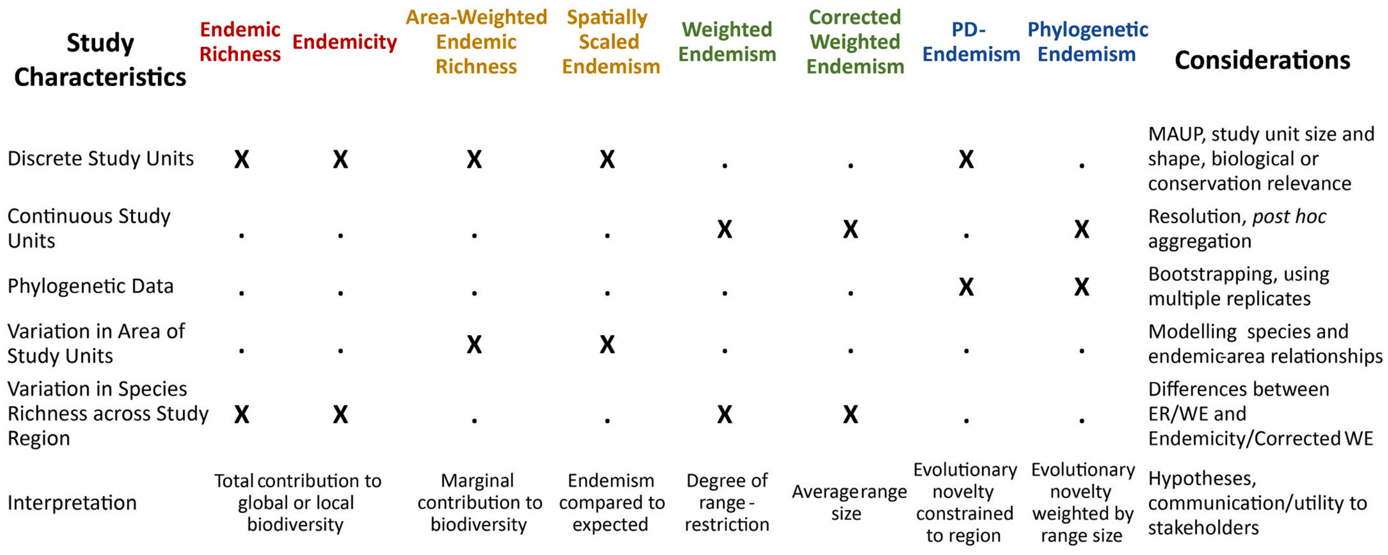


Fig. 5. Consensus endemism hotspots of Mesoamerican mammals, using 4 distinct endemism metrics and a 90% quantile threshold to determine hotspots for each metric. Only one ecoregion (Trans-Mexican Volcanic Belt) was a hotspot for all 4 metrics. The area covered by the hotspots, their total species richness, and the richness of Mesoamerican endemics and ecoregion-level endemics is shown in the bar charts, showing that despite their small area, protecting consensus hotspots can protect a disproportionate amount of biodiversity.

8. Conservation and biological implications

The methods used to manage biological communities and threatened species across the globe are incredibly varied, not only in the actual work that is done, but also in the goals and expected outcomes of the management. Species-based or “fine-filter” conservation management practices often focus on a subset of species with particular conservation importance, preserving the habitats and ecological systems used by those species (Guareschi et al., 2020; Runge et al., 2019; Tingley et al., 2014). However, these strategies are often biased towards “charismatic” animals (e.g., mega-herbivores), at the expense of other, less popular species (Ducarme et al., 2013). Instead, conservation organizations have begun to shift from a single-species approach to holistic strategies prioritizing landscape diversity and ecosystem functioning (Beier and de Albuquerque, 2015). These landscape-based or “coarse-filter” strategies attempt to prioritize landscapes and regions of high biodiversity, ecological importance, and threat (Dinerstein et al., 2017; Marchese, 2015; Myers et al., 2000). The recent expansion of global protected areas has not been particularly effective for either “coarse-filter” (ecoregions) or “fine-filter” (threatened species) strategies (Maxwell et al., 2020), necessitating new approaches including complementarity and endemism frameworks.

