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Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity

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Abstract

Aim: Species richness is often strongly correlated with climate. The most commonly invoked mechanism for this climate-richness relationship is the more-individuals-hypothesis (MIH), which predicts a cascading positive influence of climate on plant productivity, food resources, total number of individuals, and species richness. We test for a climate-richness relationship and an underlying MIH mechanism, as well as testing competing hypotheses including positive effects of habitat diversity and heterogeneity, and the species-area effect.

Location: Colorado Rocky Mountains, USA: two elevational gradients in the Front Range and San Juan Mountains.

Methods: We conducted standardized small mammal surveys at 32 sites to assess diversity and population sizes. We estimated vegetative and arthropod food resources as well as various aspects of habitat structure by sampling 20 vegetation plots and 40 pitfall traps per site. Temperature, precipitation and net primary productivity (NPP) were assessed along each gradient. Regressions and structural equation modelling were used to test competing diversity hypotheses and mechanistic links predicted by the MIH.

Results: We detected 3,922 individuals of 37 small mammal species. Mammal species richness peaked at intermediate elevations, as did productivity, whereas temperature decreased and precipitation increased with elevation. We detected strong support for a productivity-richness relationship, but no support for the MIH mechanism. Food and mammal population sizes were unrelated to NPP or mammal species richness. Furthermore, mammal richness was unrelated to habitat diversity, habitat heterogeneity, or elevational area.

Main conclusions: Sites with high productivity contain high mammal species richness, but a mechanism other than a contemporary MIH underlies the productivity–diversity relationship. Possibly a mechanism based on evolutionary climatic affiliations. Protection of productive localities and mid-elevations are the most critical for preserving small mammal richness, but may be decoupled from trends in population sizes, food resources, or habitat structure.

KEYWORDS
arthropods, elevational gradients, food resources, habitat heterogeneity, NPP, plant biomass, species richness

1 | INTRODUCTION

A positive relationship between climate and species richness is well-documented across most floral and faunal clades, especially at larger spatial scales (e.g., Ballesteros-Mejia, Kitching, Jetz, & Beck, 2017; Currie, 1991; Currie et al., 2004; Hawkins, Field, et al., 2003; Jetz & Fine, 2012; Mittelbach et al., 2001; Price et al., 2014; Stein & Kreft, 2015), but mechanisms remain contentious, largely theoretical, and generally under-evaluated empirically. Among the climate-richness hypotheses, positive temperature-richness and productivity-richness relationships are the most commonly proposed (e.g., Currie, 1991; Hawkins, Field, et al., 2003; Kaspari, O'Donnell, & Kercher, 2000), although a positive precipitation-richness hypothesis has also been proposed (Abramsky & Rosenzweig, 1984; Hawkins, Field, et al., 2003). The specific mechanisms assumed to underlie climate-richness relationships include physiological adaptations to particular climates (e.g. Currie, 1991; Hawkins, Porter, & Diniz-Filho, 2003; Turner, Gatehouse, & Corey, 1987), increased diversification rates in particular climates (e.g., Brown, Gillooly, Allen, Savage, & West, 2004; Mittelbach et al., 2007), a climatic optimum for a clade that may be contemporarily favourable (e.g., McCain, 2005), an evolutionary trait of the clade when it evolved and diversified (e.g., Wiens & Graham, 2005), and, most commonly proposed, the more-individuals-hypothesis (MIH; Storch, Bohdalková, Okie, & Gravel, 2018). MIH and parts of the related species-energy hypothesis posit that regions with high primary productivity provide more available potential energy, which leads to greater food resources and therefore larger sustainable population sizes. This results in lower local contemporary extinction rates and therefore the maintenance of greater diversity (Currie, 1991; Evans, Warren, & Gaston, 2005; Storch et al., 2018; Wright, Currie, & Maurer, 1993).

The majority of empirical tests of climate-richness hypotheses are bivariate, positive correlations between the number of species and climate or resources (e.g., Grace, Adler, Stanley Harpole, Borer, & Seabloom, 2014; Storch et al., 2018; Tilman et al., 2001), and numerous meta-analyses exist for both plants and animals (Currie, 1991; Field et al., 2009; Hawkins, Field, et al., 2003; Mittelbach et al., 2001; Storch et al., 2018; Waide et al., 1999; Whittaker, 2010). Tests of the mechanisms underlying positive climate-richness relationships are much rarer (e.g., Evans, Greenwood, & Gaston, 2005; Grace et al., 2014; and references therein). For evolutionary mechanisms, most analyses are largely theoretical or simulation-based and the few empirical studies reported mixed support (Evans & Gaston, 2005; Hurlbert & Stegen, 2014; Jetz & Fine, 2012; Mittelbach et al., 2007). Testing of physiological limits are even rarer, at least for animals (e.g. Evans, Greenwood, et al., 2005; Turner et al., 1987).

The relationships of the MIH are the most commonly-assumed ecological mechanisms for shaping environment-diversity patterns, but only one study (Classen et al., 2015) assessed all four implied variables simultaneously (i.e., climate-resources-abundance-richness). The bivariate link that higher overall abundances can support greater numbers of species, the most frequently tested aspect, alone has only mixed support (e.g., Currie et al., 2004; Gillman & Wright, 2006; Kocher & Williams, 2000; McGlynn, Weiser, & Dunn, 2010; Storch et al., 2018). Multivariate tests of two links in the climate-resources-abundance-diversity hypothesis exist, all assuming the missing link is positive. Many of these tests are artificial micro- or mesocosm studies that manipulated resource abundance (Hurlbert, 2006; Kneitel & Miller, 2002; Srivastava & Lawton, 1998; Yanoviak, 2001; Yee & Juliano, 2007). Furthermore, there is a large bias for bird and insect systems among MIH studies (~75% of MIH studies; Beck, Brehm, & Fiedler, 2011; Classen et al., 2015; Ding, Yuan, Geng, Lin, & Lee, 2005; Evans, Greenwood, et al., 2005; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Hurlbert, 2004; Kaspari, 1996; Kaspari et al., 2000; Price et al., 2014; Sanders, Lessard, Fitzpatrick, & Dunn, 2007; Storch et al., 2018), and for specialist feeders (e.g., only frugivorous or insectivorous birds; Classen et al., 2015; Ferger et al., 2014; Kaspari, 1996; Price et al., 2014). Only two recent studies have compared multiple mechanisms (birds; Ferger et al., 2014) using causal networks with structural equation modelling, and only one of those assessed all climate-food-abundance-diversity linkages (bees; Classen et al., 2015). Thus, we need more empirical studies simultaneously testing multiple possible mechanisms of the climate-diversity relationship with the latter including the complete series of MIH links. Despite the original development of the MIH on mammals (Abramsky & Rosenzweig, 1984; Brown, 1973) and the strong, well-documented productivity-richness relationships for mammals and other terrestrial vertebrates (e.g., Hawkins, Field, et al., 2003; Jetz & Fine, 2012; Rowe, 2009), mammal communities have not been tested for multiple MIH components, nor have many broad generalist feeders or most nonavian terrestrial vertebrate clades.

This study aims to test simultaneously multiple hypotheses underlying small mammal richness, including the climate-richness relationship and its underlying mechanisms along replicated elevational gradients. We measured mammal richness, mammal population sizes, estimated food resources (understorey vegetation biomass and ground-dwelling arthropod biomass), and amassed climate (temperature, precipitation) and regional plant productivity (NPP) data. We also gathered data to simultaneously assess effects of habitat diversity and complexity (e.g., MacArthur & MacArthur, 1961; Stein, Gerstner, & Kreft, 2014; Stein & Kreft, 2015; Stein et al., 2015), and the elevational species–area effect (e.g., McCain, 2007; Rosenzweig, 1995). We use individual and stepwise multivariate linear regression to detect important relationships of the various theories among the large number of variables. We then applied structural equation modelling to assess the strength, directionality, and significance of the competing theoretical mechanistic hypotheses through causal network analysis (e.g., Grace, 2006; Grace et al., 2014). Discerning the mechanistic links in climate-diversity relationships are a key for understanding how biodiversity patterns are shaped and maintained.

