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Multi-dimensional biodiversity hotspots and the future of taxonomic, ecological and phylogenetic diversity: A case study of North American rodents

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Editor: Jonathan Davies**Abstract****Aim:** We investigate geographic patterns across taxonomic, ecological and phylogenetic diversity to test for spatial (in)congruency and identify aggregate diversity hotspots in relationship to present land use and future climate. Simulating extinctions of imperilled species, we demonstrate where losses across diversity dimensions and geography are predicted.**Location:** North America.**Time period:** Present day, future.**Major taxa studied:** Rodentia.**Methods:** Using geographic range maps for rodent species, we quantified spatial patterns for 11 dimensions of diversity: taxonomic (species, range weighted), ecological (body size, diet and habitat), phylogenetic (mean, variance, and nearest-neighbour patristic distances, phylogenetic distance and genus-to-species ratio) and phyloendemism. We tested for correlations across dimensions and used spatial residual analyses to illustrate regions of pronounced diversity. We aggregated diversity hotspots in relationship to predictions of land-use and climate change and recalculated metrics following extinctions of IUCN-listed imperilled species.**Results:** Topographically complex western North America hosts high diversity across multiple dimensions: phyloendemism and ecological diversity exceed predictions based on taxonomic richness, and phylogenetic variance patterns indicate steep gradients in phylogenetic turnover. An aggregate diversity hotspot emerges in the west, whereas spatial incongruence exists across diversity dimensions at the continental scale. Notably, phylogenetic metrics are uncorrelated with ecological diversity. Diversity hotspots overlap with land-use and climate change, and extinctions predicted by IUCN status are unevenly distributed across space, phylogeny or ecological groups.**Main conclusions:** Comparison of taxonomic, ecological and phylogenetic diversity patterns for North American rodents clearly shows the multifaceted nature of biodiversity. Testing for geographic patterns and (in)congruency across dimensions of diversity facilitates investigation into underlying ecological and evolutionary processes. The geographic scope of this analysis suggests that several explicit regional

challenges face North American rodent fauna in the future. Simultaneous consideration of multi-dimensional biodiversity allows us to assess what critical functions or evolutionary history we might lose with future extinctions and maximize the potential of our conservation efforts.

KEYWORDS

biodiversity gradients, ecological diversity, North America, phyloendemism, Rodentia, species richness

1 | INTRODUCTION

Striking patterns and hotspots of biodiversity in relationship to climatic, elevational and geographic gradients are common across the globe (Antonelli et al., 2018; Badgley & Fox, 2000; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). This biodiversity encompasses many aspects of biological complexity, including not only variation in the number of species present, but also variation in the ecological attributes of species, their functional roles within ecosystems and phylogenetic history (Pagel, May, & Collie, 1991; Purvis & Hector, 2000; Stevens & Tello, 2014). Approaches to quantifying and characterizing variation in biodiversity have increased dramatically (Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009; Tucker et al., 2017), and it is now well accepted that integrating across multiple dimensions of biodiversity (e.g., species richness, phylogenetic, functional ecological) both enriches our understanding of the origin and maintenance of biodiversity patterns (Davies & Buckley, 2011; Fritz & Rahbek, 2012; Rosauer & Jetz, 2014) and informs strategies for biodiversity conservation (Chiarucci, Bacaro, & Scheiner, 2011; Cumming & Child, 2009; Dirzo & Raven, 2003; Humphries, Williams, & Vane-Wright, 1995; Mace, Gittleman, & Purvis, 2003; Myers et al., 2000; Stein et al., 2018). Although species richness is often not a one-for-one surrogate for other dimensions of biodiversity (Fergnani & Ruggiero, 2015; Safi et al., 2011; Stevens, Tello, & Gavilanez, 2013), the degree to which geographic variation across multiple dimensions of diversity represents redundant information versus unique biological patterns remains unresolved (Devictor et al., 2010; Huang, Stephens, & Gittleman, 2012; Orme et al., 2005; but see Tucker & Cadotte, 2013).

Where tested, mismatches between taxonomic richness, phylogenetic diversity and functional ecological diversity exist for some, but not all, groups and settings (Devictor et al., 2010; Stevens & Tello, 2014). Variation in the strength of correlation between different dimensions of biodiversity may correspond to environmental conditions, regional landscape and biogeographic history and the composition of the regional species pool (Davies & Buckley, 2012; Fritz & Rahbek, 2012; Mazel et al., 2014; Safi et al., 2011; Villalobos, Olalla-Tárraga, Cianciaruso, Rangel, & Diniz-Filho, 2016). Thus, identification of areas of spatial (in)congruency between various dimensions of biodiversity provides powerful insight into the underlying processes of species diversification (speciation and extinction),

biogeographic dynamics (range shifts and immigration) and community assembly. Biodiversity hotspots that emerge from the intersection of multiple axes of diversity may additionally represent special conservation targets, where taxonomic and ecological diversity, phylogenetic history and ecosystem function can be preserved simultaneously (Orme et al., 2005; Stein et al., 2018). Demonstrating how these hotspots are threatened through imminent species loss (Barnosky et al., 2011; Ceballos et al., 2015), high velocity of climate change (Burrows et al., 2011; Loarie et al., 2009) or pervasive land-use changes (Sala et al., 2000) provides additional context for the prioritization of biological conservation.

Here, we assess the geographic patterns of multiple dimensions of species biodiversity within North American rodents, emphasizing four broad categories of diversity: taxonomic, geographic range size, ecological and phylogenetic diversity. By quantifying these different dimensions, we ask the following questions:

1. Which geographic regions harbour the highest taxonomic, ecological and phylogenetic diversity?
2. Are there hotspots of multi-dimensional diversity?
3. What are the geographic patterns of (in)congruency among dimensions?
4. Which regions and dimensions are likely to be most affected by current environmental and climatic change, including predicted species loss?

In addressing these questions, we do not expect to find congruence among all dimensions of biodiversity, and we expect landscape properties and history to play determining roles in both spatial congruency and biodiversity hotspots. For example, we predict that the mountains will be regions of high diversity across multiple axes as a result of both ecological processes (e.g., species accommodation across heterogeneous habitats) and evolutionary processes (e.g., speciation across geographic barriers) (e.g., Badgley et al., 2017; Simpson, 1964). However, phylogenetic diversity need not mirror ecological diversity, because physiographical barriers to gene flow may result in geographically restricted, but not necessarily ecologically disparate, species. We also predict that regions with a shared geological and climate history will exhibit similar patterns regardless of topographic complexity. For example, we expect both high- and low-relief northern latitudes to have low species richness owing to

recent glaciation, low ecological diversity owing to strong environmental filtering, but potentially high phylogenetic variance because taxa from different rodent families dispersed into the region following glacial retreat. Finally, we expect regions with small species ranges and highly endemic faunas to be threatened across multiple biodiversity axes by environmental and climate change. This may not always align with the regions experiencing the highest rates of climate change; however, in less seasonal climates, even a small amount of climate change may be detrimental or even insurmountable to taxa that are already geographically restricted (e.g., Deutsch et al., 2008).

1.1 | Study system

The reasons for selecting rodents for a large-scale and multi-faceted analysis of biodiversity are many. North American rodents represent almost half of continental mammalian species richness and c. 5.5% of global extant mammal diversity (Burgin, Colella, Kahn, & Upham, 2018; Mammal Diversity Database, 2019). Nearly 20% of North American species are currently threatened (IUCN, 2019; Wilson & Reeder, 2005). By looking at North America, we are approximating the Nearctic; however, choosing to: (a) include all of Mexico based on a priori knowledge from the palaeontological record, in addition to modern distributions of diversity, demonstrating its importance for rodent evolution; and (b) exclude Greenland, because of its low diversity and present-day ice cover.

We focus on this clade because of its excellent phylogenetic coverage (Fabre, Hautier, Dimitrov, & Douzery, 2012), well-documented body size and geographic range size information, and detailed species-level descriptions of dietary and habitat preferences. A within-rodent approach allows us to partition diet and habitat categories more finely than would be possible for broader taxonomic studies. North America taxa, in particular, have detailed information at the species level that are lacking or inconsistently known in other continental settings with high rodent diversity (IUCN, 2019). The biogeographic history of this clade has also been well studied in North America over multiple spatio-temporal scales (Riddle, Jezkova, Hornsby, & Matocq, 2014). Over evolutionary time-scales, species richness, ecological diversity and diversification rates for rodents have varied in relationship to changes in climate and landscape (Badgley et al., 2017; Finarelli & Badgley, 2010; Samuels & Hopkins, 2017; Smiley, 2018; Zelditch, Li, Tran, & Swiderski, 2015). Over Quaternary time-scales, range dynamics, dietary shifts, extinctions, extirpations and re-colonizations have been documented for rodents in relationship to glacial–interglacial climate oscillations (Barnosky, Koch, Feranec, Wing, & Shabel, 2004; Blois, McGuire, & Hadly, 2010; Grayson, 2011; Jezkova, Olah-Hemmings, & Riddle, 2011; Lessa, Cook, & Patton, 2003; Riddle et al., 2014; Terry, Guerre, & Taylor, 2017; Terry, Li, & Hadly, 2011). Finally, over the past century, the influence of climate, land-use and vegetation change has further altered present-day rodent communities (Moritz et al., 2008; Rowe & Terry, 2014; Rowe, Terry, & Rickart, 2011; Walsh et al., 2016).

