



Patterns and drivers of leaf-litter ant diversity along a tropical elevational gradient in Mexico

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Abstract

Aim: Given their high environmental variation over relatively short distances, mountains represent ideal systems for evaluating potential factors shaping diversity gradients. Despite a long-standing interest in ecological gradients, ant diversity patterns and their related mechanisms occurring on mountains are still not well understood. Here, we (i) describe species diversity patterns (α and β) of leaf-litter ants along the eastern slope of Cofre de Perote in Veracruz, Mexico; and (ii) evaluate climatic and spatial factors in determining these patterns.

Location: Veracruz, Mexico.

Taxon: Leaf-litter ants.

Methods: We sampled 320 m² of leaf litter spread across eight equally spaced sites from sea level to 3500 m of elevation. We used regression models to predict α -diversity patterns with climatic (temperature and precipitation) and spatial (geometric constraints) variables. We also assessed, through multiple regression based on distance matrices (MRM), the relative importance of habitat filtering and dispersal limitations for shaping total dissimilarity (β_{sor}), turnover (β_{sim}) and nestedness (β_{nes}).

Results: A hump-shaped pattern was observed in the α -diversity. This pattern is best explained by the temperature gradient. β -diversity showed a nonlinear pattern along the elevational gradient with total dissimilarity and turnover components better explained by habitat filtering (i.e. temperature distances). Turnover had higher contribution to total dissimilarity rather than the nestedness component.

Main conclusions: The significance effect of temperature on both α - and β -diversity patterns reinforces its widespread importance in shaping litter ant diversity patterns across elevational gradients. The hump-shaped pattern in species richness is probably the result of harsh abiotic conditions at the base and the top of the mountain combined with biotic attrition in lowland sites. The niche specialization of ant species in their optimal thermal zones may explain total dissimilarity and ant species replacement along the studied gradient. Taken all together, these results suggest a high relevance of temperature-driven mechanisms in the origin and maintenance of the biodiversity of such insects and probably another ectothermic taxa.

KEYWORDS

alpha diversity, beta diversity, elevational patterns, habitat filtering, leaf-litter ants, taxonomic diversity, temperature



1 | INTRODUCTION

Disentangling the relative importance of mechanisms driving the natural variation in species numbers and community composition has attracted the attention of ecologists for decades (Anderson et al., 2011; Hawkins et al., 2003). Both theoretical and empirical studies have documented the interplay of environmental gradients and spatial processes as drivers of species distribution and community composition (Chase & Myers, 2011; HilleRisLambers et al., 2012; Hubbell, 2001). Mountains represent ideal scenarios to better understand the distribution of diversity (Körner, 2007; Sundqvist et al., 2013), because they represent sharp environmental gradients on relatively small geographic scales (Lomolino, 2001; Rahbek, 1995). To date, different species richness and composition patterns have been described on mountains for many taxonomic groups; however, the underlying mechanisms driving such patterns remain elusive (Peters et al., 2016; Sanders & Rahbek, 2012).

Elevational studies across multiple scales and taxa have shown that species richness decreases linearly with increasing elevation (e.g. Kwon et al., 2014; Machac et al., 2011) or peaks at intermediate elevations (e.g. Bishop et al., 2014; Longino & Branstetter, 2019). Climate-based hypotheses posit that factors such as temperature and precipitation determine species richness along elevation gradients. For instance, the general decline in temperature is generally suggested to explain the decreasing diversity with increasing elevation (e.g. Kwon et al., 2014; Machac et al., 2011; Raymond et al., 2013). Furthermore, many studies across elevational gradients including global analyses have emphasized the interaction of temperature and precipitation (Szewczyk & McCain, 2016). The relationship between these variables was formalized in the elevational climate model (ECM), wherein divergent elevational diversity patterns emerge depending on the local conditions of the mountain (McCain, 2007). According to this model, a mid-peak pattern in species diversity should appear in mountains with an arid base, because water restricts diversity towards the base, whereas temperature restricts diversity towards the summit. Conversely, on a wet mountain where water availability is relatively uniform across the mountain, temperature remains as the only factor driving species richness, resulting in a monotonic decrease of diversity (McCain, 2007). The ECM relies on the assumption that warmest and wettest elevations correspond to the highest productivity. The straightforward idea linking productivity and diversity is that productivity is equivalent to the quantity of available resources in an ecosystem, which limits the total number of individuals that a community can maintain within a region (Kaspari et al., 2000; Srivastava & Lawton, 1998). The total number of individuals in turn limits the number of species that can have viable populations in that environment (Gaston, 2000). Therefore, a region with higher population sizes is expected to have a greater number of species, either because of reduced extinction probabilities or simply because of the increased probability of sampling novel species (Evans et al., 2005).