2 | MATERIALS AND METHODS

Four elevational transects were established in the Colorado Rocky Mountains, including two in the San Juan Mountains (south-western Colorado) and two in the Front Range (north-eastern Colorado; Figure 1). Each transect consisted of eight sites placed every 200–300 m elevation between the base of the range (1,400–1,700 m) and the upper limit of vegetation on the mountain top (3,600–3,800 m). In total 32 sites were sampled between 2010–2012. A summary of the methods is detailed below; see Appendix S1 for additional methodological details and figures, and Appendix S4 for the complete dataset.

2.1 | Mammal sampling

We assessed small mammal (rodents, shrews, pika) species richness and abundance through standardized live-trapping, pitfalls, and visual surveys at each site. The survey time for each site was randomized among elevations across the four transects (e.g. early, mid, late summer) across years to eliminate bias in elevational population responses by sampling at the same time of the growing season for each elevation. Although the higher elevations could only be sampled after snow melt, thus were always trapped later in the summer season. The 300 Sherman live-traps were placed along transects established in proportion to the availability of the main habitat types at each site based on aerial imagery, which across all sites included forest, riparian, meadow, desert, tundra, and rocky outcrops. We chose sites that included most if not all of the main habitats at that elevation and were anthropogenically undisturbed. Trap pairs were located every 10 m along each transect with each trap placed 5 m on either side of each 10 m transect flag. Each site was live-trapped for five nights (1,500 trap-nights); set each late afternoon, then checked and closed each morning. Additionally, a pair of pitfall traps,

which better assess shrew species richness and abundance, were placed every 7th 10 m transect flag (40 total/site) and sampled for 90 days (~3,600 pitfall trap-nights; the same pitfall traps were used for arthropod sampling; details below). Species were identified in hand, based on voucher specimens, or with DNA sequences (Appendix S1) in cases of problematic identifications.

For diurnal rodents and pika that do not readily enter live-traps, five visual transect surveys were conducted for 1 hr during each of the trapping days. Visual surveys were stratified by time (morning, early- and late-afternoons) and location (five different routes at different start traps). Each sighted mammal was georeferenced with a hand-held GPS unit. Lastly, all mammal sightings while in camps, in transit between sites, scouting sites, or during climate and vegetation data collection were also georeferenced and elevation recorded. Mammal species richness was therefore based on all sampling methods, with species assumed to be at all elevations between their lowest and highest detection.

Mammal abundance was a sum of all individuals per site; the most common and unbiased assessment of populations for small mammals (Minimum Number Known Alive; Prevedello, Dickman, Vieira, & Vieira, 2013; Slade & Blair, 2000; Wilson, Cole, Nichils, Rudran, & Foster, 1996). If there were sufficient recaptures to estimate a species' population size from mark–recapture methods (Nichols & Conroy, 1996; Slade & Blair, 2000; Appendix S1), we added the estimate of the number of unseen individuals to species' population sizes. Both metrics of abundance, summed individuals for all species or summed individuals plus estimated individuals, were highly correlated (Figure S1.1; $r = 0.96$, $p < 0.001$), and the results were consistent for both metrics. As all methods for mammal abundance sampling (and all other site-based metrics) were employed at all sites in the same manner and intensity, sums of individuals detected among trapping, visual transects, and pitfalls allow robust, consistent, and comparable estimates of abundance across sites.
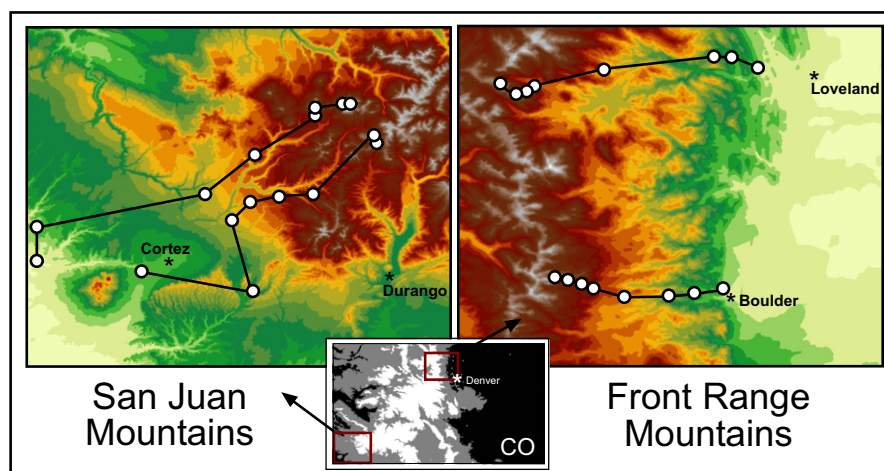

FIGURE 1 The four elevational transects in the Colorado Rocky Mountains: two in the north-east (Front Range Mountains) and two in the south-west (San Juan Mountains). Each transect includes eight sites spread between the base and top of the mountains. Coloration indicates elevation from light green at low elevation to red and grey at the highest elevations. The black and white inset is the entire state of Colorado (CO). For scale, the distance between the cities of Boulder and Loveland is about 28.5 miles or 46 km; and between Cortez and Durango is about 39 miles or 63 km [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Food biomass

We measured vegetation and arthropod biomass using 20 standardized sampling plots at each site, spaced every 70 m along the trapping transects to ensure coverage across all available habitats. Each plot consisted of concentric circles of 1, 3, and 5 m around the Sherman trap centre (Appendix S1). The vegetation measurements were conducted three times per plot—early summer, mid-summer, and late summer. Within the 1 m radius, Braun-Blanquet coverage classes (Barbour, Burk, Pitts, Gilliam, & Schwartz, 1999; Cain & De Oliveira Castro, 1959) were estimated for grasses, forbs, shrubs, cacti, and bare ground within ≤1 m from the soil surface (i.e. understorey ground cover). The height of the understorey vegetation (≤1 m height) was measured at the centre point and at the 3 m radius in the four cardinal directions. Additionally, at these same 3 m cardinal directions, we measured canopy coverage using a densiometer. Species identities, counts, and diameter at breast height (dbh) for trees >3 cm dbh were recorded within the 5 m radius circle.

As nearly all sampled mammals forage in the understorey (e.g. Armstrong, Fitzgerald, & Meaney, 2011 and references therein), usually <1 m from the soil surface, we used the understorey vegetation volume as a vegetation food biomass estimate (e.g. Niklas, 1993; Niklas & Enquist, 2003; Stevens & Tello, 2011). Plant size and height reflects the quantity of seed and fruit production as well as new growth (Hendriks & Mulder, 2008; Niklas, 1993; Niklas & Enquist, 2003; Shipley & Dion, 1992), which are important components of the mammalian herbivore and omnivore diets as used in past small mammal food resource studies (79% of sampled mammal species and more than 90% of sampled individuals consume vegetation; e.g., Armstrong et al., 2011; Pineda-Munoz & Alroy, 2014; Stevens & Tello, 2011, and references therein). The sum of the average (among three visits) understorey coverage percentage for forbs, grass, and shrubs was multiplied by the average height (among five measurements and three visits) of the understorey vegetation for an estimate of understorey plant biomass. The sum was used to include the influence of divergent times of vegetation maturity among the sites due to elevational variation in the timing and length of the growing season. Vegetation biomass is a single summer composite sum across all 20 plots per site. See Appendix S1 for additional details and metrics of vegetative food biomass, including attempts to measure seed fall.

Arthropods are an important food component of mammalian omnivores and the sole diet of shrews (84% of sampled mammal species and 83% of the sampled individuals consume arthropods; e.g., Armstrong et al., 2011; Pineda-Munoz & Alroy, 2014 and references therein). We used the traditional method for assessing shrew and insectivorous mammal diets: arthropod pitfall traps (e.g., Denneman, 1990; Pernetta, 1976; Pineda-Munoz & Alroy, 2014; Prevedello et al., 2013). The arthropod sampling was conducted using two pitfall traps in each plot at the 3 m east and west points. The pitfall traps followed standard entomological design of two nested 470 ml (16 ounce) cups, buried such that the lips were flush with the ground, covered with a small plate leaving a ~3–5 cm opening, and filled to ~1/3 with propylene glycol as a preservative (e.g. Brown & Matthews, 2016; also the standard small mammal design, although usually without a cover or preservative). To increase the surface-area of interception, three 30 cm wood shims were radiated out from the cups. The 40 pitfalls per site were set for 90 days beginning in early summer, with the various sample collections across the summer summed for a 90-day biomass estimate. All samples from arthropod pitfalls were cleaned from debris and propylene glycol, weighed, and preserved in 70% ethanol.