Rodents are additionally of broad interest, because they serve as a critical food base for many other vertebrate groups (Wolf & Ripple, 2017). Their top-down effect on plant communities is likewise critical; soil aeration, seed dispersal and burial are all key functions that rodents play across ecosystem types (Chambers & MacMahon, 1994; Laundré & Reynolds, 1993). Rodents therefore represent bellwethers of larger-scale biological change, with benefits of small-mammal conservation cascading up and down the food web.

Together, these characteristics make North American rodents an ideal case study to highlight which aspects of biodiversity (including potentially hidden dimensions and regions of diversity) are most vulnerable under present and future land-use and climate change owing to anthropogenic influences. Because of links between diversity and stability of ecosystem function (Schindler, Armstrong, & Reed, 2015; Thibaut & Connolly, 2013; Tilman & Downing, 1994), understanding the geographic congruence of diversity measures in the context of regional landscape properties is crucial for informing policy and management initiatives at a continental scale (Cadotte, Dinnage, & Tilman, 2012). Furthermore, understanding whether hotspots of biodiversity today represent accumulations of evolutionarily distant taxa, the *in situ* generation of new species, or some combination of both is important for prioritizing regions for biodiversity conservation (e.g., Mischler et al., 2014). Finally, evaluating whether ecosystems and biodiversity hotspots can remain functionally intact even with the loss of certain species is important for looking forward to the coming century, when species loss is inevitable.

2 | MATERIALS AND METHODS

2.1 | Analytical approach

To illustrate multiple dimensions of biodiversity within North American rodents, we generated maps of diversity patterns for 350 species using 100 km × 100 km equal-area grid cells on a North America Albers Conic equal area projection (following recommendations regarding scale dependence by Hurlbert & Jetz, 2007; Jarzyna & Jetz, 2018). This includes all North American taxa with range data and excludes extinct and recently synonymized taxa (for more details, see Supporting Information in Appendix S1). We used the “rgeos” (Bivand & Rundel, 2018), “raster” (Hijmans, 2017) and “sp” (Bivand, Pebesma, & Gomez-Rubio, 2013; Pebesma & Bivand, 2005) packages in R to extract and manipulate geographic data and to generate biodiversity maps. All statistical analyses were performed in the R statistical and computing environment (R Development Core Team, 2017).

2.1.1 | Taxonomic diversity

Within each grid cell, species lists were compiled based on overlapping geographic ranges of extant, native species as classified and provided by the IUCN Red List database (IUCN, 2019). To be

considered within cell, a species must span $\geq 10\%$ of a grid cell, unless it is the only grid cell that species occupies, in which case it was also retained for our analysis. We quantified taxonomic diversity, also known as species richness, as the number of species co-occurring within each grid cell.

2.1.2 | Ecological diversity

To capture the diversity of functional roles that species play within their local ecosystems, we collected three primary types of ecological information: (a) body size; (b) diet category; and (c) habitat affinity (Supporting Information Appendix S1, Tables S1.1 and S1.2). Species-level trait data were compiled from the literature, refined and cross-checked using a variety of sources, including volumes on North American mammals (Kays & Wilson, 2009; Wilson & Ruff, 1999), comprehensive body size databases and references (Silva-Aliaga & Downing, 1995; Smith et al., 2003) and previous studies (Badgley & Fox, 2000).

Given that body size has been shown to reflect many aspects of a species' ecology and to play a major role in community structure, function and dynamics (Brown & Nicoletto, 1991; Ernest, 2005; Smith et al., 2004), we assessed the number and evenness of body size classes present within grid cells across the continent. We binned species into 10 groups according to the Jenks natural break classification for the logged distribution of body sizes across all North American species (Supporting Information Appendix S1, Table S1.2) using the "classInt" package in R (Bivand, 2018). We also binned species on the basis of dietary functional group (13 categories in total, including granivores, frugivores, insectivores and succulent specialists) and habitat affinity (30 categories in total, including forest, coastal, tundra, shrubland and freshwater habitats), both of which are axes along which niche partitioning and competitive exclusion can occur in rodent communities (e.g., Brown & Lieberman, 1973; Price & Brown, 1983). Although an individual species may span several diet and habitat categories, we chose the dominant category represented in the literature and quantified ecological diversity based on the number of categories filled per grid cell. We then calculated the evenness of all three ecological measures using Simpson's evenness metric or the probability of interspecific encounter (PIE), as formulated by Hurlbert (1971). Species-depauperate grid cells (i.e., fewer than five species present) were excluded from analyses.

2.1.3 | Range-related diversity patterns

We first calculated the mean and minimum geographic range area of species present in a grid cell. We then combined taxonomic richness and range data to calculate range-weighted taxonomic richness, a metric that assigns greater proportional weight to spatially restricted than geographically widespread species and reflects endemism (Crisp, Laffan, Linder, & Monro, 2001; Rosauer & Jetz, 2014).

2.1.4 | Phylogenetic diversity patterns

To investigate phylogenetic diversity for rodents, we used the maximum likelihood phylogeny generated by Fabre et al. (2012) from a supermatrix of mitochondrial and nuclear genes (obtained via personal communication). Given that North American rodents do not form a monophyletic group, we pruned the phylogeny to our dataset; 99% of species for which geographic distributions were available were also present in the phylogeny ($n = 348$; for additional taxonomic considerations, see Supporting Information, Appendix S1). We used four metrics to quantify phylogenetic diversity (Faith, 1992; Tucker et al., 2017) for the assemblages occupying each 100 km \times 100 km grid cell: (a) the mean of all pairwise branch lengths (mean patristic distance, MPD); (b) the mean of pairwise shortest branch lengths (patristic nearest neighbour distance, PNN); (c) the variance of pairwise branch lengths (variance in patristic distance, VPD); and (d) Faith's phylogenetic diversity (PD). The MPD and PNN describe the distribution of divergence dates among species, with PNN specifically highlighting recent divergences. The use of MPD is further justified because it is not mathematically correlated with richness. The VPD describes the regularity of species composition, or how evenly evolutionary history is distributed among species within a set (Tucker et al., 2017). In conjunction with ecological diversity, VPD provides useful information about the overall structure of biodiversity across spatial scales. Although known to be correlated strongly with species richness (Fritz & Rahbek, 2012), Faith's PD was also included and describes the accumulated evolutionary history represented by a set of species (Faith, 1992). We additionally used a purely taxonomic approach and calculated genus-to-species ratios (GSR) for each suite of species to demonstrate the distribution of shallower (species-level) divergences relative to deeper (genus-level) divergences.

Finally, we integrated range size data with phylogenetic branch lengths to calculate phylogenetic endemism (PE; Rosauer et al., 2009), a metric that identifies regions that host both phylogenetically isolated and spatially restricted biota (Gonzalez-Orozco et al., 2016; Rosauer & Jetz, 2014). All phylogenetic analyses were conducted in R, using the "ape" package (Paradis, Claude, & Strimmer, 2004).

2.1.5 | Assessment of multi-dimensional hotspots and imperilled species

To assess congruency in spatial patterns of taxonomic, ecological and phylogenetic diversity, we applied Dutilleul's *t*-test (Dutilleul, Clifford, Richardson, & Hemon, 1993), which is a modified test of association between spatially autocorrelated variables, using the "SpatialPack" package in R (Osorio, Vallejos, & Cuevas, 2014). Owing to the large number of comparisons conducted, we applied a Bonferroni sequential adjustment to test for significant relationships (Rice, 1989). For diversity metrics that were significantly correlated (i.e., adjusted

p -value < .05) or exhibited a clear linear relationship with species richness, we also mapped residuals to identify areas where ecological or phylogenetic diversity differed from expectations based on species richness in a cell (e.g., Fergnani & Ruggiero, 2015; Fritz & Rahbek, 2012).