In the last few decades, research on biodiversity hotspots has been successfully integrated into biological conservation, with exceptional results (de Albuquerque et al., 2015; Marchese, 2015; Wilson et al., 2006). Studying endemic species through a hotspots framework provides an excellent opportunity to link species-based and habitat-based conservation strategies. Endemic species have inherent conservation relevance for fine-filter practices because of their propensity for population declines and their vulnerability to habitat loss. Furthermore, targeting endemism hotspots allows for the protection of a larger proportion of species' ranges than similar-sized areas outside of endemism hotspots. For example, conserving a small area in the Trans-Mexican Volcanic Belt can preserve the entire range of several species, including all the habitats and requirements necessary for a viable population of those species. In contrast, conserving a comparatively small region in the relatively endemic-depauperate Yucatán Peninsula may not preserve enough habitat for the resident species to maintain viable populations. At the same time, examining which landscape holds the highest endemism (irrespective of definition) can help to highlight entire landscapes of interest for “coarse-filter” strategies.



Study Characteristics	Endemic Richness	Endemicity	Area-Weighted Endemic Richness	Spatially Scaled Endemism	Weighted Endemism	Corrected Weighted Endemism	PD-Endemism	Phylogenetic Endemism	Considerations
Discrete Study Units	X	X	X	X	.	.	X	.	MAUP, study unit size and shape, biological or conservation relevance
Continuous Study Units	.	.	.	.	X	X	.	X	Resolution, *post hoc* aggregation
Phylogenetic Data	.	.	.	.	.	.	X	X	Bootstrapping, using multiple replicates
Variation in Area of Study Units	.	.	X	X	.	.	.	.	Modelling species and endemic-area relationships
Variation in Species Richness across Study Region	X	X	.	.	X	X	.	.	Differences between ER/WE and Endemicity/Corrected WE
Interpretation	Total contribution to global or local biodiversity		Marginal contribution to biodiversity	Endemism compared to expected	Degree of range-restriction	Average range size	Evolutionary novelty constrained to region	Evolutionary novelty weighted by range size	Hypotheses, communication/utility to stakeholders

Fig. 6. A table describing which endemism metrics may be most informative for a variety of study characteristics (e.g., the study has discrete areal units). X's indicate that metric is effective for each case. The right-most column details considerations that must be taken into account when choosing or applying metrics for that particular study. The biological and conservation interpretations of each metric is provided in the bottom row.

In particular, using complementary-based prioritization can help to highlight a greater variety of ecosystems and can more effectively lead to the preservation of a representative sample of habitats on Earth (Fig. 4). Indeed, the complementarity-based prioritization method used by Zonation was more effective at preserving overall species richness than some of the endemism metrics (in particular the range-size metrics), even when aggregated by ecoregion (Fig. 4). However, when limited to Mesoamerican endemics and ecoregion-level endemics, the relative efficacy of the endemism metrics outstripped the results from Zonation (Appendix S6). Further, the complementarity method does not automatically distinguish between different geographical regions or habitats, nor does it necessarily suggest contiguous regions for conservation (Moilanen et al., 2014). Although it is unfeasible and undesirable to conserve the entire land area of endemism hotspots, consensus hotspots of endemism can suggest targets to focus efforts for developing new or expanded protected areas or for strengthening restrictions on habitat degradation, trapping, and other exploitative practices (Sarkar et al., 2009). Therefore, for conservation prioritization, we suggest using endemism metrics and the consensus hotspots definition to determine broad regions and habitats with high endemism and conservation priority, and using a complementarity-based approach such as Zonation to determine the areas *within* those ecoregions to prioritize.

By prioritizing only one or a few metrics when identifying endemism hotspots and evaluating regions, we inadvertently minimize and neglect aspects of endemism that may well contribute to important dimensions of global biodiversity. To provide effective and informed conservation based on biodiversity and endemism hotspots, we will require strategies based on multiple metrics of endemism, spanning all aspects of endemic species. To that end, we propose applying a framework of overlapping hotspots based on multiple endemism metrics like the one conducted in this study (Fig. 5) that integrates across endemism metrics to provide nuance to hotspot-based conservation.

9. Conclusion

Studying global and continental trends in endemism can provide unique insight into the distribution, threat, and evolution of species and communities. In addition, discovering regions with high endemism can help to focus and refine our global conservation efforts, prioritizing areas with many range-restricted species. As many species ranges continue to contract through increasing habitat loss, urbanization, and climate change, research on the dynamics and distribution of endemism has begun to take a prominent role in both ecological and conservation studies. However, much of this research has not applied the requisite nuance to properly examine endemism. First, as evidenced by our case study using Mesoamerican mammals, differences in the scale and extent of analyses may significantly influence the apparent trends in endemism. Although much research has been conducted on spatial biases in the interpretation of biodiversity trends, few studies have examined these influences on endemism, especially across continents. This case study demonstrates these influences and, although it was limited to Mesoamerican mammals, can easily be applied to global scales.