Marmot and bear disturbance interrupted arthropod collection at a few sites, particularly the highest sites. In order to account for the variability in days each pitfall was actively collecting arthropods and the number of intact pitfalls per site, we calculated an adjusted arthropod biomass. For each pitfall this was based on a calculated daily pitfall accumulation rate during the days undisturbed, then adjusted for the total 90 days of sampling to be comparable among all pitfalls. Then at the site level, the 90-day total biomass of the 40 pitfalls were summed for a total biomass, but to account for unequal numbers of intact pitfalls at some sites the median 90-day biomass was substituted for missing pitfalls (see Appendix S1 for more details). Only at two sites were too few pitfalls functional to estimate arthropod biomass. Arthropod biomass is a single summer sum to estimate the combined arthropod food resources.

For equally-weighted food variables, we standardized the vegetation biomass and arthropod biomass across sites using z-transformations (x_{site}−mean$_{all\ sites}$)/$SD_{all\ sites}$) plus an added constant (+2) for consistently positive values. Standardized vegetation volume and standardized arthropod biomass were summed to estimate total food biomass at each site. See Appendix S1 for figures of unstandardized vegetation and arthropod biomass trends along each gradient.

We would have ideally measured multiple years of vegetation and food resources, but this was not possible given our financial and logistical limitations, and a single season is the norm in the MIH literature. Nevertheless, we feel that this is an adequate index of food resources for this system. The mostly arid, coniferous, and relatively unproductive environments of the south-western USA do not tend to feature a high year-to-year variability as seen in more productive systems, such as the seed masting effects common in eastern deciduous forests. Additionally, our study systems reflect the seasonal dynamics of high latitude, high elevation populations; therefore, populations of plants and animals are dominated by a postwinter rebound throughout each spring and summer. Thus, the food conditions of a given year should be most closely related to the overall small mammal populations attainable in that year. For more details on the vegetation measurements and alternative food assessments, see Appendix S1.

2.3 | Climate and productivity data

At each site we established a climate station (air and soil temperature, rainfall gauge) that was in place for 12 months. For the watershed surrounding each transect, we calculated mean annual precipitation and temperature from PRISM data (30-year averages;

800 m resolution), and mean annual net primary productivity (NPP) (gC/m²/yr); stomatal closure-modified MODIS (Moderate Resolution Imaging Spectroradiometer; NASA Satellite) data (Running et al., 2004; 1 km resolution; Figure 3), averaged for each 100 m band of elevation (Appendix S1). Local temperature values were 94%–95% correlated with PRISM data across sites, but because a few climate stations did not have continuous 12-month collections for both variables, we used the PRISM data for analyses.

2.4 | Competing hypotheses data

To assess various aspects of habitat structure that may serve as a potential indicator of greater niche diversity and thus coexistence mechanisms (e.g., MacArthur, MacArthur, & Preer, 1962; Stein & Kreft, 2015), we measured habitat diversity and three measures of habitat complexity. Habitat diversity was estimated from the number of land cover types in the elevational band of each site within its watershed using the National Land Cover Database (2011; excluding perennial ice/snow, open water, and human development; 30 m resolution). Habitat complexity was measured as (1) the average number of trees per plot, (2) the total number of tree species documented in the plots at each site, and (3) a heterogeneity metric calculated as a sum of coefficients of variation for (a) each ground cover type (grass, forb, shrub, cacti, and bare ground), (b) understorey vegetation height, (c) canopy cover, and (d) tree diameter at breast height. The species–area relationship was tested using the spatial extent for each 100 m elevational band calculated in an equal area projection of a digital elevational model (90 m resolution) in a GIS following McCain (2007). We did not consider the mid-domain effect, as it has been repeatedly shown to be a poor predictor of small mammal elevational species richness (McCain, 2005) and elevational species richness in general (Dunn, McCain, & Sanders, 2007).

2.5 | Statistical analyses

As a result of the large number of explanatory variables, we first ran individual linear regressions and only further included variables that meet four criteria: (a) met the expected positive relationship with species richness (since all hypotheses predict a positive relationship); (b) independence (i.e., only best abundance or habitat complexity measure used), which was determined by r^2 and p-values, and (c) any variable necessary to test the climate-species richness mechanisms. We then used step-wise multivariate linear regressions to test for support of the climate-species richness relationship as well as the competing hypotheses using the small-sample Akaike information criterion (AICc) and the Bayesian information criterion (BIC) to evaluate models due to their basis in maximum likelihood fits and penalties for model complexity. We tested the entire dataset as well as the separate Front Range and San Juan mountains datasets to account for potential differences among the two mountain regions.

To simultaneously test the causal implications of the proposed mechanisms underlying the climate-species richness relationship, we constructed structural equation models (SEM; e.g., Grace, 2006; Grace

et al., 2014) using the *lavaan* package (Rosseel, 2012) in R. In addition to the composition food variable as mentioned above, all other variables also were z-transformed to a mean of zero and a standard deviation of one, so that all variables were of a comparable magnitude. To assess model quality, we used a multi-index approach with viable models determined by cut-off values (in parentheses): comparative fit index (CFI >0.95; high values indicate good models), standardized root mean square residual (SRMR <0.1; this and all following metrics: low values indicate good models), root mean square error of approximation (RMSEA <0.08), and the AIC value (Browne & Cudeck, 1992; Grace, 2006; Hu & Bentler, 1999; Kline, 2010; Shipley, 2000).

The full theoretical model with both direct and indirect relationships (MIH: climate→food resources→abundance→species richness) between climate and mammal species richness was compared to the optimal model (best quality according to the four indices [Schermelleh-Engel, Moosbrugger, & Müller, 2003]) chosen among progressively simplified models from the full theoretical model. Again, we ran separate sets of SEM models for the Front Range Mountains and for the San Juan Mountains. Lastly, we also ran the SEM models using the best habitat heterogeneity or habitat complexity variable to detect whether a positive productivity–species richness relationship is mediated through NPP's positive influence on habitat structure and thus positive habitat impacts on mammal abundance. This is to test the alternative hypothesis that productivity increases niche complexity leading to increased abundance and species richness (e.g., Eisenhauer, Schulz, Scheu, & Jousset, 2013; Hurlbert, 2004; Kohn & Leviten, 1976; and references therein). To avoid false conclusions due to spatial autocorrelation, we retested significant univariate correlations with spatial correlation (i.e., Dutilleul's corrected degrees of freedom; software SAM 4.0).

3 | RESULTS

We detected 3,922 individuals of 37 small mammal species (7,338 captures & sightings), including eight soricid species (shrews), six arvicoline rodents (voles), 11 sciurid rodents (chipmunks and squirrels), 11 neotomine rodents (North American mice and rats), and one small lagomorph (pika; see Appendix S5). Small mammal elevational species richness peaked at mid-elevations with some variability among gradients (Figure 2). Both Front Range transects and the western San Juan transect all displayed very similar mid-elevation species richness pattern (average $r > 0.82$), whereas the eastern San Juan transect detected lower species richness and almost no trend with elevation. This indicates either an undersampling effect (although the identical effort was employed), or poorer quality habitats due to historical disturbance or greater pitfall disturbances. This latter transect also was sampled in a summer where multiple sites were impacted by nearby wildfires. This eastern transect may not be equivalent to the other transects or representative of the overall species richness pattern, hence we compare analyses with and without this transect below. Temperature declined and precipitation increased with elevation on both mountains, while regional NPP was

unimodal with maximum productivity at mid-elevations (Figure 3). The abundance of mammals (Figure 2), understorey vegetation, arthropod biomass, habitat diversity, and habitat complexity were highly variable among sites and elevations (Figure 3).