To identify regions that represented high multi-dimensional biodiversity, we generated aggregate hotspot maps (e.g., Stein et al., 2018). Hotspots of species richness comprised cells within the top 10% for taxonomic richness, range-weighted taxonomic richness and phylogenetic endemism. Likewise, hotspots of ecological richness comprised cells within the top 10% for body size, diet and habitat richness. Finally, regions that harboured elevated deep diversity (top 10% of MPD and VPD) and elevated shallow diversity (bottom 10% of PNN and GSR) were identified as phylogenetic diversity hotspots.

Given that multi-dimensional hotspots are likely to represent regions of particular conservation concern, we also related hotspots to the current and future geography of habitat transformation (e.g., Sala et al., 2000) and climate change velocity (Burrows et al., 2011; Loarie et al., 2009). Mapping the geographic distribution of biodiversity hotspots in relationship to regions of high human impact and rapidly shifting climates serves to identify regions disproportionately at risk (Finnegan et al., 2015; Garcia et al., 2014; Ohlemüller et al., 2008). We assigned human-impacted habitats to cells for which the maximum land-cover type was cropland, pasture or urban, using a business-as-usual scenario of modern (1970) and future (2080) land use from the IMAGE 3.0 database (<https://data.knmi.nl/datasets>). We determined regions of high climate velocity using the general circulation model ensemble-based forward velocity datasets for moderate (RCP4.5) and high (RCP8.5) emissions scenarios (Carroll, Lawler, Roberts, & Hamann, 2015; <https://adapt.west.databasin.org>). Forward velocity refers to the rate (in kilometres per year) at which organisms in the current landscape would have to migrate in order to maintain constant climate conditions in 2080. We designated cells as having a high velocity if they were within the 90th percentile of velocity values under the moderate emissions scenario.

Finally, to demonstrate potential losses of biodiversity, be it taxonomic, ecological or phylogenetic, we simulated future extinctions by culling currently imperilled rodent species and reanalysing diversity patterns. We defined imperilled species as those categorized by the IUCN Red List as Critically Endangered, Endangered or Vulnerable. To demonstrate the impact of species loss, we compared both geographic diversity patterns and distributions of diversity metrics across taxa for the current biodiversity state versus a future “post”-extinction state.

2.2 | Sensitivity analyses

Using the following approaches, we also tested the sensitivity of our analysis to two factors: (a) influence of wide-ranging species; and (b) choice of phylogeny.

2.2.1 | Wide-ranging species

To test the sensitivity of these metrics to wide-ranging species (Jetz & Rahbek, 2002), we performed additional analyses that excluded species with geographic range sizes above the 90% quantile, such as *Castor canadensis* and *Peromyscus maniculatus*. A total of 35 species with ranges > 2,620,000 km² were excluded, and all analyses were re-run to test for statistical over-representation of wide-ranging taxa in correlation tests of spatial congruence across different dimensions of biodiversity. We note that range-weighted diversity and phylogenetic endemism measures mitigate the potential impacts of wide-ranging taxa by down-weighting those taxa in diversity calculations.

2.2.2 | Phylogeny choice

To test the sensitivity of phylogenetic metrics to tree choice, we conducted all phylogenetic analyses (MPD, VPD, PNN, PD and PE) using an alternative molecular-based 4,254-taxon mammal phylogeny from Faurby and Svenning (2015a), updated to v.1.2 in the Phylacine database (Faurby et al., 2018). From a posterior distribution of 1,000 trees, we generated the maximum clade credibility tree for use in our analyses, calculated with the R package “phangorn” v.2.5.5 (Schliep, 2011), and pruned it to North American rodent taxa. When reanalysing geographic patterns of phylogenetic diversity, 36 taxa were excluded owing to lack of phylogenetic information in the Faurby and Svenning tree.

3 | RESULTS

Taxonomic richness varies considerably over the North American continent, ranging from fewer than five species per 100 km × 100 km grid cell (Arctic) to > 45 species per cell (intermontane west) (Figure 1a). The species-rich western region (including the Rocky Mountain Front Range, the Great Basin and the Sierra Madres) also hosts species with small mean and minimum range sizes (Figure 1b). Small geographic ranges contribute to elevated range-weighted taxonomic richness (Figure 1c) and phylogenetic endemism (Figure 3e), highlighting regions with small-ranging and phylogenetically isolated taxa along the Pacific Coast and in Mexico.

Ecological richness metrics (based on body size, diet and habitat affinity) demonstrate similar east-to-west gradients in diversity. The number of body size classes varies with longitude and latitude, peaking in the Great Basin and southern Mexico (Figure 2a). High dietary richness is found in southwest deserts of the USA, whereas habitat richness is highest in western regions with increased topographic relief and habitat heterogeneity (Figure 2b,c). In contrast, ecological evenness varies little and remains high across the continent for all three metrics (Figure 2d-f), suggesting that communities are composed of equally filled body size, diet and habitat categories within the local environment. A

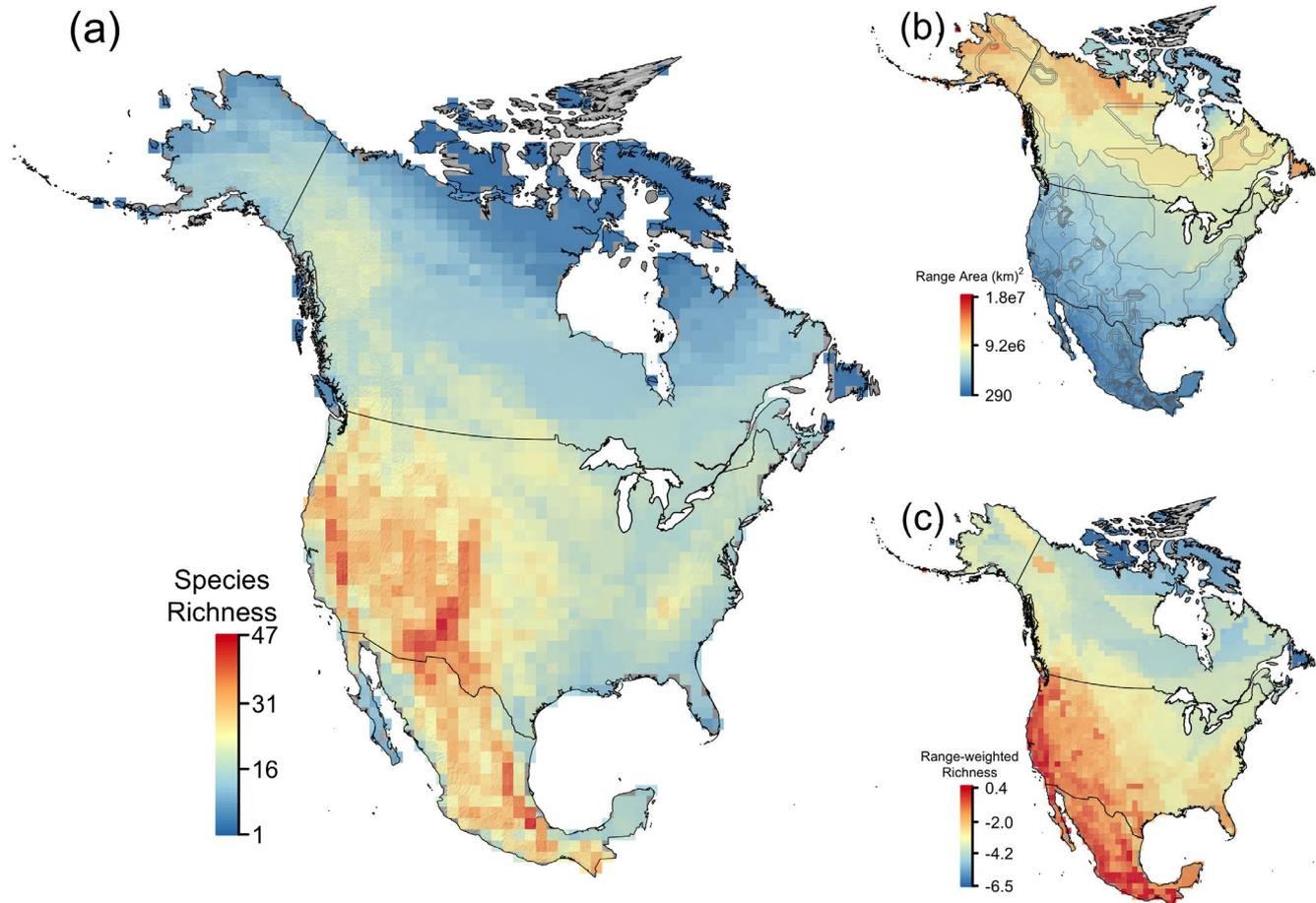


FIGURE 1 Maps of North American rodent diversity metrics: (a) taxonomic richness; (b) mean geographic range size for each suite of species present within a grid cell overlain by contour lines representing the logarithm of the minimum geographic range size to illustrate a higher concentration of smaller rodent ranges in the western USA and Mexico; and (c) range-weighted taxonomic richness (logarithmic scale) [Colour figure can be viewed at wileyonlinelibrary.com]

few notable exceptions are low (0.5–0.7) body size evenness localized to the Baja Peninsula and southeastern California and a moderate increase (from 0.6 to 0.8) in dietary evenness from Great Plains to intermontane west communities.