Second, we have shown that the metric used to define endemism can have a major effect on its interpretation and also the distribution of hotspots across landscapes (Fig. 3). Many metrics for quantifying endemism have arisen somewhat independently of each other, and as a result, these metrics measure different aspects of the range size, evolutionary novelty, or uniqueness of a given species (Fig. 6). Understanding the research question and how the different endemism metrics converse with that question is necessary for effective research into the trends and drivers of endemism. Ecological studies must be especially precise, as hypotheses about the drivers and correlates of endemism may not be adequately answered with a hastily-chosen endemism metric (Smiley et al., 2020). In addition to the differences in interpretation, the different endemism metrics often show divergent spatial patterns of endemism hotspots. The metric comparisons we have conducted in this paper reveal this discrepancy in Mesoamerican mammals, but research expanding this analysis to broader scales, different types of study region subdivisions, and other taxa are necessary to fully examine how the different endemism metrics communicate with one another.

It is clear that any single metric of endemism paints an incomplete picture of the geographical distribution of endemism across landscapes, so, lastly, we promote applying consensus hotspots frameworks to evaluate trends in endemism. The consensus hotspots we calculated for Mesoamerican mammals highlighted regions that may not appear when using just a single metric (Fig. 5). The scope of our hotspot calculation was necessarily limited, but future research should consider evaluating different methods of generating consensus hotspots of endemism and applying them across different scales. Regardless, overlapping hotspots based on the different endemism metrics demonstrates the complexity of endemism and the importance of considering multiple dimensions of endemism in studies of conservation hotspots. The ecology and conservation of range-restricted species is becoming more complex and unpredictable with global effects on the environment like climate change and land conversion. As a result, understanding endemism in an integrative, holistic way, through the incorporation of different scales, endemism metrics and consensus hotspots is necessary for effective research across the world, both now and in the near future.

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Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

A list of recent papers quantifying and examining endemism hotspots (Supplementary Table 1), an analysis of the range size threshold used in this study (Appendix S1), detailed discussions of spatially-scaled endemism (Appendix S2), a sensitivity analysis of the number of phylogeny replicates needed (Appendix S3), the results of the Mesoamerican case study (Appendix S5), and an expansion on the MAUP (Appendix S4) and the conservation efficacy of the various metrics (Appendix S6) may be found online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supplementary data to this article can be found online at doi: https://doi.org/10.1016/j.biocon.2021.109403.

References

Albuquerque, F., Beier, P., 2015. Rarity-weighted richness: a simple and reliable alternative to integer programming and heuristic algorithms for minimum set and maximum coverage problems in conservation planning. PLoS ONE 10, e0119905. https://doi.org/10.1371/journal.pone.0119905.

de Albuquerque, F.S., Benito, B., Beier, P., Assunção-Albuquerque, M.J., Cayuela, L., 2015. Supporting underrepresented forests in mesoamerica. Natur. Conserv. 13, 152–158. https://doi.org/10.1016/j.ncon.2015.02.001.

Astudillo-Scalia, Y., de Albuquerque, F.S., 2020. The geography of high-priority conservation areas for marine mammals. Glob. Ecol. Biogeogr. 29, 2097–2106. https://doi.org/10.1111/geb.13175.

Bacon, C.D., Molnar, P., Antonelli, A., Crawford, A.J., Montes, C., Vallejo-Pareja, M.C., 2016. Quaternary glaciation and the Great American biotic interchange. Geology 44, 375–378. https://doi.org/10.1130/G37624.1.

Bailey, R.G., 1983. Delineation of ecosystem regions. Environ. Manag. 7, 365–373. https://doi.org/10.1007/BF01866919.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57. https://doi.org/10.1038/nature09678.

Beier, P., de Albuquerque, F.S., 2015. Environmental diversity as a surrogate for species representation. Conserv. Biol. 29, 1401–1410. https://doi.org/10.1111/cobi.12495.

Bryson, R.W., García-Vázquez, U.O., Riddle, B.R., 2011. Phylogeography of middle American gophersnakes: mixed responses to biogeographical barriers across the Mexican transition zone. J. Biogeogr. 38, 1570–1584. https://doi.org/10.1111/j.1365-2699.2011.02508.x.

Bykov, B.A., 1979. On a quantitative estimate of endemism. In: Botaniceskie materialy Gerbarija Instituta botaniki Akademii nauk Kazahskoj, 11. SSR, pp. 3–8.