In a comparison of the various species richness hypotheses using univariate linear regressions (Appendix S2) only NPP and two habitat complexity measures (number of trees and tree species richness) met our statistical criteria for model inclusion. When included with the other climate-species richness mechanism variables (mammal abundance, temperature, precipitation, and food biomass) in stepwise multivariate models, only NPP was supported. This was consistent for an analysis excluding the eastern San Juan transect, as well as for the Front Range transects alone (Appendix S2). The San Juan transects separately found little support for any variables, which is likely due to the inclusion of the species-deficient eastern transect.

In the mechanistic SEM with the simultaneous direct climate effects on mammal species richness through temperature, precipitation, and NPP plus the indirect NPP effects on species richness via food resources and mammal abundance, the model only detected a significant, direct relationship between regional productivity and mammal species richness (Figure 4b). Similarly, the optimal model with the
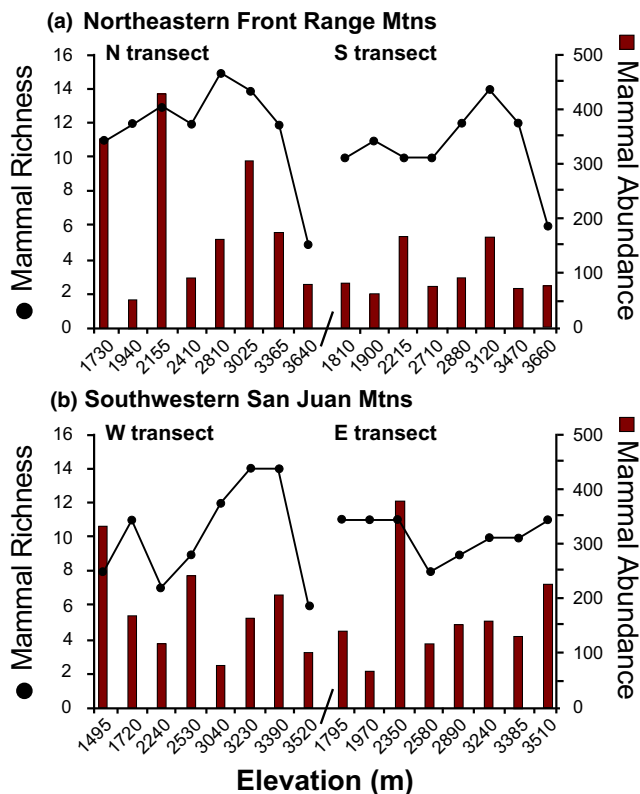

FIGURE 3 Within the 32 sites spread between the four elevational transects, two in the Front Range and two in the San Juan Mountains (shown combined), we estimated (a) food biomass as the sum of standardized understory vegetation and ground-dwelling arthropods (shown here in standard deviations (SD) with arbitrary added constant to avoid negative axis values), and net primary productivity (NPP) based on MODIS data for the elevational bands within each watershed; and (b) three habitat variables: habitat diversity (white circles; sum of habitat types within site's elevational band; multiplied by a factor of two for ease of visualization); habitat heterogeneity (black circles; sum of coefficients of variation in each ground cover category, tree diameters, and canopy cover within a site), and the number of trees, an indication of habitat complexity (green bars). Tree species diversity (not shown) is similarly distributed as the number of trees (OLS, $r^2 = 0.68$) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 The species richness and abundance patterns for small mammals on the four elevational transects in the Colorado Rocky Mountains: (a) the northern (left; Big Thompson Watershed) and southern (right; Boulder Creek Watershed) transects in the north-eastern Front Range Mountains; and (b) the western (left; Lizardhead Wilderness Watershed) and eastern (right; Dolores Watershed) transects in the south-western San Juan Mountains [Colour figure can be viewed at wileyonlinelibrary.com]
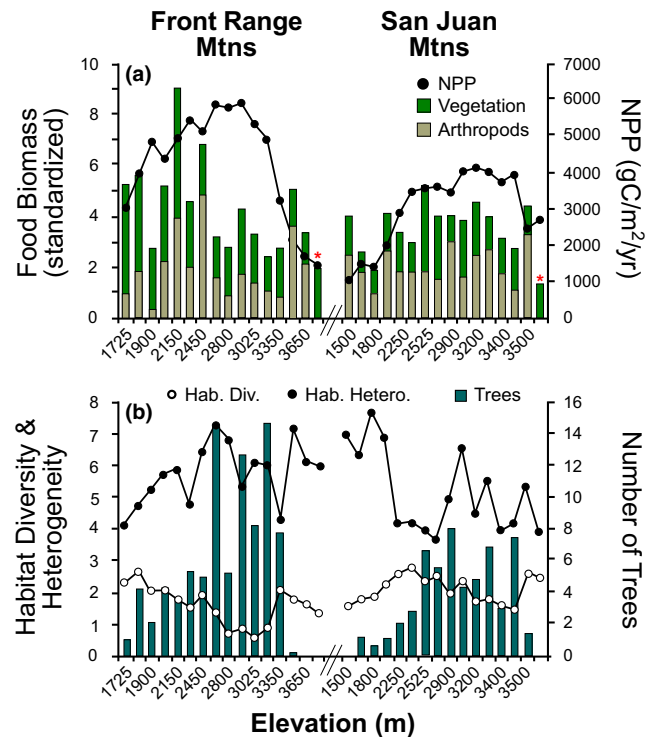
strongest support across all five quality indices (Figure 4a) also includes only a significant positive direct relationship between productivity and mammal species richness. In fact, in all SEMs from the most complex to the simplest, the direct productivity–species richness relationship was the only significant relationship, whereas the models with any of the indirect relationships (food resources and/or mammal abundances) included were the least supported across the fit indices (Appendix S3). SEM models with a latent variable construction for food resources, as opposed to the sum of standardized vegetation and arthropod biomass, were not supported due to negative latent variable variances (Grace, 2006; Grace et al., 2014; Appendix S3). The direct productivity–species richness relationship was the only significant relationship when using either of the mammal abundance measures (sums with and without population estimates; Appendix S1). Individual relationship scatterplots and regressions clearly show the lack of strong fits among MIH-predicted relationships, but a relatively strong

fit between NPP and species richness, which was also supported in spatially explicit testing (Figure 5; Appendix S2).

For SEMs of the two mountain ranges separately, the Front Range sites detected nearly identical results to the complete results (Appendix S3) whereas those based on San Juan sites were uniformly poor (i.e., no single model met the highest support across all five indices and none of the models with any index support included a significant individual variable). A set of SEMs without the eastern San Juan sites also detected the same results as the complete dataset and the Front Range dataset, and resulted in an improved r^2 value over the complete dataset (Appendix S3).

Lastly, for the same set of SEMs as above, we also compared whether the strongest habitat complexity variable, the average number of trees, may have influenced mammal species richness indirectly through NPP and/or abundance (Appendix S3). Similar to the indirect MIH relationships, including the number of trees either directly or indirectly through NPP and/or mammal abundance was not significantly supported. The average number of trees was significantly related to NPP, unlike food resources, but had no significant influence on mammal species richness when NPP was included in the model.

4 | DISCUSSION

Based on replicated elevational transects, small mammal species richness was highest at midelevations and was linked directly to contemporary, regional productivity (NPP; Figures 3–5; e.g. Francis & Currie, 2003; McCain, 2005; Rowe, 2009; Wiens et al., 2010). One of the transect replicates (eastern San Juan Mountains) featured lower species richness per site than the other transects and almost no elevational species richness pattern, possibly due to higher pitfall trap disturbance or fire prevalence in that year. Regardless, the remaining three transects individually as well as the combined dataset showed consistent species richness patterns and support across the various hypotheses. This mid-elevational species richness trend in small mammals is consistent for other small mammal studies in the mountains of the south-western USA and across the globe, many of which also detected a positive productivity–species richness relationship (e.g. Chen, He, Cheng, Khanal, & Jiang, 2017; McCain, 2004, 2005; Rowe, 2009). Despite the strong productivity–species richness relationship in mammals, this is the first test of the mechanistic underpinning of that relationship other than bivariate analyses.