Each phylogenetic diversity metric reveals a distinct pattern across North America (Figure 3). The MPD varies little with geography (Figure 3a), whereas VPD (Figure 3b) is lowest in the Great Plains (low relief, environmentally homogeneous) and parts of the Great Basin and southwestern deserts (high relief, environmentally heterogeneous), indicating relatively uniform distributions of branch lengths independent of absolute branch length in these regions. The PNN and GSR are both low in the intermontane west of the USA, indicating concentrations of recently diverged taxa in these regions spanning multiple genera (Figure 3c,f). In contrast, low PNN values in the eastern USA do not correspond to low GSR values, where fewer species are found within genera, but these species tend to have at least one within-genus nearest neighbour. Faith's PD tightly follows the species richness geographic pattern, with highest values along the southern Rocky Mountain Front Range. Finally, strong gradients in phylogenetic diversity exist in Canada owing to low taxonomic richness, especially in the Arctic.

To assess whether different dimensions of biodiversity represent novel or redundant information, we also tested the spatial congruence of these patterns and, using a Bonferroni sequential correction, found significant correlations between < 15% of the diversity metric pairs (Figure 4a; Supporting Information Appendix S1, Table S1.3). Lack of significant correlation between metrics is reflected in non-congruent geographic gradients at both continental and regional scales. The notable exception is Faith's PD, which exhibits significant positive correlations ($r = .94$, adjusted p -value = .001) and similar spatial patterns with species richness and its correlates, including body size, diet and habitat richness. The residuals from regression models of ecological diversity against species richness also exhibit spatial variation, including lower than expected body size richness in the taxonomically diverse desert southwest (Figure 4b) and higher than expected dietary richness in the Great Plains and intermontane west (Figure 4c). Likewise, habitat richness was lower than expected in the Sierra Madres, but higher than expected along strong regional ecotones (e.g., Northern Great Basin, Rocky Mountain Front Range). Although not significantly correlated using a Bonferroni sequential adjustment, higher species richness generally corresponded to higher range-weighted species richness

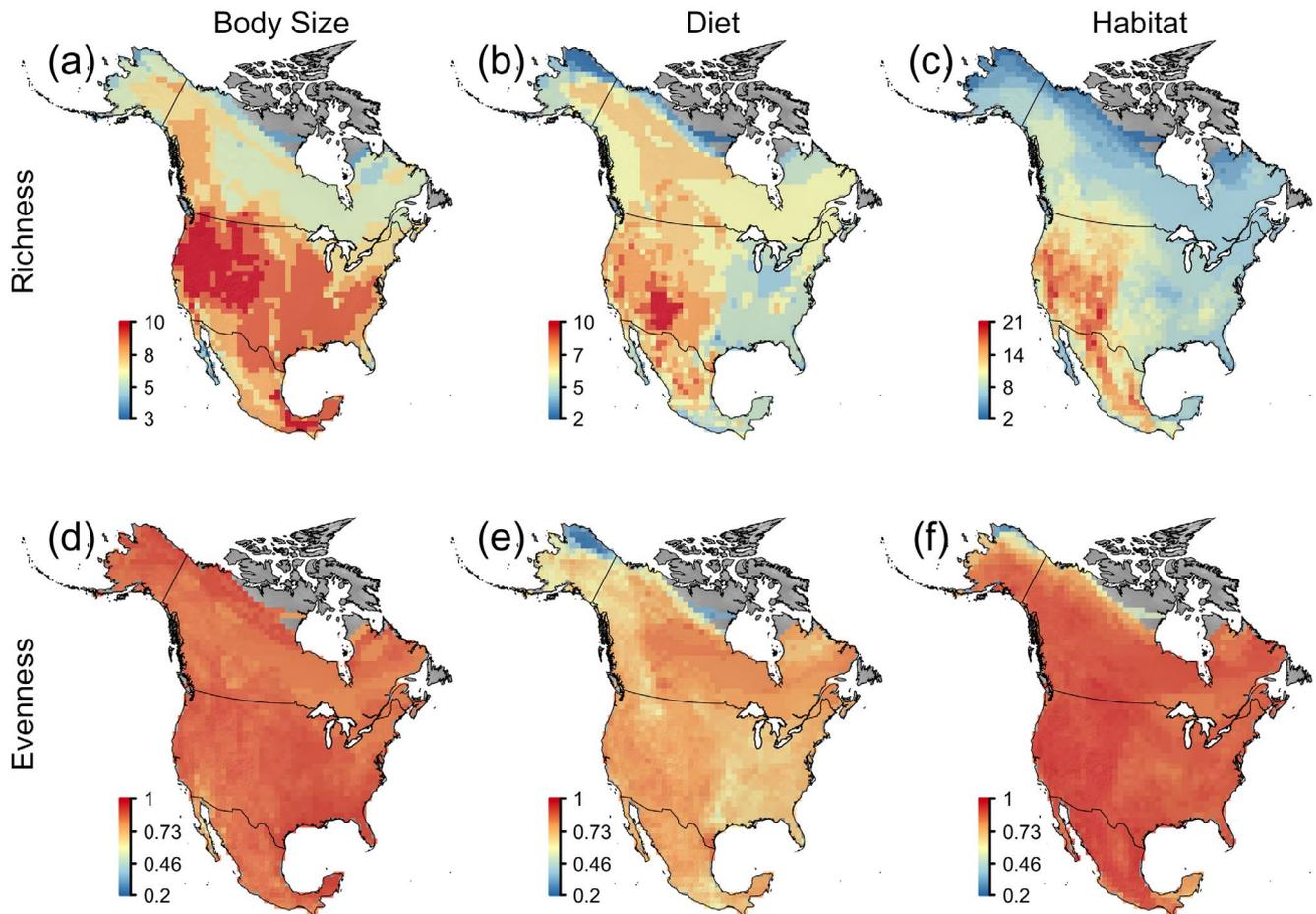


FIGURE 2 For North American rodent species, categorical richness (a–c) and Simpson's evenness (d–f) for three indices of ecological diversity, calculated for cells with a minimum of five species present. Indices include body size class, determined using Jenks natural breaks optimization from the North American rodent body size distribution (a,d), diet category (b,e), and habitat affinity (c,f) [Colour figure can be viewed at wileyonlinelibrary.com]

and phylogenetic endemism, and lower GSR at the continental scale ($r > .8$). These three metrics include species richness in their calculation; however, correlation need not be expected (Reig, 1989; Tucker & Cadotte, 2013), and spatial differences in gradients, especially the location of high richness, exist among these metrics (Figures 1 and 3e,f). Phylogenetic endemism was generally uncorrelated with other phylogenetic metrics and therefore reveals novel information about geographic patterns of species relatedness and diversity. Finally, phylogenetic diversity metrics were only weakly correlated, suggesting that each metric also reflects a unique aspect of clade diversity and history.

Sensitivity tests that excluded wide-ranging species revealed where our analysis might be influenced by the over-representation of species with ranges spanning much of the continent. Although we find an increase in the number of significantly correlated relationships among diversity dimensions (Supporting Information Appendix S1, Table S1.4), the spatial patterns remain similar (Supporting Information Appendix S1, Figure S1.1). Losses of ecological diversity patterns at high latitudes and in eastern USA are notable, where taxonomic lists are composed of numerous wide-ranging taxa. In

comparison with the full dataset, MPD, PNN and VPD also differ in spatial patterns in these northern and eastern regions; however, phylogenetic diversity hotspots remain in the intermontane West and Mexico, where species ranges are smaller on average (Figure 1b). Measures of phylogenetic diversity calculated from the phylogenies of Fabre et al. (2012) and Faurby and Svenning (2015a) exhibited highly correlated patterns ($r > .89$; $p < .001$). Therefore, all results and discussion herein pertain to the phylogeny of Fabre et al. (2012); for further information about tree choice and interpretation of phylogenetic diversity metrics across trees, see the Supporting Information (Appendix S1, Figure S1.2). In combination, these sensitivity analyses show that the results of the (in)congruency analysis remain robust to the influence of wide-ranging taxa and choice of phylogeny.