Cadena, C.D., Kozak, K.H., Gómez, J.P., Parra, J.L., McCain, C.M., Bowie, R.C.K., Carnaval, A.C., Moritz, C., Rahbek, C., Roberts, T.E., Sanders, N.J., Schneider, C.J., VanDerWal, J., Zamudio, K.R., Graham, C.H., 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proc. R. Soc. B Biol. Sci. 279, 194–201. https://doi.org/10.1098/rspb.2011.0720.

Calderon, R., Boucher, T., Bryer, M., Sotomayor, L., Kappelle, M., 2004. Setting biodiversity conservation priorities in Central America: Action site selection for the development of a first portfolio. The Nature Conservancy (TNC), San Jose, Costa Rica.

Cárdenes-Sandí, G.M., Shadik, C.R., Correa-Metrio, A., Gosling, W.D., Cheddadi, R., Bush, M.B., 2019. Central American climate and microrefugia: a view from the last interglacial. Quat. Sci. Rev. 205, 224–233. https://doi.org/10.1016/j.quascirev.2018.12.021.

Collins, M.B., Mitchard, E.T.A., 2017. A small subset of protected areas are a highly significant source of carbon emissions. Sci. Rep. 7, 1–11. https://doi.org/10.1038/srep41902.

Crisp, M.D., Laffan, S., Linder, H.P., Monro, A., 2001. Endemism in the Australian flora. J. Biogeogr. 28, 183–198. https://doi.org/10.1046/j.1365-2699.2001.00524.x.

Dalsgaard, B., Carstensen, D.W., Fjeldsa, J., Maruyama, P.K., Rahbek, C., Sandel, B., Sonne, J., Svenning, J.-C., Wang, Z., Sutherland, W.J., 2014. Determinants of bird species richness, endemism, and island network roles in Wallacea and the West Indies: is geography sufficient or does current and historical climate matter? Ecol. Evol. 4, 4019–4031. https://doi.org/10.1002/ece3.1276.

Daru, B.H., le Roux, P.C., Gopalraj, J., Park, D.S., Holt, B.G., Greve, M., 2019. Spatial overlaps between the global protected areas network and terrestrial hotspots of evolutionary diversity. Glob. Ecol. Biogeogr. 28, 757–766. https://doi.org/10.1111/geb.12888.

Daru, B.H., Farooq, H., Antonelli, A., Faurby, S., 2020. Endemism patterns are scale dependent. Nat. Commun. 11, 2115. https://doi.org/10.1038/s41467-020-15921-6.

Dávila, P., Arizmendi, M.D.C., Valiente-Banuet, A., Villaseñor, J.L., Casas, A., Lira, R., 2002. Biological diversity in the Tehuacán-Cuicatlán Valley, Mexico. Biodivers. Conserv. 11, 421–442. https://doi.org/10.1023/A:1014888822920.

Dawson, M.N., Axmacher, J.C., Beierkuhnlein, C., Blois, J.L., Bradley, B.A., Cord, A.F., Dengler, J., He, K.S., Heaney, L.R., Jansson, R., Mahecha, M.D., Myers, C., Nogués-Bravo, D., Papadopoulou, A., Reu, B., Rodríguez-Sánchez, F., Steinbauer, M.J., Stigall, A., Tuanmu, M.-N., Gavin, D.G., 2016. A second horizon scan of biogeography: Golden Ages, Midas touches, and the Red Queen. Frontiers of Biogeography 8. https://doi.org/10.21425/F58429770.

DeClerck, F.A.J., Chazdon, R., Holl, K.D., Milder, J.C., Finegan, B., Martinez-Salinas, A., Imbach, P., Canet, L., Ramos, Z., 2010. Biodiversity conservation in human-modified landscapes of mesoamerica: past, present and future. In: Biological Conservation, Conserving complexity: Global change and community-scale interactions, 143, pp. 2301–2313. https://doi.org/10.1016/j.biocon.2010.03.026.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 67, 534. https://doi.org/10.1093/biosci/bix014.

Ducarme, F., Luque, G.M., Courchamp, F., 2013. What are "charismatic species" for conservation biologists?. In: Ecole Normale Superieure de Lyon: BioSciences Master Reviews, pp. 1–8.

Fagua, J.C., Ramsey, R.D., 2019. Geospatial modeling of land cover change in the Chocó-Darien global ecoregion of South America; one of most biodiverse and rainy areas in the world. PLoS ONE 14, e0211324. https://doi.org/10.1371/journal.pone.0211324.