The NPP-species richness relationship we observed for small mammals is not mechanistically produced via greater food resources or higher mammal abundances, contrary with the predictions of several hypotheses on indirect mechanisms, particularly the more individuals hypothesis (MIH) (Figure 2; Evans, Greenwood, et al., 2005; Grace et al., 2014; Storch et al., 2018; Wright, 1983). Neither understorey plant biomass nor arthropod biomass were positively related to regional NPP (Figure 3c), nor were those (well-justified) proxies of food resources positively related to mammal abundances (Figure 3d). Mammal abundances were also not positively related to mammal
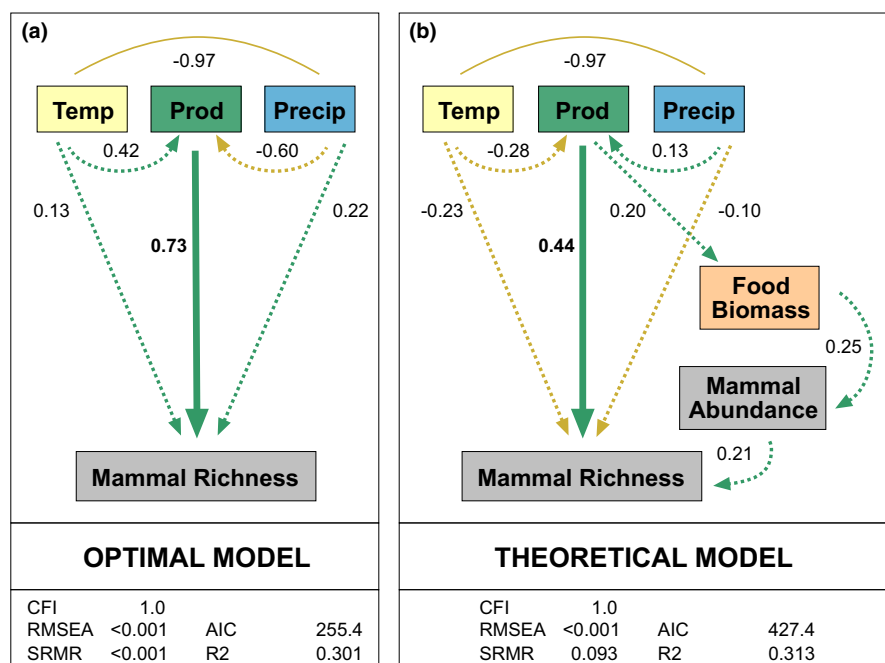

FIGURE 4 Structural equation models representing the proposed mechanisms for the productivity-species richness relationship for the optimal model (a) and the complete theoretical model (b). The theoretical model (b) includes both direct mechanisms of climate on mammal richness (temperature [Temp], precipitation [Precip], net primary productivity [Prod], and the indirect mechanism of productivity mediated through Prod→food biomass→mammal abundance→species richness. All productivity-species richness relationships and their indirect pathways should all be positive (green arrows). Negative arrows are yellow, significant relationships are solid lines, and dotted lines indicate nonsignificant relationships. For structural equation model fit criteria (CFI, RMSEA etc. see explanations in the text) [Colour figure can be viewed at wileyonlinelibrary.com]
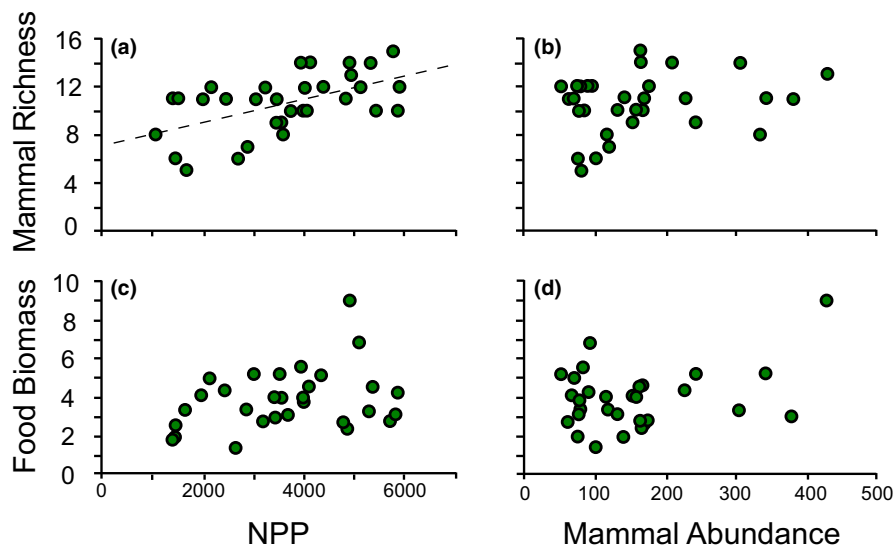
FIGURE 5 For the 32 sites along four elevational transects in the Colorado Rocky Mountains, the univariate relationships of mammal species richness with (a) net primary productivity (NPP) and (b) mammal abundance, and food biomass with (c) NPP, and (d) mammal abundance. All relationships are non-significant except a significant positive regression between mammal richness and NPP ($r^2 = 0.3$; $p < 0.001$; fitted coefficients for untransformed data: small mammal richness = 6.343 + 0.00115*NPP; spatial correlation: $n = 32$, spatially corrected $F = 10.5$, corrected degrees of freedom = 24.9, corrected $p = 0.003$) [Colour figure can be viewed at wileyonlinelibrary.com]

species richness (Figure 3b). All structural equation models including food resources or mammal abundance were the weakest models in our comparison (Appendix S3).

Despite the prevalence of the MIH as a theoretical explanation of observed productivity–species richness relationships in the literature, the weak support detected here is corroborated by other studies on nonmammalian animals. Overall only about half of the published studies testing these mechanisms were supportive, including artificial microcosms, mesocosms, and field experiments (e.g., Classen et al., 2015; Currie et al., 2004; McGlynn et al., 2010; Srivastava & Lawton, 1998; Storch et al., 2018; Yanoviak, 2001). Additionally, only one other study has examined all of the mechanistic links for the MIH hypothesis—climate–food resources–abundance–species richness. In that case, bees of Mt. Kilimanjaro displayed a strong direct temperature–species richness relationship and only a weak indirect food resource-mediated trend (Classen et al., 2015). Of the studies exploring three of the four predictions of the MIH: (a) several detected that food resources were linked to abundance and species richness but the climate-food resource relationship was not tested (Kneitel & Miller, 2002; Loiselle & Blake, 1991; Price et al., 2014; Yee & Juliano, 2007), while Kaspari (1996) did not find support for resource effects; (b) one study detected a strong climate-food resources-species richness relationship but abundance was not included (Ferger et al., 2014); and (c) two studies detected support for a climate-abundance-species richness relationship but NPP and food resources were not included (Beck et al., 2011; Sanders et al., 2007). Therefore, across studies, the support for indirect mechanisms of climate–species richness hypotheses is mixed and weak. More rigorous studies are needed to test simultaneously the direct and complete indirect mechanisms as conducted here for small mammals in the Rocky Mountains and by Classen et al. (2015) for bees on Mt. Kilimanjaro.