Despite their different spatial patterns at the continental scale, high diversity values across multiple metrics are roughly congruent, concentrated in the western USA and Mexico. Aggregate hotspots of taxonomic (raw and range-weighted) richness and phylogenetic endemism (Figure 5a) overlap broadly with aggregate hotspots of ecological diversity along body size, diet and

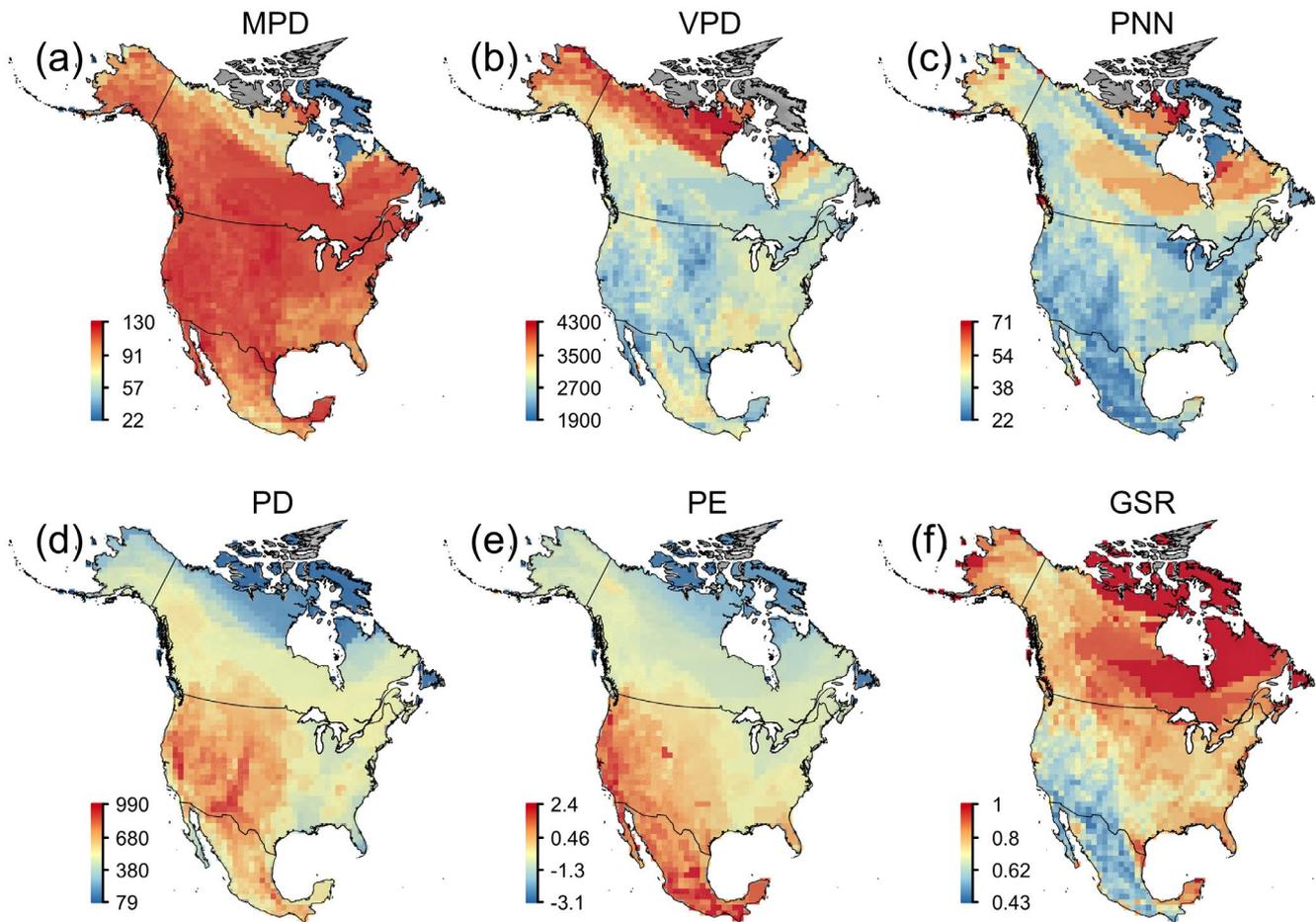


FIGURE 3 Six phylogenetic diversity metrics calculated for each suite of North American rodents present in a 100 km × 100 km grid cell: (a) mean pairwise distance (MPD); (b) variance of pairwise distances (VPD); (c) mean pairwise nearest-neighbour distance (PNN); (d) Faith's phylogenetic diversity (PD); (e) phylogenetic endemism (PE; logarithmic scale); and (f) genus-to-species ratio (GSR) [Colour figure can be viewed at wileyonlinelibrary.com]

habitat axes (Figure 5b). In contrast, hotspots of shallow (bottom 10% PNN and GSR) and deep (top 10% MPD and VPD) phylogenetic diversity are not spatially congruent (Figure 5c). Summing across all biodiversity hotspots, the Great Basin, the southwest deserts and the Sierra Madres capture a high degree of taxonomic, ecological and phylogenetic diversity (Figure 5d). Comparison of multi-dimensional biodiversity hotspots with regions that have undergone human-driven changes in land use (agriculture, pasture or urbanization) in the last century (Figure 5e) reveals considerable overlap: 33.3 and 34.4% of hotspot area overlaps with highly affected regions owing to modern and future human land use, respectively. Overlap of multi-dimensional diversity hotspots with regions predicted to experience rapidly changing climates over the coming decades may also be high, depending on the emissions scenario (Figure 5f); 10.4 and 37.9% of hotspot area overlaps with high climate change velocity under moderate and high CO₂ emission scenarios, respectively.

Under hypothetical future extinctions of imperilled IUCN species attributable to these and other drivers, the impact of species loss on taxonomic, ecological or phylogenetic diversity is concentrated

geographically along the western coast of the USA and Mexico, in southern Mexico and in Florida (Figure 6a,b). Typically, only a single species went extinct in a cell; however, up to three species were lost in southern California and up to six species within regions of southern Mexico (Supporting Information Appendix S1, Figure S1.3). For cells that experienced extinction, we found significant differences in several diversity metrics pre- and post-extinction (Supporting Information Appendix S1, Figure S1.4). Lost species represented a mix of deep and shallow divergence events, and all but one had restricted geographic range areas (Figure 6a,b). The loss of ecological diversity varied in geographic extent and intensity, with body size, dietary and habitat richness loss in certain regions (e.g., southwestern Mexico) but not in others (e.g., Florida) during species extinction (Figure 6c). Ecological loss was distributed across all body size classes and dietary categories, but was most pronounced among medium-sized rodents and insectivore and carnivore specialists (Figure 6d). Lost species spanned several different habitat categories; in particular, a large percentage (64%) of species occupying particularly fragmented and fragile cloud forest habitats of central Mexico were imperilled.