Faith, D.P., Reid, C.A.M., Hunter, J., 2004. Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. Conserv. Biol. 18, 255–261. https://doi.org/10.1111/j.1523-1739.2004.00330.x.

Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli, A., Svenning, J.-C., 2018. PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. Ecology 99. https://doi.org/10.1002/ecy.2443.

Ferreira, P.M.A., Boldrini, I.I., 2011. Potential reflection of distinct ecological units in plant endemism categories. Conserv. Biol. 25, 672–679. https://doi.org/10.1111/j.1523-1739.2011.01675.x.

Ferrier, S., Watson, G., 1997. An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity. Environment Australia.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J., Velichko, A.A., 2007. Ecosystems, their properties, goods, and services. In: Climate Change 2007: Impacts, Adaptation and Vulnerability., Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Fritz, S.A., Bininda-Emonds, O.R.P., Purvis, A., 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol. Lett. 12, 538–549. https://doi.org/10.1111/j.1461-0248.2009.01307.x.

García, A., 2006. Using ecological niche modelling to identify diversity hotspots for the herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. Biol. Conserv. 130, 25–46. https://doi.org/10.1016/j.biocon.2005.11.030.

García-Llamas, P., Calvo, L., De la Cruz, M., Suárez-Seoane, S., 2018. Landscape heterogeneity as a surrogate of biodiversity in mountain systems: what is the most appropriate spatial analytical unit? Ecol. Indic. 85, 285–294. https://doi.org/10.1016/j.ecolind.2017.10.026.

Gavin, D.G., 2015. Vegetation stability and the habitat associations of the endemic taxa of the Olympic Peninsula, Washington, USA. Frontiers of biogeography 7.

Gorman, C.E., Potts, B.M., Schweitzer, J.A., Bailey, J.K., 2014. Shifts in species interactions due to the evolution of functional differences between endemics and non-endemics: an endemic syndrome hypothesis. PLoS ONE 9, e111190. https://doi.org/10.1371/journal.pone.0111190.

Guareschi, S., Laini, A., Viaroli, P., Bolpagni, R., 2020. Integrating habitat- and species-based perspectives for wetland conservation in lowland agricultural landscapes. Biodivers. Conserv. 29, 153–171. https://doi.org/10.1007/s10531-019-01876-8.

Guerin, G.R., Lowe, A.J., 2015. 'Sum of inverse range-sizes' (SIR), a biodiversity metric with many names and interpretations. Biodivers. Conserv. 24, 2877–2882. https://doi.org/10.1007/s10531-015-0977-6.

Guerin, G.R., Ruokolainen, L., Lowe, A.J., 2015. A georeferenced implementation of weighted endemism. Methods Ecol. Evol. 6, 845–852. https://doi.org/10.1111/2041-210X.12361.

Gutiérrez-Pesquera, L.M., Tejedo, M., Olalla-Tárraga, M.Á., Duarte, H., Nicieza, A., Solé, M., 2016. Testing the climate variability hypothesis in thermal tolerance limits of tropical and temperate tadpoles. J. Biogeogr. 43, 1166–1178. https://doi.org/10.1111/jbi.12700.

Harrison, S., Noss, R., 2017. Endemism hotspots are linked to stable climatic refugia. Ann. Bot. 119, 207–214. https://doi.org/10.1093/aob/mcw248.

Heino, M., Kummu, M., Makkonen, M., Mulligan, M., Verburg, P.H., Jalava, M., Räsänen, T.A., 2015. Forest loss in protected areas and intact forest landscapes: a global analysis. PLoS ONE 10, e0138918. https://doi.org/10.1371/journal.pone.0138918.

Herkt, K.M.B., Barnikel, G., Skidmore, A.K., Fahr, J., 2016. A high-resolution model of bat diversity and endemism for continental Africa. Ecol. Model. 320, 9–28. https://doi.org/10.1016/j.ecolmodel.2015.09.009.

Hijmans, R.J., van Etten, J., 2021. raster: Geographic analysis and modeling with raster data. R package version 3.4-5. http://CRAN.R-project.org/package=raster.

Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163, 192–211. https://doi.org/10.1086/381004.

Hobohm, C., 2003. Characterization and ranking of biodiversity hotspots: centres of species richness and endemism. Biodivers. Conserv. 12, 279–287. https://doi.org/10.1023/A:1021934910722.

Hobohm, C. (Ed.), 2014. Endemism in Vascular Plants, Plant and Vegetation. Springer, Netherlands. https://doi.org/10.1007/978-94-007-6913-7.