Besides the importance of climatic factors, some authors have proposed that the geometry of bounded domains may account for the hump-shaped patterns in richness (Colwell et al., 2004; Dunn et al., 2007). Such geometric effect is called the mid-domain effect (MDE) and is usually considered in the form of null models. The MDE results from a random placement of species ranges within a constrained geographical domain, such as the lower and upper parts of the mountain (Colwell & Hurr, 1994; Colwell et al., 2004). Hence, a higher overlap of species ranges increasing towards the middle of the domain is expected, predicting a peak of species richness at intermediate elevations (hump-shaped pattern; Colwell et al., 2004). Although the MDE is subject to some scepticism (Brehm et al., 2007; Currie & Kerr, 2008), since it cannot provide biological explanations, the empirical evidence supporting MDE in predicting hump-shaped patterns across many elevational gradient studies (e.g. Fu et al., 2006; McCain, 2004) suggests that the MDE should not be simply rejected.

Further information can be gained about the processes that create and maintain biodiversity through the evaluation of β -diversity (e.g. Anderson et al., 2011; Kraft et al., 2011; Tuomisto, Ruokolainen & Yli-Halla, 2003). β -diversity is a crucial component reflecting the dissimilarity between local assemblages, as well as the relationship between local (α) and regional (γ) diversity (Anderson et al., 2011; Chase & Myers, 2011; Kraft et al., 2011; Tuomisto, 2010). Overall, studies on many taxa across regions have consistently shown that higher site-to-site dissimilarity is found at lower elevations, while lower site-to-site dissimilarity is rather found at higher elevations (Kraft et al., 2011; Tello et al., 2015). This pattern has been attributed to several non-mutually exclusive processes, particularly the interplay of dispersal limitation and habitat filtering (Morlon et al., 2008; Wang et al., 2011). For instance, higher habitat specialization of species in some regions may lead to increased community dissimilarity (Lenoir et al., 2010; Leprieur et al., 2011), but greater dispersal ability promotes the ubiquitousness of species, therefore decreasing community dissimilarity (Qian, 2009). Whereas the interest in the relationship between β -diversity and elevation has increased greatly over the years, it has focused mainly on plant taxa (e.g. Myers et al., 2013; Sabatini et al., 2018; Tello et al., 2015), thus both patterns and causes of taxonomic β -diversity for several taxa, particularly for insects, remain largely unknown.

Here, we studied neotropical leaf-litter ant assemblages along a tropical elevational gradient. We focused on litter ants because they comprise a large fraction of tropical ant species, with high levels of ecological diversity (Delabie et al., 2000), easily sampled with a standardized protocol and with a highly solved taxonomy (Fichaux et al., 2021). Further, leaf-litter ant distributions are strongly constrained by local and regional climate (Dunn et al., 2009; Warren & Chick, 2013). The studies of leaf-litter ant diversity along elevational gradients across the globe have documented a decrease in species richness with increasing elevation (e.g. Brühl et al., 1999; Colwell et al., 2008; Fisher, 1995; Liu et al., 2018; Olson, 1994; Robertson, 2002;), as well as peaks at intermediate elevations (Longino & Branstetter,

2019; Sabu et al., 2008). The majority of these studies have demonstrated that both temperature (e.g. Longino & Branstetter, 2019; Machac et al., 2011) and precipitation (e.g. Smith et al., 2014; Szweczyk & McCain, 2016), and in some instances geometric constraints (Marathe et al., 2020; Sanders, 2002), have a strong effect in shaping ant diversity patterns along elevational gradients. Similarly, compositional dissimilarity of litter ants in relation to changes in elevation has also been observed to decrease with elevation (e.g. Liu et al., 2018), although an increase in β -diversity with increasing elevations has also been reported (e.g. Fontana et al., 2020; Fontanilla et al., 2019). This variety of elevational ant diversity patterns highlights the importance of more comprehensive studies across replicated gradients to identify the general patterns of ant distribution in mountains and to untangle different potential drivers (Szweczyk & McCain, 2016).