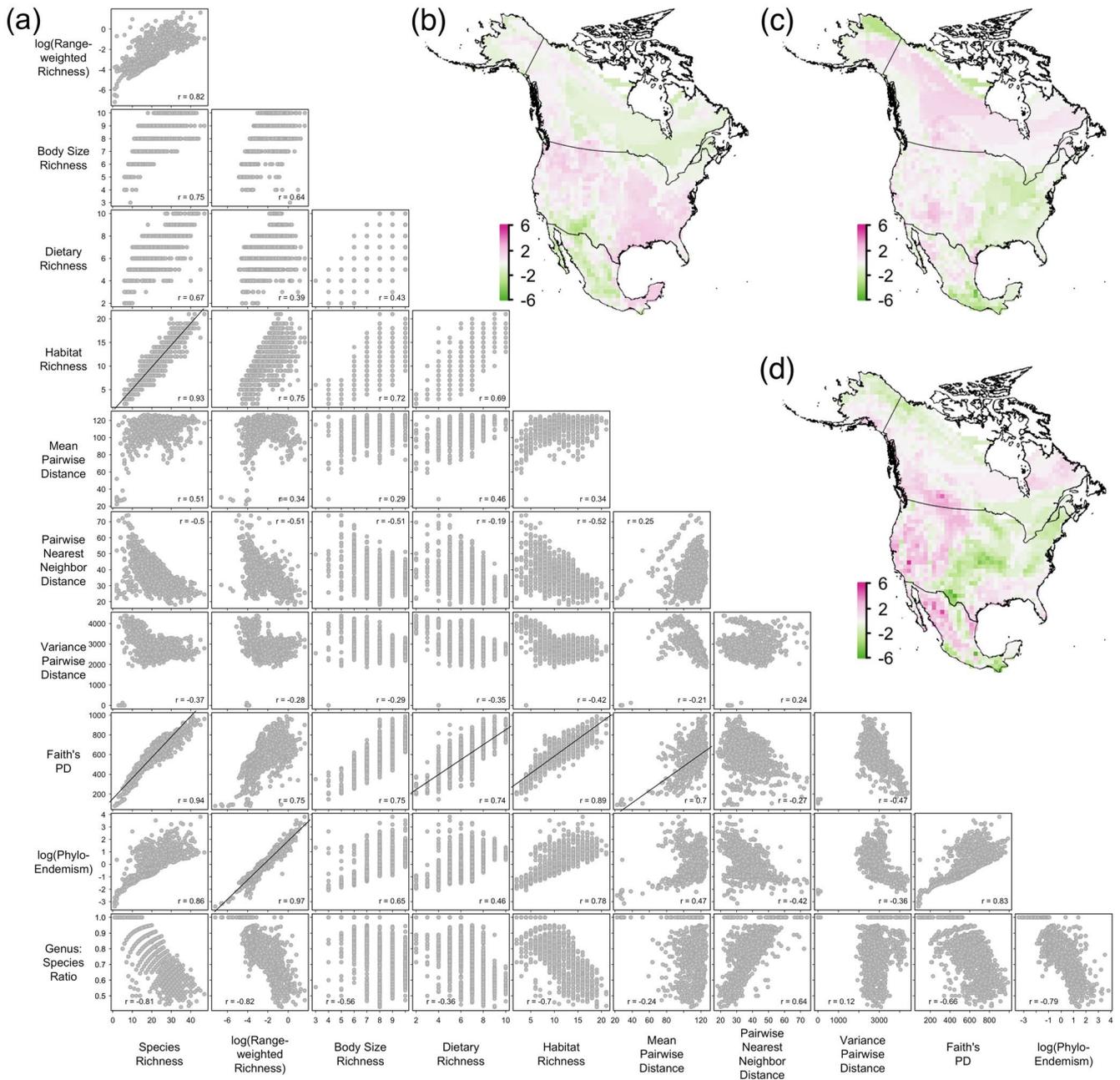


FIGURE 4 (a) Pairwise correlations among biodiversity metrics. Correlation coefficients (r) and significance are determined using Dutilleul's t -test, with linear regression lines shown for significant correlations, according to a Bonferroni sequential correction (adjusted p -value $< .05$), only. (b–d) Maps of residuals from a regression model of body size richness (b), dietary category richness (c) and habitat affinity richness (d) against taxonomic richness [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our comparison of taxonomic, ecological and phylogenetic diversity patterns for North American rodents clearly shows the multifaceted nature of biodiversity. Familiar patterns emerge from this analysis, such as a strong, positive relationship between topographic complexity and taxonomic diversity (Antonelli et al., 2018; Badgley & Fox, 2000; Badgley, Smiley, & Cable, 2018; Quintero & Jetz, 2018; Simpson, 1964). Yet this study adds several new dimensions of diversity that, in conjunction, suggest potential mechanisms driving

elevated species richness in topographically complex regions and reduced diversity in others.

4.1 | Patterns and hotspots of multi-dimensional diversity

As predicted, we find that the influence of topography and environmental heterogeneity extends beyond species richness to novel dimensions of biodiversity (Figure 5d): high-relief landscapes and

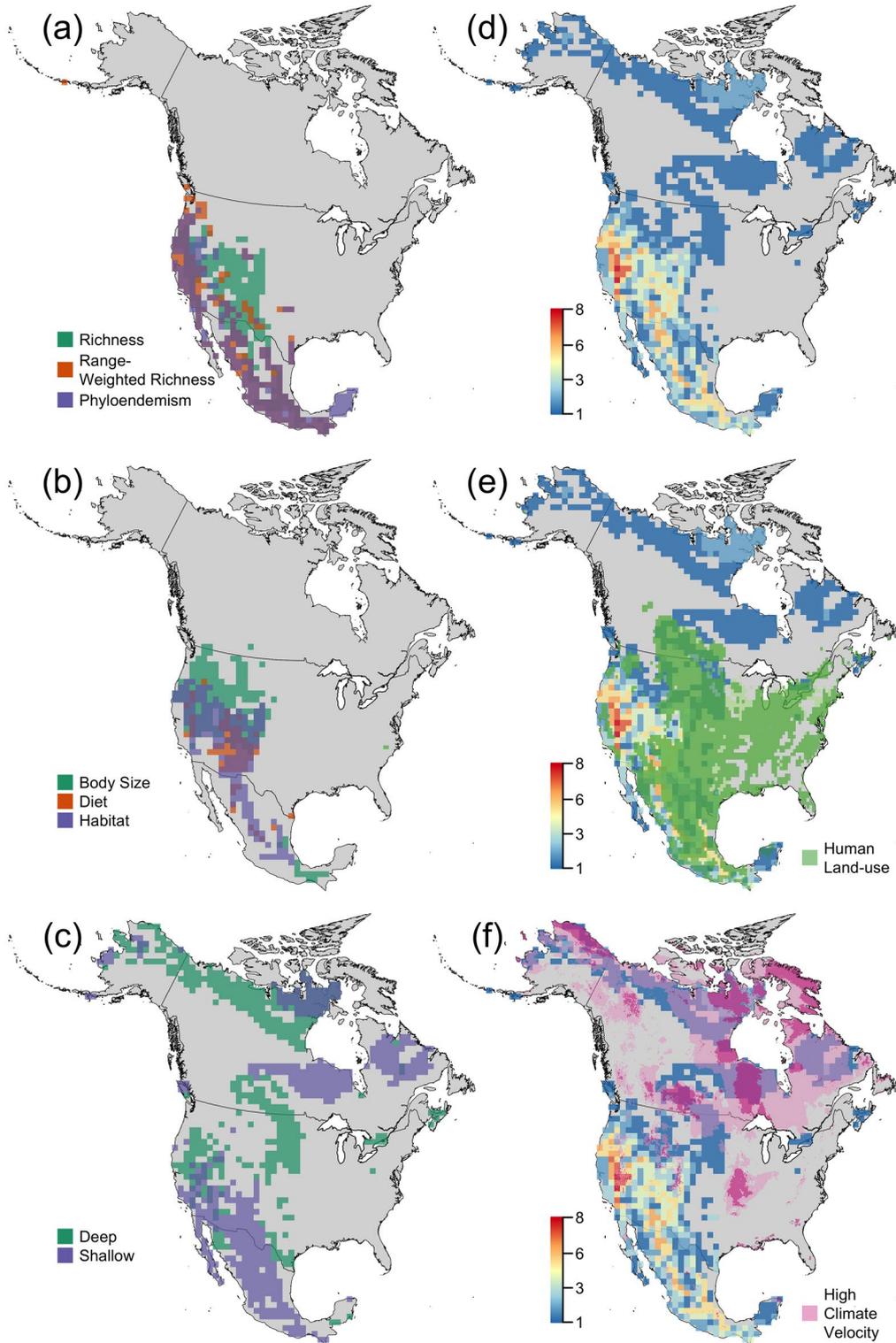


FIGURE 5 Multi-dimensional hotspots for cells with the top 10% of values for: (a) taxonomic richness, log(range-weighted taxonomic richness) and log(phylogenetic endemism); and (b) ecological diversity, including body size, diet and habitat richness. (c) Multi-dimensional hotspots of shallow [bottom 10% pairwise nearest-neighbour distance (PNN) and genus-to-species ratio] and deep [top 10% mean pairwise distance (MPD) and variance of pairwise distances (VPD)] phylogenetic diversity. For (a–c), the hotspot locations are unique to each metric; however, colours are transparent, to illustrate regions of hotspot overlap. (d) Aggregate (sum) hotspot map for all diversity metrics. This map is overlain by: (e) cells dominated by human land use (cropland, pasture and urban) in 1970 and projected into 2080 (each a translucent green layer); and (f) cells experiencing high climate velocity (now to 2080) under moderate- and high-emissions scenarios (each a translucent pink layer, with the high-emissions scenario being more widespread) [Colour figure can be viewed at wileyonlinelibrary.com]