Hobohm, C., Tucker, C.M., 2014. How to quantify endemism. In: Hobohm, C. (Ed.), Endemism in Vascular Plants, Plant and Vegetation. Springer, Netherlands, Dordrecht, pp. 11–48. https://doi.org/10.1007/978-94-007-6913-7_2.

Hurlbert, A.H., Jetz, W., 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. PNAS 104, 13384–13389. https://doi.org/10.1073/pnas.0704469104.

Irl, S.D.H., Harter, D.E.V., Steinbauer, M.J., Puyol, D.G., Fernández-Palacios, J.M., Jentsch, A., Beierkuhnlein, C., 2015. Climate vs. topography – spatial patterns of plant species diversity and endemism on a high-elevation island. J. Ecol. 103, 1621–1633. https://doi.org/10.1111/1365-2745.12463.

IUCN, 2020. The IUCN Red List of Threatened Species, 2019th–3. ed.

Jansson, R., 2003. Global patterns in endemism explained by past climatic change. Proc. R. Soc. B 270, 583–590. https://doi.org/10.1098/rspb.2002.2283.

Jelinski, D.E., Wu, J., 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecol 11, 129–140. https://doi.org/10.1007/BF02447512.

Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M., Mucina, L., 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. Ann. Bot. 122, 927–934. https://doi.org/10.1093/aob/mcy173.

Kier, G., Barthlott, W., 2001. Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. Biodivers. Conserv. 10, 1513–1529. https://doi.org/10.1023/A:1011812528849.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. PNAS 106, 9322–9327. https://doi.org/10.1073/pnas.0810306106.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W., Shugart, H.H., 2006. Global tests of biodiversity concordance and the importance of endemism. Nature 440, 212–214. https://doi.org/10.1038/nature04291.

de Lima, R.A.F., Souza, V.C., de Siqueira, M.F., ter Steege, H., 2020. Defining endemism levels for biodiversity conservation: tree species in the Atlantic Forest hotspot. Biol. Conserv. 252, 108825 https://doi.org/10.1016/j.biocon.2020.108825.

Loucks, C., Ricketts, T.H., Naidoo, R., Lamoreux, J., Hoekstra, J., 2008. Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural suitability. J. Biogeogr. 35, 1337–1348. https://doi.org/10.1111/j.1365-2699.2008.01899.x.

Marchese, C., 2015. Biodiversity hotspots: a shortcut for a more complicated concept. Glob. Ecol. Conserv. 3, 297–309. https://doi.org/10.1016/j.gecco.2014.12.008.

Matthews, T.J., Rigal, F., Triantis, K.A., Whittaker, R.J., 2019. A global model of island species–area relationships. PNAS 116, 12337–12342. https://doi.org/10.1073/pnas.1818190116.

Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S.L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O., Watson, J.E.M., 2020. Area-based conservation in the twenty-first century. Nature 586, 217–227. https://doi.org/10.1038/s41586-020-2773-z.

McDonald, R.I., Güneralp, B., Huang, C.-W., Seto, K.C., You, M., 2018. Conservation priorities to protect vertebrate endemics from global urban expansion. Biol. Conserv. 224, 290–299. https://doi.org/10.1016/j.biocon.2018.06.010.

McGuinness, K.A., 1984. Species–area curves. Biol. Rev. 59, 423–440. https://doi.org/10.1111/j.1469-185X.1984.tb00711.x.

Mishler, B.D., Knerr, N., González-Orozco, C.E., Thornhill, A.H., Laffan, S.W., Miller, J.T., 2014. Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian acacia. Nat. Commun. 5, 1–10. https://doi.org/10.1038/ncomms5473.

Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. R. Soc. B Biol. Sci. 272, 1885–1891. https://doi.org/10.1098/rspb.2005.3164.

Moilanen, A., Pouzols, F.M., Meller, L., Veach, V., Arponen, A., Leppänen, J., Kujala, H., 2014. Zonation–spatial conservation planning methods and software. Version 4. User Manual 290.

Munguía, M., Peterson, A.T., Sánchez-Cordero, V., 2008. Dispersal limitation and geographical distributions of mammal species. J. Biogeogr. 35, 1879–1887. https://doi.org/10.1111/j.1365-2699.2008.01921.x.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Owens, I.P.F., 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436, 1016. https://doi.org/10.1038/nature03850.

Paradis, E., Schliep, K., 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Pejchar, L., 2015. Introduced birds incompletely replace seed dispersal by a native frugivore. AoB Plants 7. https://doi.org/10.1093/aobpla/plv072.