In the last decades, several elevational studies focusing on the leaf-litter assemblages have been conducted in the tropics (e.g. Fichaux et al., 2021; Lapolla et al., 2007; Longino et al., 1990; Olson, 1994). However, to date, we lack such studies from Mexico. Studying new regions and thus surveying ant assemblages from different species pools, influenced by different evolutionary histories, may help to uncover the mechanisms shaping ant biodiversity along elevational gradients and also to investigate whether similar mechanisms are at place across continents (Bernadou et al., 2015). A case in point is the Cofre de Perote, a tropical mountain located at the Mexican Transition Zone (MTZ). MTZ is a complex evolutionary and active area where the Neotropical and Nearctic regions converge (Escalante et al., 2004; Morrone, 2015). It extends from the south of the United States to the plain of southern Nicaragua (Halftter & Morrone, 2017). Mountains located in the MTZ were primarily dispersion tracks for the northern fauna adapted to cold conditions, whereas the lowlands allowed neotropical species to pass through northern areas (Halftter, 1987; Halftter & Morrone, 2017). All these characteristics make the Cofre de Perote an interesting scenario for analysing biodiversity patterns along elevation and their related mechanisms.

In this study, we describe the α - and β -diversity patterns of leaf-litter ants and evaluate the effect of different drivers along an entire elevational gradient. More specifically, we have the following objectives: (i) to describe the α -diversity elevational pattern and assess whether this pattern is best explained by temperature, precipitation and/or MDE factors; (ii) to document the pattern of total pairwise dissimilarity (β -diversity) across the elevational gradient and test whether this dissimilarity is driven by species turnover or by nestedness-resultant component; and (iii) to evaluate whether these β -diversity components are driven by either habitat filtering or dispersal limitation. Following the proposed effect of temperature, precipitation and geometric constraints on ant diversity patterns across elevation, we expected that (i) ant richness will decrease monotonically with increasing elevation, resulting from the linear decrease of temperature restricting ant species richness at higher elevations given their thermophilic affinity; (ii) total dissimilarity will decrease

linearly with increasing elevation as a consequence of lowland species with more restricted ranges than highland species, which in turn can be related to higher species turnover in lowlands resulting from niche specialization of species at warm sites. Conversely, total dissimilarity at higher elevation will largely be caused by nestedness given only a subset of ant species that occur in more benign environments (lower sites) is well adapted to the harsher conditions found at those elevations. Finally, (iii) if ant dispersal rates are sufficient to allow species to spread to all potential habitats, then habitat filtering will have a higher importance in shaping the three components of β -diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted along the eastern slope of the Cofre de Perote mountain, in Veracruz, Mexico. This region is located at the junction of the Trans-Mexican volcanic belt and the Sierra Madre Oriental. We selected eight study sites spanning an elevational gradient of 3500 m of altitude (Figure 1). Regardless of the geographical distance, all sites were systematically separated with an elevational difference of 500 m on average between each other. We placed our study sites at the following elevations above sea level: 30–50 m, 610–670 m, 900–1010 m, 1470–1650 m, 2020–2230 m, 2470–2600 m, 3070–3160 m and 3480–3540 m; however, for simplicity, we will refer to each site as the discrete unit (i.e. 0, 600, 1000, 1500, 2100, 2500, 3100 and 3500 m). For summarized characteristics of sites, see Table 1 and Table S1.