There are a number of potential sampling artefacts that may have obscured a positive relationship between food resources and mammal abundance, but we can reject most of these conjectures. First, it is possible that omnivorous mammals respond less to our estimates of food biomass than would specialists, due to omnivores' diffuse use of resources and potential for switching among types of resources if one becomes scarce (Evans, Greenwood, et al., 2005; Groner & Novoplansky, 2003). To exclude this possibility, we also explored separately the links for insectivorous mammals (shrews) with arthropod biomass, and for herbivorous mammals (voles) with plant biomass and grass coverage, finding no support of any indirect relationships (all links nonsignificant; many negative; OLS; $p \gg 0.05$). Second, it may be that accounting for body size differences by evaluating mammalian biomass rather than abundance would lead to improved fits (Blackburn & Gaston, 1996; Srivastava & Lawton, 1998; Wright, 1983). We recalculated mammal abundance as mammal biomass (sum of the number of individuals of each species multiplied by the average weight for that species at the site), but conclusions from structural equation models were unaltered. Third, potentially the only important effect of climatically determined NPP is on plant biomass, while it may be only loosely related to arthropod biomass (e.g. Currie, 1991; Hawkins, Field, et al., 2003). We ran the SEMs with only plant biomass as an estimate of food resources and again our results and conclusions did not change. Alternatively, it could be that only food resources from arthropods, the next lowest trophic level to small mammals, are a strong proxy of food resources (Groner & Novoplansky, 2003), but this also did not change our results. Fourth, it is possible that our estimates of food resources were too narrow—based on a single, although completely sampled, growing season. This may be the case for arthropods which potentially fluctuate widely in population size from year to year, but our

plant biomass assessments should not change drastically year to year as the majority of the understorey species are dry-adapted perennials. If the estimates of food biomass from a single growing season are not sufficient to detect a long-term food resource average, and multiyear (5–10+ years) food estimates across many sites are cost-prohibitive, then a food-resource-abundance relationship may be hard to detect in any predominantly omnivorous system. Lastly, many other ecological factors like predation pressure, population time-lags, or complex food web dynamics may alter the food abundance-population size relationship, but in such cases these still negate the simple four-factor energy-species richness hypothesis. Ecology allows an almost indefinite post hoc extension of hypotheses to explain away nonsupportive results. However, only testing and rejecting a priori hypotheses will truly advance our understanding of species richness mechanisms, and such extensions (if reasonable) should be taken as new hypotheses to be tested in further study (Forstmeier, Wagenmakers, & Parker, 2017).

Based on our understanding of this highly seasonal set of elevational transects, it is likely that the mammal populations are not food limited. For mammals that need to survive harsh winters, many of which do not hibernate and are among the smallest species (shrews and voles), mammal abundances are likely kept low by high winter mortality when temperatures drop too low for activity and feeding (Armstrong et al., 2011; Brady & Slade, 2004; Schorr, Lukacs, & Florant, 2009; Swihart & Slade, 1990; Turbill, Bieber, & Ruf, 2011). Although populations may be rebounding in the spring and summer, this time of year also produces an abundant flush of plant and arthropod resources, hence unlimited food. Such a scenario would decouple the relationship between food resources and mammal abundance, and mammal abundance and species richness, and exhibit patterns such as we detected (i.e., high resource abundance at high elevations but low abundances and species richness of mammals). Regardless of how the food resources were measured or supported, the MIH links with NPP, mammal population sizes, and mammal species richness were not supported. Thus, on multiple levels there is no support for the tested mechanism.

Without support for the MIH, the mechanism for a climate–species richness or NPP-species richness relationship needs to be more direct (e.g., Evans, Greenwood, et al., 2005; Evans, Warren, et al., 2005). This could include evolutionary rates influenced by climate (e.g., Brown et al., 2004; Mittelbach et al., 2007), phylogenetic niche conservatism (e.g., Wiens & Graham, 2005; Wiens et al., 2010), species sorting by a contemporary climatic optimum (e.g., Francis & Currie, 2003; McCain, 2005), climate's influence on structural diversity and thus mammal species richness (mammals; e.g., Heaney, 2001; Stein et al., 2015), or an effect of physiological limitations (Evans, Greenwood, et al., 2005; MacArthur, 1972; Turner et al., 1987). The mammal communities investigated here were assembled by dispersal, not by in situ speciation and extinction, as both mountain ranges experienced complete (Front Range) or partial (San Juans) glaciation during the Last Glacial Maximum (e.g. Price et al., 2014; Richmond, 1965), hence any hypothesized contrasting evolutionary rates across elevations (e.g. Wiens, Parra-Olea, & Wake, 2007) appear

unconvincing. Additionally, faster evolutionary rates as theoretically proposed rely on a greater mutation rate, and thus speciation rates, due to higher temperatures (Evans, Greenwood, et al., 2005; Mittelbach et al., 2007), but temperature was not supported directly in our models and no effect on evolutionary rates are hypothesized for NPP.

Montane mammals do appear to track a high-NPP climatic optimum (e.g., Chen et al., 2017; McCain, 2005; Rowe, 2009), but this optimum could be either ecologically caused by elevational filtering by dispersal over relatively short time periods (Francis & Currie, 2003; McCain, 2005), or by climatic niche conservatism within which the clades evolved (Wiens & Graham, 2005; Wiens et al., 2010). Direct physiological limits appear less likely as a mechanism underlying this productivity–species richness pattern, as it is difficult to propose physiological limits tied to productivity, rather than temperature (Evans, Greenwood, et al., 2005; MacArthur, 1972). Some small mammal endotherms are capable of heterothermy (i.e., hibernation and torpor) whereas others are active and feed all year even under the snow (Armstrong et al., 2011), thus there is little evidence of clear physiological limits leading to a peak in species richness at high productivity midelevations.

Lastly, our competing hypotheses for mammal species richness—habitat structure and elevational species-area effect—were also not supported across these replicated gradients (Appendix S2, S3). Habitat diversity, heterogeneity, and complexity have been proposed to underlie species richness with a long history as an example of 'diversity begets diversity' (Hutchinson, 1959; MacArthur, 1972; MacArthur et al., 1962). For small mammals, habitat heterogeneity has been shown to be associated with species richness in certain systems (e.g. Rowe, 2009; Stein et al., 2014; Stevens & Tello, 2011; and references therein). One complication with habitat diversity, heterogeneity, or complexity is that they are difficult to define and are often taxon and/or system dependent (Stein & Kreft, 2015; Stein et al., 2014). Therefore, in this system we tested four habitat structure variables (habitat diversity, habitat heterogeneity, number of trees, and number of tree species) to test for a relationship with mammal species richness. However, none of those indices were related to species richness when NPP was included as a predictor in the models (Appendix S2, S3). A climate–habitat structure relationship on mammal abundance or species richness was also not supported with the SEMs. Thus, along these elevational gradients, habitat diversity or complexity are not critical elements for mammal species richness, either directly nor as an intermediate of a climate or population effect. Lastly, the elevational species–area relationship, which has been shown to be significantly related to insect elevational species richness patterns (e.g. Beck et al., 2017; Beck et al. unpub. ms; Szewczyk & McCain, 2016), appears to be unsupported for small mammals in this study and others (e.g. McCain, 2005, 2007; Rowe, 2009).

In conclusion, our study detected only strong support for a direct productivity (NPP)-species richness relationship in small mammals but not by the mechanism of the MIH. Discerning between the contemporary climate *versus* niche conservatism drivers of a direct mechanism is the next challenge. As a mammalian midelevation

climatic optimum is nearly universal across mountains in the tropics and temperate zone (Chen et al., 2017; McCain, 2005; Rowe, 2009), presumably the species within these clades from the various mountainous regions have different regional species pools with divergent underlying evolutionary histories and climatic niche evolution. Such reasoning then suggests that mammals would be assorting more strongly to contemporary climate (e.g. Francis & Currie, 2003) or climatically driven attractors (Colwell et al., 2016), but time-calibrated phylogenetic analyses with reconstructed productivity for various time slices, and tests of niche conservatism are needed at a much finer elevational scale than currently available (e.g., Jetz & Fine, 2012; Price et al., 2014; Wiens et al., 2010).

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REFERENCES

Abramsky, Z., & Rosenzweig, M. L. (1984). Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature*, *309*, 150–151. https://doi.org/10.1038/309150a0

Armstrong, D. M., Fitzgerald, J. P., & Meaney, C. A. (2011). *Mammals of Colorado* (2nd ed.). Denver, CO: University Press of Colorado.

Ballesteros-Mejia, L., Kitching, I. J., Jetz, W., & Beck, J. (2017). Putting insects on the map: Near-global variation in sphingid moth richness along spatial and environmental gradients. *Ecography*, *40*, 698–708. https://doi.org/10.1111/ecog.02438

Barbour, M. G., Burk, J. H., Pitts, W. D., Gilliam, F. S., & Schwartz, M. W. (1999). *Terrestrial plant ecology* (3rd ed.). Menlo Park, CA: Benjamin/ Cummings.