Pellissier, L., Heine, C., Rosauer, D.F., Albouy, C., 2018. Are global hotspots of endemic richness shaped by plate tectonics? Biol. J. Linn. Soc. 123, 247–261. https://doi.org/10.1093/biolinnean/blx125.

Procheş, Ş., Ramdhani, S., Perera, S.J., Ali, J.R., Gairola, S., 2015. Global hotspots in the present-day distribution of ancient animal and plant lineages. Sci. Rep. 5, 15457. https://doi.org/10.1038/srep15457.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation forStatistical Computing, Vienna, Austria. https://www.R-project.org/.

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x.

Rodrigues, A.S.L., Brooks, T.M., 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annu. Rev. Ecol. Evol. Syst. 38, 713–737. https://doi.org/10.1146/annurev.ecolsys.38.091206.095737.

Rosauer, D.F., Jetz, W., 2015. Phylogenetic endemism in terrestrial mammals. Glob. Ecol. Biogeogr. 24, 168–179. https://doi.org/10.1111/geb.12237.

Rosauer, D.F., Laffan, S.W., Crisp, M.D., Donnellan, S.C., Cook, L.G., 2009. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. Mol. Ecol. 18, 4061–4072. https://doi.org/10.1111/j.1365-294X.2009.04311.x.

Rovito, S.M., Wake, D.B., Papenfuss, T.J., Parra-Olea, G., Muñoz-Alonso, A., Vásquez-Almazán, C.R., 2012. Species formation and geographical range evolution in a genus of central american cloud forest salamanders (Dendrotriton). J. Biogeogr. 39, 1251–1265. https://doi.org/10.1111/j.1365-2699.2012.02696.x.

Runge, C.A., Withey, J.C., Naugle, D.E., Fargione, J.E., Helmstedt, K.J., Larsen, A.E., Martinuzzi, S., Tack, J.D., 2019. Single species conservation as an umbrella for management of landscape threats. PLoS ONE 14, e0209619. https://doi.org/10.1371/journal.pone.0209619.

Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J., Svenning, J.-C., 2011. The influence of Late Quaternary climate-change velocity on species endemism. Science 334, 660–664. https://doi.org/10.1126/science.1210173.

Sandel, B., Weigelt, P., Kreft, H., Keppel, G., van der Sande, M.T., Levin, S., Smith, S., Craven, D., Knight, T.M., 2020. Current climate, isolation and history drive global patterns of tree phylogenetic endemism. Glob. Ecol. Biogeogr. 29, 4–15. https://doi.org/10.1111/geb.13001.

Sarkar, S., Sanchez-Cordero, V., Cecilia Londono, M., Fuller, T., 2009. Systematic conservation assessment for the mesoamerica, Choco, and tropical Andes biodiversity hotspots: a preliminary analysis. Biodivers. Conserv. 18, 1793–1828. https://doi.org/10.1007/s10531-008-9559-1.

Shrestha, N., Shen, X., Wang, Z., 2019. Biodiversity hotspots are insufficient in capturing range-restricted species. Conserv. Sci. Pract. 1, e103 https://doi.org/10.1111/csp2.103.

Slatyer, C., Rosauer, D.F., Lemckert, F., 2007. An assessment of endemism and species richness patterns in the Australian Anura. J. Biogeogr. 34, 583–596. https://doi.org/10.1111/j.1365-2699.2006.01647.x.

Smiley, T.M., Title, P.O., Zelditch, M.L., Terry, R.C., 2020. Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological and phylogenetic diversity: a case study of north american rodents. Glob. Ecol. Biogeogr. 29, 516–533. https://doi.org/10.1111/geb.13050.

Sobral, F.L., Lees, A.C., Cianciaruso, M.V., 2016. Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. Ecol. Lett. 19, 1091–1100. https://doi.org/10.1111/ele.12646.

Sonne, J., Martín González, A.M., Maruyama, P.K., Sandel, B., Vizentin-Bugoni, J., Schleuning, M., Abrahamczyk, S., Alarcón, R., Araujo, A.C., Araújo, F.P., Mendes de Azevedo, S., Baquero, A.C., Cotton, P.A., Ingversen, T.T., Kohler, G., Lara, C., Guedes Las-Casas, F.M., Machado, A.O., Machado, C.G., Maglianesi, M.A., Moura, A.C., Nogués-Bravo, D., Oliveira, G.M., Oliveira, P.E., Ornelas, J.F., Rosero-Lasprilla, L., Rui, A.M., Sazima, M., Timmermann, A., Varassin, I.G., Wang, Z., Watts, S., Fjeldså, J., Svenning, J.-C., Rahbek, C., Dalsgaard, B., Rodrigues, L. da C., 2016. High proportion of smaller ranged hummingbird species coincides with ecological specialization across the Americas, 283, 20152512. https://doi.org/10.1098/rspb.2015.2512.