2.2 | Sampling design

Sampling sites were old-growth forests characterized by no obvious forest use and highly dominance of mature forests, except in the case of the lowest site (i.e. La Mancha), where most of its original vegetation has been transformed. To overcome the effect of perturbation in the studied patterns, we sampled La Mancha in a secondary forest with up to 30 years of regeneration. All sampling sites were closed-canopy forests in which a leaf-litter layer could be guaranteed. During the rainy season (July–September) of 2018 one 300-m transversal transect was located at each one of the eight study locations where we established 10 equidistantly sampling points (i.e. 30 m between each other). Two independent 1-m² samples were taken perpendicularly to each sampling point: one 10 m on the right side and the other 10 m from the left side. This procedure was repeated in a second transect placed during the dry season (March–May) of 2019 in order to increase our sample coverage (see below) as well as reduce any seasonality effect on our diversity patterns. Transects within an elevational site were separated at least 1 km away from each other. Thus, 320 leaf-litter samples characterized the whole

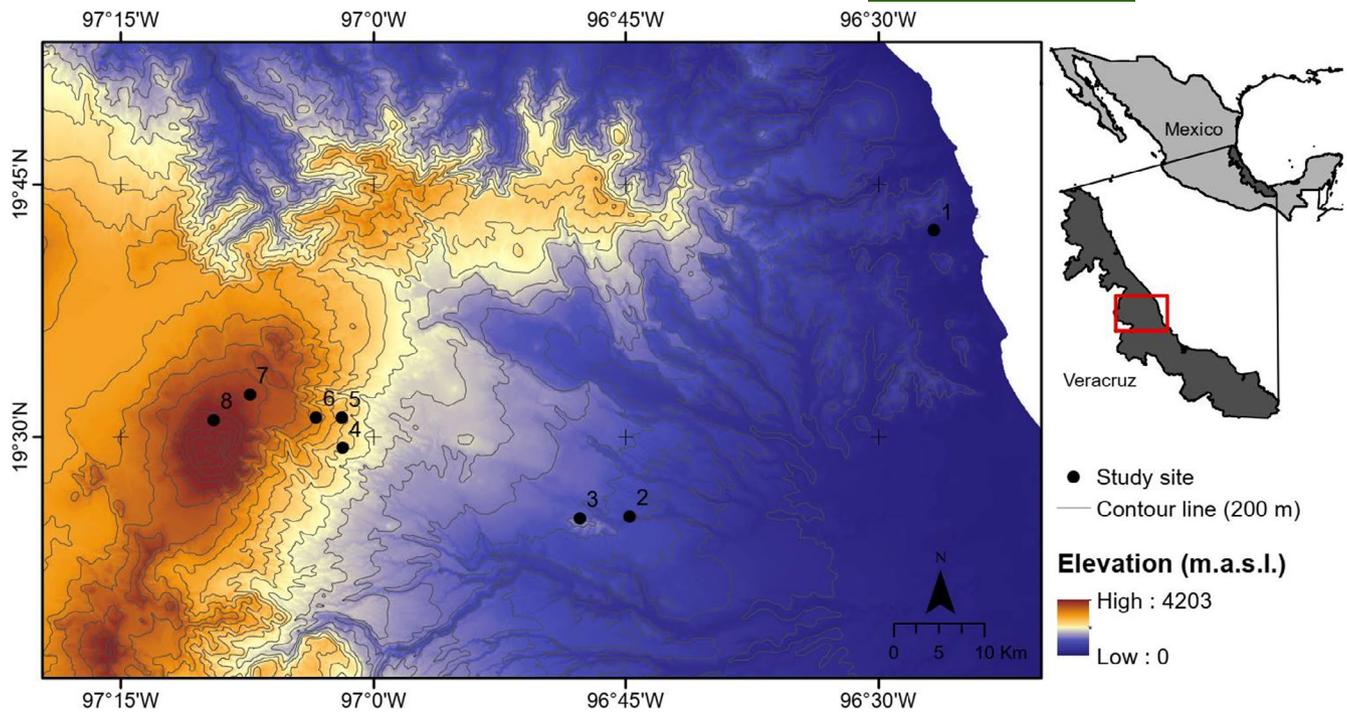


FIGURE 1 Location of eight sample sites in the eastern slope of Cofre de Perote down to the sea level in the Gulf of Mexico. Study sites are represented by black dots and numbers: 1 = La Mancha, 2 = Palmarejo, 3 = Chavarrillo, 4 = Los Capulines, 5 = El Zapotal, 6 = El Encinal, 7 = Los Pescados and 8 = El Conejo. Elevation data were downloaded from INEGI (<https://www.inegi.org.mx/app/geo2/elevacionesmex/>), whereas contour lines from CONABIO (<https://www.gob.mx/conabio>, CONABIO, 1998). Map is displayed on a WGS 1984 World Mercator projection (Datum: WGS 1984)