Beck, J., Brehm, G., & Fiedler, K. (2011). Links between the environment, abundance and diversity of Andean moths. *Biotropica*, *43*, 208–217. https://doi.org/10.1111/j.1744-7429.2010.00689.x

Beck, J., McCain, C. M., Axmacher, J. C., Ashton, L. A., Bärtschi, F., Brehm, G., … Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Global Ecology and Biogeography*, *26*, 412–424. https://doi.org/10.1111/geb.12548

Blackburn, T. M., & Gaston, K. J. (1996). A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Letters*, *3*, 44–53. https://doi.org/10.2307/2999768

Brady, M. J., & Slade, N. A. (2004). Long-term dynamics of a grassland rodent community. *Journal of Mammalogy*, *85*, 552–561. https://doi.org/10.1644/1545-1542(2004)085<0552:LDOAGR>2.0.CO;2

Brown, J. H. (1973). Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology*, *54*, 775–787. https://doi.org/10.2307/1935672

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Brown, G. R., & Matthews, I. M. (2016). A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecology and Evolution*, *6*, 3953–3964. https://doi.org/10.1002/ece3.2176

Browne, M. W., & Cudeck, R. (1992). Alternative ways of assessing model fit. *Sociological Methods & Research*, *21*, 230–258. https://doi.org/10.1177/0049124192021002005

Cain, S. A., & De Oliveira Castro, G. M. (1959). *Manual of vegetation analysis*. New York, NY: Harper & Brothers Publishers.

Chen, Z., He, K., Cheng, F., Khanal, L., & Jiang, X. (2017). Patterns and underlying mechanisms of non-volant small mammal richness along two contrasting mountain slopes in southwestern China. *Scientific Reports*, *7*, 13277. https://doi.org/10.1038/s41598-017-13637-0

Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., … Steffen-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Global Ecology and Biogeography*, *24*, 642–652. https://doi.org/10.1111/geb.12286

Colwell, R. K., Gotelli, N. J., Ashton, L. A., Beck, J., Brehm, G., Fayle, T. M., … Novotny, V. (2016). Midpoint attractors and species richness: Modelling the interaction between environmental drivers and geometric constraints. *Ecology Letters*, *19*, 1009–1022. https://doi.org/10.1111/ele.12640

Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, *137*, 27–49. https://doi.org/10.1086/285144

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J.-F., Hawkins, B. A., … Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, *7*, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x

Denneman, W. D. (1990). A comparison of diet composition of two *Sorex araneus* populations under different heavy metal stress. *Acta Theriologica*, *35*, 25–38. https://doi.org/10.4098/0001-7051

Ding, T.-S., Yuan, H.-W., Geng, S., Lin, Y.-S., & Lee, P.-F. (2005). Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan. *Global Ecology and Biogeography*, *14*, 299–306. https://doi.org/10.1111/j.1466-822X.2005.00159.x

Dunn, R. R., McCain, C. M., & Sanders, N. J. (2007). When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography*, *16*, 305–312. https://doi.org/10.1111/j.1466-8238.2006.00284.x

Eisenhauer, N., Schulz, W., Scheu, S., & Jousset, A. (2013). Niche dimensionality links biodiversity and invasibility of microbial communities. *Functional Ecology*, *27*, 282–288. https://doi.org/10.1111/j.1365-2435.2012.02060.x

Evans, K. L., & Gaston, K. J. (2005). Can the evolutionary-rates hypothesis explain species-energy relationships? *Functional Ecology*, *19*, 899–915. https://doi.org/10.1111/j.1365-2435.2005.01046.x

Evans, K. L., Greenwood, J. J. D., & Gaston, K. J. (2005). Dissecting the species–energy relationship. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2155–2163. https://doi.org/10.1098/rspb.2005.3209

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews*, 80, 1–25. https://doi.org/10.1017/S1464793104006517

Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M., & Böhning-Gaese, K. (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, 23, 541–549. https://doi.org/10.1111/geb.12151

Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Guégan, J.-F., … Turner, J. R. G. (2009). Spatial species-richness gradientsacross scales: A meta-analysis. *Journal of Biogeography*, 36, 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

Forstmeier, W., Wagenmakers, E.-J., & Parker, T. H. (2017). Detecting and avoiding likely false-positive findings – a practical guide. *Biological Reviews*, 92, 1941–1968. https://doi.org/10.1111/brv.12315

Francis, Anthony. P., & Currie, D. J. (2003). A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, 161, 523–536. https://doi.org/10.1086/368223

Gillman, L. N., & Wright, S. D. (2006). The influence of productivity on the species richness of plants: A critical assessment. *Ecology*, 87, 1234–1243. https://doi.org/10.1890/0012-9658(2006)87[1234:TIOPOT]2.0.CO;2

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511617799

Grace, J. B., Adler, P. B., Stanley Harpole, W., Borer, E. T., & Seabloom, E. W. (2014). Causal networks clarify productivity–richness interrelations, bivariate plots do not. *Functional Ecology*, 28, 787–798. https://doi.org/10.1111/1365-2435.12269

Groner, E., & Novoplansky, A. (2003). Reconsidering diversity–productivity relationships: Directness of productivity estimates matters. *Ecology Letters*, 6, 695–699. https://doi.org/10.1046/j.1461-0248.2003.00488.x

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J.-F., Kaufman, D. M., … Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. https://doi.org/10.1890/03-8006

Hawkins, B. A., Porter, E. E., & Diniz-Filho, J. A. F. (2003). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, 84, 1608–1623. https://doi.org/10.1890/0012-9658(2003)084[1608:PAHAPO]2.0.CO;2

Heaney, L. R. (2001). Small mammal diversity along elevational gradients in the Philippines: An assessment of patterns and hypotheses. *Global Ecology and Biogeography*, 10, 15–39. https://doi.org/10.1046/j.1466-822x.2001.00227.x

Hendriks, A. J., & Mulder, C. (2008). Scaling of offspring number and mass to plant and animal size: Model and meta-analysis. *Oecologia*, 155, 705–716. https://doi.org/10.1007/s00442-007-0952-3

Hu, L. T., & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal*, 6, 1–55. https://doi.org/10.1080/10705519909540118

Hurlbert, A. H. (2004). Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, 7, 714–720. https://doi.org/10.1111/j.1461-0248.2004.00630.x

Hurlbert, A. H. (2006). Linking species–area and species–energy relationships in Drosophila microcosms. *Ecology Letters*, 9, 287–294. https://doi.org/10.1111/j.1461-0248.2005.00870.x

Hurlbert, A. H., & Stegen, J. C. (2014). When should species richness be energy limited, and how would we know? *Ecology Letters*, 17, 401–413. https://doi.org/10.1111/ele.12240

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *The American Naturalist*, 93, 145–159. https://doi.org/10.1086/282070

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, 10, e1001292. https://doi.org/10.1371/journal.pbio.1001292

Kaspari, M. (1996). Testing resource-based models of patchiness in 4 Neotropical litter ant assemblages. *Oikos*, 76, 443–454. https://doi.org/10.2307/3546338

Kaspari, M., O'Donnell, S., & Kercher, J. R. (2000). Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *The American Naturalist*, 155, 280–293. https://doi.org/10.1086/303313

Kline, R. B. (2010). *Principles and practice of structural equation modeling* (3rd ed.). New York, NY: Guilford Press.

Kneitel, J. M., & Miller, T. E. (2002). Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology*, 83, 680–688. https://doi.org/10.1890/0012-9658(2002)083[0680:RATPRI]2.0.CO;2

Kocher, S. D., & Williams, E. H. (2000). The diversity and abundance of North American butterflies vary with habitat disturbance and geography. *Journal of Biogeography*, 27, 785–794. https://doi.org/10.1046/j.1365-2699.2000.00454.x

Kohn, A. J., & Leviten, P. J. (1976). Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia*, 25, 199–210. https://doi.org/10.1007/BF00345098

Loiselle, B. A., & Blake, J. G. (1991). Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology*, 72, 180–193. https://doi.org/10.2307/1938913

MacArthur, R. H. (1972). *Geographical ecology*. New York, USA: Harper and Rowe Publishers.

MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42, 594–598. https://doi.org/10.2307/1932254

MacArthur, R. H., MacArthur, J. W., & Preer, J. (1962). On bird species diversity. II. Prediction of bird census from habitat measurements. *The American Naturalist*, 96, 167–174. https://doi.org/10.1086/282219

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, 31, 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

McCain, C. M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, 86, 366–372. https://doi.org/10.1890/03-3147

McCain, C. M. (2007). Area and mammalian elevational diversity. *Ecology*, 88, 76–86. https://doi.org/10.1890/0012-9658(2007)88[76:AAMED]2.0.CO;2

McGlynn, T. P., Weiser, M. D., & Dunn, R. R. (2010). More individuals but fewer species: Testing the 'more individuals hypothesis' in a diverse tropical fauna. *Biology Letters*, 6, 490–493. https://doi.org/10.1098/rsbl.2010.0103

Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., … Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, 10, 315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., … Gough, L. (2001). What is the observed relationshipbetween species richness and productivity? *Ecology*, 82, 2381–2396. https://doi.org/10.1890/0012-9658(2001) 082[2381:WITORB]2.0.CO;2

Nichols, J. D., & Conroy, M. J. (1996). Estimation of species richness. In D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, & M. S. Foster (Eds.), *Measuring and monitoring biological diversity: Standard methods for mammals* (pp. 226–234). Washington, DC: Smithsonian Institution Press.

Niklas, K. J. (1993). The allometry of plant reproductive biomass and stem diameter. *American Journal of Botany*, 80, 461–467. https://doi.org/10.1002/j.1537-2197.1993.tb13824.x

Niklas, K. J., & Enquist, B. J. (2003). An allometric model for seed plant production. *Evolutionary Ecology Research*, 5, 79–88.

Pernetta, J. C. (1976). Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. *Journal of Animal Ecology*, 45, 899–912. https://doi.org/10.2307/3588

Pineda-Munoz, S., & Alroy, J. (2014). Dietary characterization of terrestrial mammals. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141173. https://doi.org/10.1098/rspb.2014.1173

Prevedello, J. A., Dickman, C. R., Vieira, M. V., & Vieira, E. M. (2013). Population responses of small mammals to food supply and predators: A global meta-analysis. *Journal of Animal Ecology*, 82, 927–936. https://doi.org/10.1111/1365-2656.12072

Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alstrom, P., … Mohan, D. (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509, 222–225. https://doi.org/10.1038/nature13272

Richmond, G. M. (1965). Glaciation of the Rocky Mountains. In H. E. J. Wright & D. G. Frey (Eds.), *The Quaternary of the United States* (pp. 217–230). Princeton, NJ: Princeton University Press.

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511623387

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48, 1–36.

Rowe, R. J. (2009). Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. *Ecography*, 32, 411–422. https://doi.org/10.1111/j.1600-0587.2008.05538.x

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., & Hashimoto, H. (2004). A continuous satellite-derived measure of global terrestrial primary production. *BioScience*, 54, 547–560. https://doi.org/10.1641/0006-3568(2004)054[0547:ACSMOG]2.0.CO;2

Sanders, N. J., Lessard, J.-P., Fitzpatrick, M. C., & Dunn, R. R. (2007). Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, 16, 640–649. https://doi.org/10.1111/j.1466-8238.2007.00316.x

Schermelleh-Engel, K., Moosbrugger, H., & Müller, H. (2003). Evaluating the fit of structural equation models: Tests of significance and descriptive goodness-of-fit measures. *Methods of Psychological Research Online*, 8, 23–74.

Schorr, R. A., Lukacs, P. M., & Florant, G. L. (2009). Body mass and winter severity as predictors of overwinter survival in Preble's meadow jumping mouse. *Journal of Mammalogy*, 90, 17–24. https://doi.org/10.1644/07-MAMM-A-392.1

Shipley, B. (2000). *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511605949

Shipley, B., & Dion, J. (1992). The allometry of seed production in herbaceous angiosperms. *The American Naturalist*, 139, 467–483. https://doi.org/10.1086/285339

Slade, N. A., & Blair, S. M. (2000). An emprical test of using counts of individuals captured as indices of population size. *Journal of Mammalogy*, 81, 1035–1045. https://doi.org/10.1644/1545-1542(2000)081<1035:AETOUC>2.0.CO;2

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *The American Naturalist*, 152, 510–529. https://doi.org/10.1086/286187

Stein, A., Beck, J., Meyer, C., Waldmann, E., Weigelt, P., & Kreft, H. (2015). Differential effects of environmental heterogeneity on global mammal species richness. *Global Ecology and Biogeography*, 24, 1072–1083. https://doi.org/10.1111/geb.12337

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880. https://doi.org/10.1111/ele.12277

Stein, A., & Kreft, H. (2015). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, 90, 815–836. https://doi.org/10.1111/brv.12135

Stevens, R. D., & Tello, J. S. (2011). Diversity begets diversity: Relative roles of structural and resource heterogeneity in determining rodent community structure. *Journal of Mammalogy*, 92, 387–395. https://doi.org/10.1644/10-MAMM-A-117.1

Storch, D., Bohdalková, E., Okie, J., & Gravel, D. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, 21, 920–937. https://doi.org/10.1111/ele.12941

Swihart, R. K., & Slade, N. A. (1990). Long-term dynamics of an early successional small mammal community. *American Midland Naturalist*, 123, 372–382. https://doi.org/10.2307/2426565

Szewczyk, T., & McCain, C. M. (2016). A systematic review of global drivers of ant elevational diversity. *PLoS ONE*, 11, e0155404. https://doi.org/10.1371/journal.pone.0155404

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845. https://doi.org/10.1126/science.1060391

Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3355–3363. https://doi.org/10.1098/rspb.2011.0190

Turner, J. R. G., Gatehouse, C. M., & Corey, C. A. (1987). Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48, 195–205. https://doi.org/10.2307/3565855

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G. G., Gough, L., Dodson, S. I., … Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, 30, 257–300. https://doi.org/10.1146/annurev.ecolsys.30.1.257

Whittaker, R. J. (2010). Meta-analyses and mega-mistakes: Calling time on meta-analysis of the species richness–productivity relationship. *Ecology*, 91, 2522–2533. https://doi.org/10.1890/08-0968.1

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., … Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, 13, 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wiens, J. J., & Graham, C. H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics*, 36, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wiens, J. J., Parra-Olea, G., & Wake, D. B. (2007). Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society of London (B)*, 274, 919–928. https://doi.org/10.1098/rspb.2006.0301

Wilson, D. E., Cole, F. R., Nichils, J. D., Rudran, R., & Foster, M. S. (Eds.) (1996). *Measuring and monitoring biological diversity: Standard methods for mammals*. Washington, D.C.: Smithsonian.

Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41, 496–506. https://doi.org/10.2307/3544109

Wright, D. H., Currie, D. J., & Maurer, B. A. (1993). Energy supply and patterns of species richness on local and regional scales. In R. E. Ricklef, & D. Schluter (Eds.), *Species diversity in ecological communities: Historical and geographical perspectives* (pp. 66–74). Chicago, IL: University of Chicago Press.

Yanoviak, S. P. (2001). Predation, resource availability, and community structure in Neotropical water-filled tree holes. *Oecologia*, 126, 125–133. https://doi.org/10.1007/s004420000493

Yee, D. A., & Juliano, S. A. (2007). Abundance matters: A field experiment testing the more individuals hypothesis for richness-productivity relationships. *Oecologia*, *153*, 153–162. https://doi.org/10.1007/s00442-007-0707-1

DATA ACCESSIBILITY

The entirety of the dataset analysed herein is included as an online Appendix S4, including transect, locality, year sampled, elevation, mammal diversity and abundance, vole diversity and abundance, shrew diversity and abundance, average annual temperature, precipitation, and net primary productivity (NPP), elevational area, standardized arthropod, understory vegetation and food biomass, habitat diversity, habitat heterogeneity, number of trees, tree diversity, and grass coverage for each of the 32 sites. GIS layers from which the average annual temperature, precipitation, and NPP were extracted are publicly available at http://www.worldclim.org/bioclim and http://www.ntsg.umt.edu/project/modis/default.php.

BIOSKETCH

Christy McCain, **Sarah King**, **Tim Szewczyk**, and **Jan Beck** are ecologists and evolutionary biologists interested in conservation, montane biogeography, climate change, and theoretical and empirical aspects of the causes and maintenance of species diversity.

Author contributions: CMM designed the study and analysed the data, supported by SK and JB; CMM, SK, and TS collected and compiled the field data; CMM wrote the manuscript, with input from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.