Sosa, V., Vásquez-Cruz, M., Villarreal-Quintanilla, J.A., 2020. Influence of climate stability on endemism of the vascular plants of the Chihuahuan Desert. J. Arid Environ. 177, 104139 https://doi.org/10.1016/j.jaridenv.2020.104139.

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., Ludwig, C., 2015. The trajectory of the anthropocene: the great acceleration. Anthr. Rev. 2, 81–98. https://doi.org/10.1177/2053019614564785.

Steinbauer, M.J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A.V., Cardoso, P., Chou, C.-H., Sanctis, M.D., de Sequeira, M.M., Duarte, M.C., Elias, R.B., Fernández-Palacios, J.M., Gabriel, R., Gereau, R.E., Gillespie, R.G., Greimler, J., Harter, D.E.V., Huang, T.-J., Irl, S.D.H., Jeanmonod, D., Jentsch, A., Jump, A.S., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M.M., Strasberg, D., Stuessy, T., Svenning, J.-C., Vetaas, O.R., Beierkuhnlein, C., 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation. Glob. Ecol. Biogeogr. 25, 1097–1107. https://doi.org/10.1111/geb.12469.

Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am. Nat. 133, 240–256. https://doi.org/10.1086/284913.

Storch, D., Keil, P., Jetz, W., 2012. Universal species–area and endemics–area relationships at continental scales. Nature 488, 78–81. https://doi.org/10.1038/nature11226.

Tingley, M.W., Darling, E.S., Wilcove, D.S., 2014. Fine- and coarse-filter conservation strategies in a time of climate change. Ann. N. Y. Acad. Sci. 1322, 92–109. https://doi.org/10.1111/nyas.12484.

Turpie, J.K., Crowe, T.M., 1994. Patterns of distribution, diversity and endemism of larger african mammals. S. Afr. J. Zool. 29, 19–32. https://doi.org/10.1080/02541858.1994.11448322.

United Nations Educational, Scientific, and Cultural Organization (UNESCO), n.d.United Nations Educational, Scientific, and Cultural Organization (UNESCO), n.d. Talamanca Range-La Amistad Reserves / La Amistad National Park [WWW Document]. UNESCO World Heritage Centre. URL https://whc.unesco.org/en/list/205/ (accessed 8.13.20).

Vargas, P., Jiménez-Mejías, P., Fernández-Mazuecos, M., 2020. 'Endangered living fossils' (ELFs): long-term survivors through periods of dramatic climate change. In: Environmental and Experimental Botany, The climatic challenge: learning from past survivors and present outliers, 170, p. 103892. https://doi.org/10.1016/j.envexpbot.2019.103892.

Veach, V., Minin, E.D., Pouzols, F.M., Moilanen, A., 2017. Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. Divers. Distrib. 23, 715–726. https://doi.org/10.1111/ddi.12571.

Velázquez, A., Guerrero, J.A., 2019. Romerolagus diazi. In: The IUCN Red List of Threatened Species, 2019. e.T19742A45180356. https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T19742A45180356.en. Downloaded on 01 October 2021.

Veron, S., Haevermans, T., Govaerts, R., Mouchet, M., Pellens, R., 2019. Distribution and relative age of endemism across islands worldwide. Sci. Rep. 9, 1–12. https://doi.org/10.1038/s41598-019-47951-6.

van der Werff, H., Consiglio, T., 2004. Distribution and conservation significance of endemic species of flowering plants in Peru. Biodivers. Conserv. 13, 1699–1713. https://doi.org/10.1023/B:BIOC.0000029334.69717.f0.

Williams, P.H., 1998. Key sites for conservation: area-selection methods for biodiversity. In: Mace, G.M., Balmford, A., Ginsberg, J.R. (Eds.), Conservation in a Changing World. Cambridge University Press, Cambridge, pp. 211–249.

Wilson, K.A., McBride, M.F., Bode, M., Possingham, H.P., 2006. Prioritizing global conservation efforts. Nature 440, 337–340. https://doi.org/10.1038/nature04366.

Zuloaga, J., Currie, D.J., Kerr, J.T., 2019. The origins and maintenance of global species endemism. Glob. Ecol. Biogeogr. 28, 170–183. https://doi.org/10.1111/geb.12834.