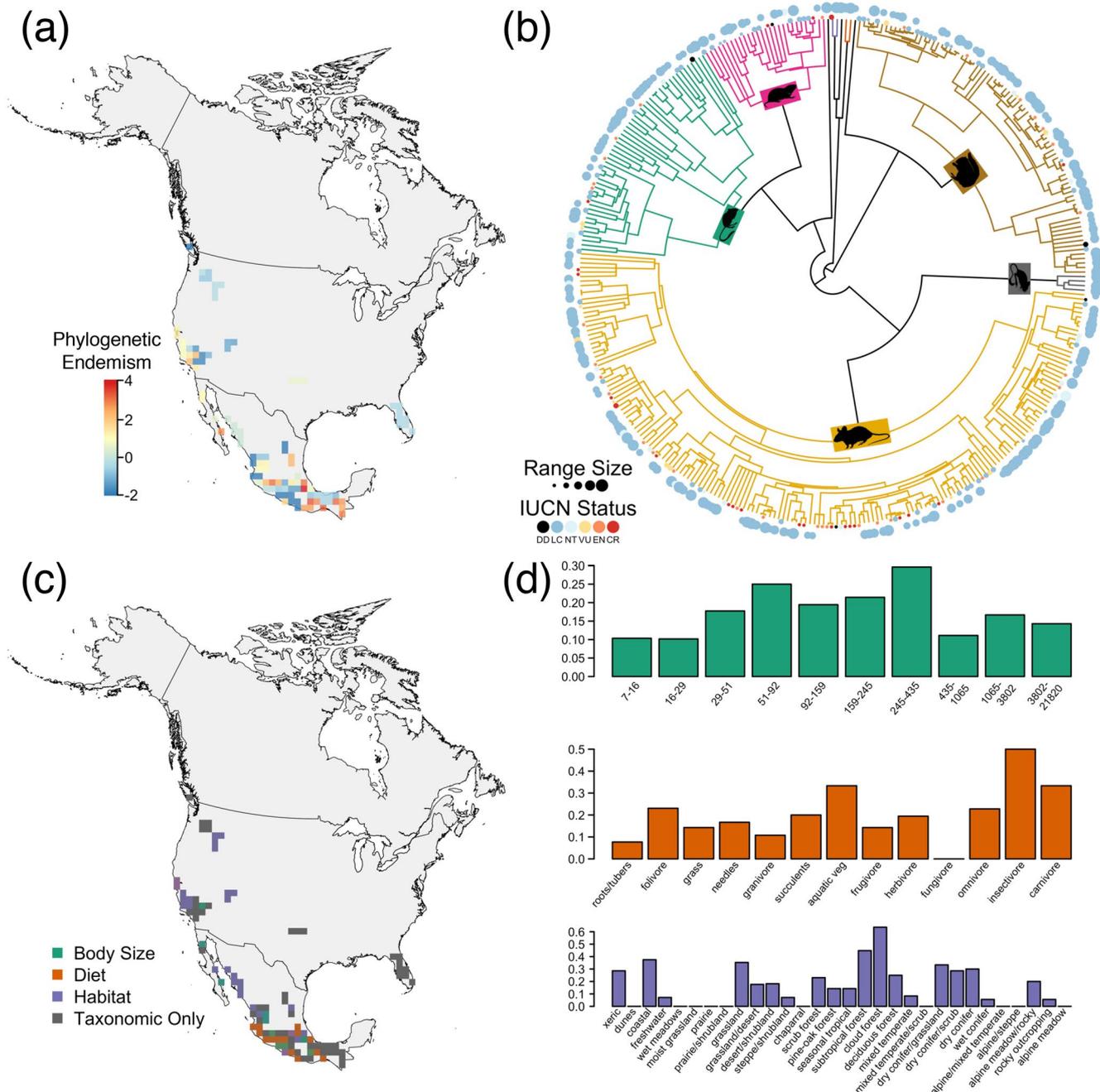


FIGURE 6 (a) The geographic regions facing the greatest change under future species extinction are represented by the difference in phylogenetic endemism after the removal of imperilled taxa, where imperilled refers to Vulnerable (VU), Endangered (EN) and Critically Threatened (CR) IUCN status. (b) Phylogenetic endemism captures branch length data from the phylogenetic tree of rodents (pruned from Fabre et al., 2012 to North American taxa used in the present study) and geographic range area. In the phylogeny, branch colours correspond to the major rodent families, circle size at the end of each branch is relative to species range area (points are jittered to see variation better), and colour indicates the IUCN status of the species. (c) Cells with species extinction are shown in dark grey, and cells that experience further loss in ecological diversity (loss of one or more body size classes, diet or habitat categories) are coloured accordingly. (d) The proportion lost for each ecological category after extinction of imperilled species within those cells [Colour figure can be viewed at wileyonlinelibrary.com]

heterogeneous habitats harbour high diversity in rodent body size, dietary and habitat classes (Figures 3a–c and 5b) and in phylogenetic endemism (Figures 3e and 5a). Furthermore, rodent communities in these regions comprise species that span a broader range of evolutionary history than elsewhere on the continent (Figures 2 and 5c). Thus, high

regional diversity in western North America not only fuels high local diversity during community assembly (Ernest, Brown, Thibault, White, & Goheen, 2008; Mittelbach & Schemske, 2015; Ricklefs, 1987), but also highlights the importance of topographically complex landscapes as potential species source regions (e.g., “out-of-the-mountains” model;

Badgley et al., 2017) and refugia (Grayson, 2011; Holderegger, Thiel-Egenter, & Whittaker, 2009) over evolutionary time-scales.

Previous work has attributed the high taxonomic richness in topographically complex regions to ecological, evolutionary and geohistorical mechanisms (Badgley et al., 2017; Simpson, 1964). We find high dietary and habitat richness (Figure 3a,c), even after removing the effect of taxonomic diversity (Figure 4c,d), in intermontane regions, adding support to a species accommodation model for explaining macroecological patterns, with tighter species packing along steep environmental and elevational gradients (Coblentz & Riitters, 2004; Kotler & Brown, 1988). Evolutionary hypotheses additionally propose that topographic relief increases the likelihood of population-level divergence and, ultimately, speciation events, especially during intervals of climate change and corresponding range shifts (Barnosky & Carrasco, 2002; Flantua & Hooghiemstra, 2018; Jezkova et al., 2011; Machac, Graham, & Storch, 2017; Quintero & Jetz, 2018; Riddle et al., 2014). Modern and fossil records have demonstrated that tectonically active landscapes promote diversification pulses and high regional species richness (Cracraft, 1985; Finarelli & Badgley, 2010; Hoorn et al., 2010; Moen & Morlon, 2014; Mulch, 2016; Smiley, 2018). Thus, isolated mountain ranges and intervening basins can generate and maintain high regional diversity through increases in both deep and shallow divergence events.

These evolutionary and geohistorical hypotheses are supported by our results, and notable patterns in phylogenetic diversity arise in relationship to topographic complexity. In particular, although MPD does not change substantially across most of the continent, steep gradients in VPD in the intermontane west indicate high turnover in the phylogenetic make-up of species assemblages. High variance could reflect the combined influence of speciation, extinction and immigration into intermontane regions during intervals of climate change (Davies & Buckley, 2011). Patterns of PNN and GSR additionally illustrate hotspots of “young” diversity (low values) found across the heterogeneous habitats of the western USA and Mexican highlands (Figure 3c,f). Thus, our findings are consistent with mountains as sites of recent radiations and current hotspots of neoendemism (Antonelli et al., 2018; Badgley et al., 2018; Davis, Koo, Conroy, Patton, & Moritz, 2008). Furthermore, topographically complex landscapes can preserve “old” lineages through various mechanisms (e.g., refugia effect). We find a concentration of phylogenetically distinct and long-branched taxa with small geographic ranges leading to increased phyloendemism in the western USA and Mexican highlands (Figure 3e).

Our focus on the intermontane west stems from identifying and examining multi-dimensional hotspots, but equally interesting hypotheses could be proposed and tested for regions that harbour low diversity across multiple dimensions, such as the Great Plains. Likewise, this analysis is applicable to other topographically complex landscapes globally. Next steps might include assessing patterns in other mountain ranges and taxonomic groups to: (a) investigate whether concordant patterns emerge; and (b) test whether similar ecological and evolutionary drivers of high diversity in relationship to topographic relief and history are at play. In addition, at the spatial

scale of our analysis, we are not able to distinguish whether taxa co-occur locally or experience high turnover along elevational gradients within our grid cells. Incorporating elevational range data to assess patterns of taxonomic, ecological and phylogenetic diversity along topographic gradients (e.g., Quintero & Jetz, 2018) would be a promising future direction.

4.2 | Incongruence in geographic patterns sheds light on potential drivers of diversity gradients

Although regions of topographic complexity harbour high multi-dimensional biodiversity, spatial congruence across diversity metrics is not the dominant trend (Figure 4), as predicted and previously demonstrated at other spatial and taxonomic scales (Devictor et al., 2010; Fritz & Rahbek, 2012; Huang et al., 2012; Safi et al., 2011; Stein et al., 2018; Stevens & Tello, 2014). Although many factors may contribute to spatial incongruency, the geographic scope of our study allows us to address whether processes of faunal assembly appear localized or if general patterns emerge across regional scales. With this aim, we highlight three observations from our results: (a) regional diversity is shaped by processes of speciation, immigration and extinction, and the relative contribution of each may lead to incongruency in some regions but not in others; (b) phylogenetic and ecological diversity measures are not interchangeable; and (c) diversity and evenness patterns in the desert southwest depart from regional patterns.