TABLE 1 Environmental characteristics at the study sites

Site	Elevation (m)	Vegetation type	MAT (°C)	MAP (mm.)
La Mancha	0	Tropical semi-deciduous forest	24.9	1160.7
Palmarejo	600	Tropical semi-deciduous forest	22.4	983.8
Chavarrillo	1000	Tropical <i>Quercus</i> forest	20.1	1381.8
Los Capulines	1500	Cloud mountain forest	16.1	1678
El Zapotal	2000	Cloud mountain forest	13.7	1367.4
El Encinal	2500	<i>Pinus-Quercus</i> forest	11.9	882.4
Los Pescados	3000	<i>Pinus</i> forest	9.7	1102.6
El Conejo	3500	<i>Abies</i> forest	8.2	829.3

Information is given on elevational (m a.s.l.) and vegetation type.

Vegetation types according to Leopold (1950), mean annual temperature (MAT) and mean annual precipitation (MAP) according to bioclimatic rasters at ~90 m.

mountain (8 study sites \times 20 m² per transect \times 2 transects = 320 m²). In each 1-m² quadrat, we collected the leaf litter inside and sifted it through a coarse mesh screen of 1-cm grid size to remove the largest fragments and concentrate the fine litter. The concentrated fine litter from each sample was suspended in independent mini-Winkler sacks for 3 days in the laboratory. Falling arthropods were collected into a container with 95% ethanol. Ant workers were removed from each container for identification. When possible, specimens were identified at the species level. If not, we assigned a morphospecies number.

2.3 | α -Diversity pattern

We calculated the sample coverage (\hat{C}_n , Chao & Jost, 2012) to assess the completeness of our samples to represent leaf-litter ant assemblages at each sampling site. These calculations were conducted on an occurrence matrix constructed by pooling the species occurrence (i.e. the number of samples in which a species is present) out of the forty 1-m² samples of each elevational band. Given that we did not collect any ant species at 3500 m, these calculations were



conducted only on the first seven sites (i.e. from 0 to 3000 m; see Results). We assigned a zero-raw value to the 3500 m site to conduct downstream analyses. Sample coverage calculation varied from 0.801 to 0.976 (Table S1), therefore we extrapolated the species richness of the location with the lowest \hat{C}_n (i.e. 3000 m) by doubling the reference sample sizes (Chao & Jost, 2012). Through this extrapolation technique, we achieved an \hat{C}_n of 0.88. Comparisons were made after the richness values of the rest of the sites were standardized (hereafter standardized richness) to the minimum value of sample coverage (i.e. 0.88). Statistical differences between sites were inferred by the non-overlapping 95% CI associated with each richness estimation. Furthermore, we addressed the pattern at the 1-m² scale across the mountain by calculating the mean number of species per sample (hereafter mean species richness). For this, at each elevation, we summed the number of species present in each sample and then divided by 40 (i.e. samples taken per site). Sample coverage calculations were carried out with 'iNEXT' package (Hsieh et al., 2016) in R project (R Core Team, 2019).

2.4 | β -Diversity pattern

To assess the variation of β -diversity between adjacent sites along the elevational gradient, we transformed the site-level matrix with species occurrences into a presence/absence matrix (1 for presences and 0 for absences). Using this matrix, we calculated the pairwise Sørensen dissimilarity (total dissimilarity) between adjacent sites going from the base to the top of the mountain (i.e. 0–500, 500–1000, 1000–1500, 1500–2000, 2000–2500, 2500–3000). Total dissimilarity (β_{sor}) was further partitioned into its two antithetic components, namely turnover (β_{sim}) and nestedness-resultant (β_{nes}) following the framework of Baselga (2010). Additionally, we addressed the β -diversity patterns within each elevational site by evaluating the total dissimilarity among all points with ant species recorded. Similarly, we partitioned total dissimilarity into its turnover and nestedness-resultant components. Matrix transformations were carried out using the 'vegan' package (Oksanen et al., 2013), whereas beta diversity calculations were conducted using the 'betapart' package (Baselga & Orme, 2012) in R project software (R Core Team, 2019).

2.5 | Diversity predictors

To evaluate the effect of current climate in terms of temperature and precipitation on species richness, we used BIO1: mean annual temperature (°C; hereafter MAT) and BIO12: mean annual precipitation (mm.; hereafter MAP). In each elevation, we extracted MAT and MAP values from the bioclimatic rasters available for Mexico at 3 arc-second resolution (~90 m; Cuervo-Robayo et al., 2014) using the geographic coordinates of the 40 points where samples were taken. For practical purposes, each site was characterized by averaging these 40 values.

For testing the effect of MDE on species richness, we used simulation models that randomly arrange species distributions across elevation. For this purpose, we determined the empirical elevational range for each species, which is defined by its minimum and maximum elevation of occurrence. Then, we randomly place this empirical range within the entire geographical domain, represented by the lowest and highest elevation (0–3500 m). We ran this procedure 1000 times after which the mean predicted richness for each study site was calculated by averaging over the 1000 predicted richness values. These analyses were conducted using the *rangemod1d* function incorporated in the 'RangeModelR' package (<https://CRAN.R-project.org/package=rangemod1d>) in R project software (R Core Team, 2019).

To assess the relative contributions of environmental differences (i.e. habitat filtering) and geographical distance (i.e. dispersal limitation) in explaining β -diversity patterns, we constructed an environmental distance matrix independently for MAT and MAP. These matrices were based on the Mahalanobis pairwise distances between all pairwise sites (hereafter MATd and MAPd). Additionally, a geographical distance matrix (hereafter GEOd) was obtained between pairwise centroids of sites using the *earth.dist* function from the 'fossil' package (Vavrek, 2011) in the R project software (R Core Team, 2019).

2.6 | Statistical analyses

To evaluate whether the climatic variables (i.e. temperature and precipitation) or geometric constraints (i.e. MDE) better explained the standardized ant richness, we constructed three simple linear models with standardized richness as the response variable and MAT, MAP and MDE as independent explanatory variables. Additionally, we conducted a multiple regression in which standardized richness was modelled through the additive effect of both climatic variables (i.e. MAT + MAP). Because of our low number of observational units (elevational sites), we did not consider the interaction effect of MAT and MAP on the multiple regression models. Models were validated by checking for normality of the residuals by Shapiro's test with $\alpha = 0.05$ (Zuur et al., 2009), and in all cases, model assumptions were met (MAT: $W = 0.9518$, p -value = 0.729; MAP: $W = 0.8784$, p -value = 0.165; MDE: $W = 0.9063$, p -value = 0.3293; and MAT + MAP: $W = 0.97669$, p -value = 0.9447). To select the best fit model, we used the Akaike information criterion with correction for small sample sizes (AICc), where the lowest AIC was considered to be the best. We considered a model equally probable to the best fit model if the difference in AIC (Δ AIC) between the focal model and the model with the lowest AICc was <2. We obtained the coefficients of determination (R^2) to evaluate the proportion of the standardized richness variance explained by each model. Analyses were conducted using the 'AICmodavg' package (Mazerolle, 2006) in the R project software (R Core Team, 2019).

To test the relative contribution of different factors that might explain β -diversity variation between adjacent sites, we used a



multiple regression on distance matrices (MRM) approach coupled with variance partitioning (Lichstein, 2007; Swenson, 2014). This method is conceptually similar to traditional multiple regression but with all variables being distance matrices instead of raw data and coefficient significance being calculated through permutation tests (10,000 runs). For this purpose, the full triangular β -dissimilarity matrices (i.e. β_{SOR} , β_{SIM} and β_{NES}) including all pairwise comparisons between elevational sites were modelled with the full triangular climatic- and geographic distance matrices (i.e. MATd, MAPd and GEOd). The standardized partial regression coefficients (β) were estimated to evaluate the relative importance of each predictor variable on the patterns of β -diversity. Finally, the *lm* function was used to obtain the portion of the variance explained (R^2) by each model (Swenson, 2014). MRM analysis was conducted using the 'ecodist' package (Goslee & Urban, 2007) in the R project software (R Core Team, 2019).