Our findings, especially the wedge-shaped relationship between taxonomic richness and MPD, PNN and VPD, reflect high variability across local and regional assemblages in phylogenetic diversity, especially among taxonomically impoverished regions. As predicted, the Arctic exhibits high phylogenetic variance attributable, in part, to the temporally and spatially asynchronous immigration and refugia histories of disparate phylogenetic lineages into the region following the end-Pleistocene glacial retreat that, via extinctions, “wiped” the slate clean for incoming taxa (e.g., Lessa et al., 2003; Lyons, 2003; Shafer, Cullingham, Côté, & Coltman, 2010). This history of extinction and assembly via immigration contrasts sharply with the pattern of high phylogenetic variance found elsewhere on the continent (e.g., desert southwest) due to a combination of recently diverged taxa (which are likely to have diverged *in situ*) coexisting with deep, endemic lineages. Further examination of the lack of correspondence between different biodiversity measures and phylogenetic diversity residuals (Supporting Information Appendix S1, Figure S1.5) might help to illuminate the diversification and immigration processes that help to generate and maintain biodiversity gradients.

Early emphasis on phylogenetic diversity rested on the assumption that closely related species exhibit high functional overlap due to phylogenetic signal (Faith, 1992). Thus, regions of high phylogenetic diversity, especially phylogenetic variance, were assumed to capture a higher degree of ecological diversity and promote functional stability of ecosystems (Cadotte et al., 2012). However, we

and others (e.g., Devictor et al., 2010; Fritz & Purvis, 2010) do not find that expected correspondence between phylogenetic and ecological diversity (Figure 4), especially across space (Figures 2 and 3), stressing the importance of placing these measures in geographic context. Furthermore, phylogenetic diversity measures are not interchangeable across our dataset, nor are ecological diversity measures, each representing distinct information about the evolutionary make-up and history of a local assemblage (Figures 3 and 5a,c). Spatial structure within the residuals of ecological versus taxonomic richness demonstrate regions of “functional” deficits (Fergnani & Ruggiero, 2015; Safi et al., 2011) or areas where more species are presumably packed into a smaller ecological space (negative residuals in Figure 4b–d). Conversely, regions with high ecological diversity for the number of species present (positive residuals in Figure 4b–d) might reflect communities that fill more of the available body size, dietary or habitat space.

A good example of how geographic incongruity informs ecological hypotheses across spatial scales is in the desert southwest. Rodent communities in the desert southwest have long been used to test hypotheses centred on community ecology, such as competitive exclusion, niche partitioning, and energetics and resource utilization (e.g., Bowers & Brown, 1982; Ernest, 2005; Holling, 1992); however, our analysis reveals that the granivore-dominated communities occurring in this region might follow different assembly rules from elsewhere in North America. Ecological evenness varies surprisingly little at the continental scale, suggesting that despite highly structured richness patterns, ecological roles are partitioned in a relatively uniform manner across body size and functional ecological classes, regardless of how densely packed those classes are locally. In contrast, the southern desert region (characterized by mosaic habitats, high-relief terrain and elevated taxonomic richness and turnover; Figure 1) departs notably from these patterns. Body size richness, in particular, is lower than expected based on the number of species present (Figure 4b), and strikingly low body size evenness is found in the desert southwest and around the Gulf of California (Figure 2d). Integrating across different dimensions of diversity elucidates important geographic variation in the structure of faunal assemblages and demonstrates that the drivers of local patterns (e.g., size-mediated utilization of resources, facilitating coexistence of highly competitive desert granivores; Bowers & Brown, 1982; Ernest, 2005) might not be generalizable at broader spatial scales. Assembling a multi-dimensional viewpoint of biodiversity gradients and their drivers based on North American rodents is a useful starting point, and broadening the taxonomic or geographic scope of analyses (e.g., Fergnani & Ruggiero, 2015) will help us to understand the generality of patterns emerging from this well-known and diverse group.

4.3 | Conserving species, ecological diversity and evolutionary history

The threats to biodiversity are numerous, with losses portended not only for taxonomic richness, but also for evolutionary

history and ecosystem functioning (Cardinale et al., 2006; Davis & Buckley, 2011; Dirzo & Raven, 2003; Dobson et al., 2006; Stein et al., 2018). Analyses that consider multiple dimensions of biodiversity thus allow us to ask what we might be losing, aside from a raw species count, with future extinctions, and therefore maximize the potential of our conservation efforts. It is clear that phylogenetic and ecological diversity promote ecosystem stability and resilience in myriad ways (Cadotte et al., 2012; Davies, Urban, Rayfield, Cadotte, & Peres-Neto, 2016). Greater diversity in existing form and function, and in evolutionary lability and depth, across species within communities translates to a broader range of potential niches and thus increased capacity of communities and their species to respond to changing climates, environments and resource availability (Hooper et al., 2005; Purvis, Cardillo, Grenyer, & Collen, 2005). Furthermore, preserving regions with deep and shallow phylogenetic diversity and diverse evolutionary modes (e.g., Davies, 2015) protects both past evolutionary heritage and future potential centres of species generation. Conservation aimed at protecting (phylo-)endemic species is also crucial, because these species capture biodiversity components with little representation elsewhere in terms of geographic and phylogenetic space (Ceballos & Ehrlich, 2006; Myers et al., 2000; Rosauer & Jetz, 2014).

Biodiversity scenarios can be forecast over the coming century based on the current trajectory of individual taxa (i.e., IUCN Red List Status). We find that future losses felt along phylogenetic and ecological axes are concentrated in the western USA, and notably throughout Mexico, with the highest losses being experienced among geographically restricted species (Figure 6a–c). Although certain small rodent clades are at risk of being lost entirely to extinction, imperilled species are distributed throughout the rodent phylogeny (Figure 6b). Likewise, loss of ecological diversity is not spread evenly across body size, dietary and habitat categories. Although most ecological categories experience some degree of loss, the greatest impacts are felt by medium-sized rodents, rodents at higher trophic levels and rodents occupying higher elevation habitats in the tropics (Figure 6d). These findings provide further evidence that not all species are at equal risk of extinction (Ohlemüller et al., 2008; Ripple et al., 2017). Non-uniform species loss across ecological categories also influences ecological evenness, possibly compounding negative impacts on ecosystem function (Chiarucci et al., 2011). In particular, the loss of functional redundancy places a greater burden on the remaining members of the community, with potentially more disastrous consequences if those species also then go extinct (Tilman, Knops, & Wedin, 1997; Tilman, Wedin, & Knops, 1996).

Looking to the coming century via projections of land-use and climate change, we find that anthropogenic impacts will be felt in many regions that represent multi-dimensional biodiversity hotspots today (Figure 5d,e). It is important to note that today's snapshot of biodiversity has already been highly influenced by anthropogenic drivers over both long (Faurby & Svenning, 2015b; Smith, Elliott-Smith, Lyons, & Payne, 2018) and short (Parmesan & Yohe, 2003; Weinzettel, Vačkář, & Medková, 2018) time-scales. Climate change velocity, or the rate at which species would have to move to maintain their current climate

conditions, reveals especially looming challenges to species response. Not surprisingly, these effects will be more intense and geographically widespread under higher emission scenarios (Figure 5f; Carroll et al., 2015). In addition to the direct influence of land-use and climate stressors, indirect and synergistic interactions among different local, regional and global change factors might lead to unpredictable biodiversity outcomes (Newbold et al., 2016; Sala et al., 2000). For example, with habitat fragmentation and increased urbanization, species are increasingly left without suitable corridors at the regional scale to track thermal niche requirements during climate change (Bennett, 2003; McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Thus, as the window of opportunity for action begins to close, understanding the geographic context of our existing biodiversity hotspots, and the multiple dimensions of biodiversity that they represent, is key to safeguarding them into the future.

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DATA ACCESSIBILITY

Data associated with this manuscript are openly available in the Dryad repository at <https://doi.org/10.5061/dryad.4xgxd2559> (Smiley, Title, Zelditch, & Terry, 2019).

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BIOSKETCH

Tara M. Smiley led this work as an National Science Foundation postdoctoral research fellow at Oregon State University with co-author Rebecca C. Terry. Tara M. Smiley has recently moved to the Environmental Resilience Institute at Indiana University. She is interested in biodiversity patterns across space and time in relationship to landscape and climate change. Her research integrates studies from modern and fossil records of mammals in North America, focusing on biogeography, ecomorphology and diversification history.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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