3 | RESULTS

3.1 | Myrmecofauna overview

A total of 24,373 ant workers were collected, belonging to 145 species of 47 genera, 17 tribes and 10 subfamilies (Table S2). The genera with the highest number of species were *Pheidole* and *Strumigenys* (15 species each), followed by *Stenammina* and *Hypoponera* (10 species each); *Solenopsis* and *Adelomyrmex* (seven species each); *Themnothorax* (six species); *Crematogaster*, *Nylanderia* and *Octostruma* (five species each); *Camponotus*, *Gnamptogenys* and *Rogeria* (four species each); *Brachymyrmex*, *Odontomachus* and *Syscia* (three species each); *Carebara*, *Eurhopalothrix*, *Megalomyrmex*, *Monomorium*, *Neivamyrmex*, *Pseudomyrmex* and *Rhopalothrix* (two species each); the rest 25 genera were represented by only one species. The most collected species overall was *Stenammina vexator* with

5.4% of all species records. Eighty ant species (54%) were restricted to one site, whereas *Strumigenys brevicornis* had the widest distribution, occupying five out of seven sites (see Figure S1).

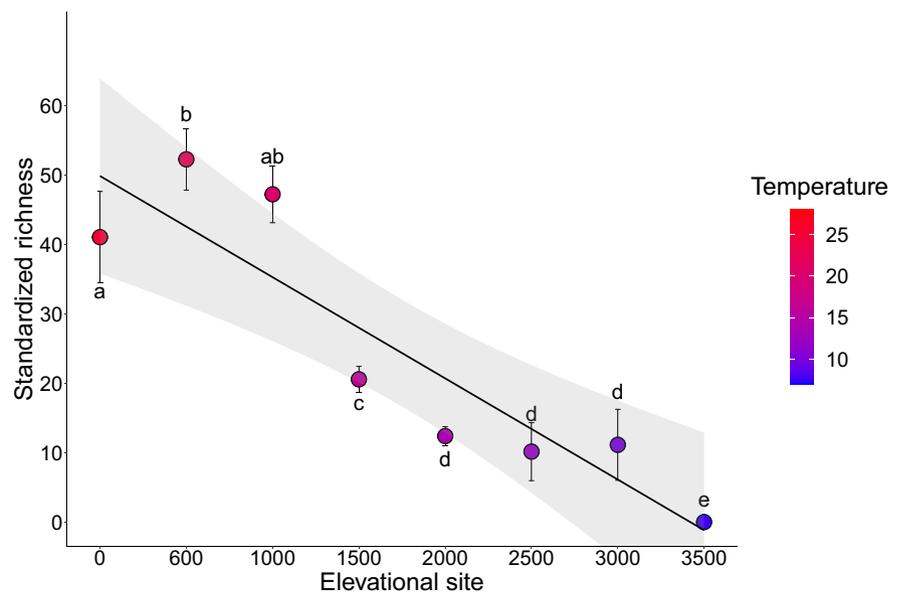
3.2 | α -Diversity

The mean species richness and standardized richness of leaf-litter ants clearly showed a hump-shaped pattern along our studied elevational gradient. The mean species richness peaked at 1000 m (see Figure S2), whereas the standardized richness at 600 and 1000 m were similar and statistically higher than the rest of the sites. Intermediate richness sites were at 0 and 1500 m. Sites with the lowest richness were observed when elevation reaches 2000 m or greater (Figure 2), while we did not observe any ant species at 3500 m. According to generalized linear models, temperature was the best supported variable (lowest AIC) and explained a high proportion of species richness variation ($\approx 86\%$; Table 2). Model performance did not improve when precipitation was included. MDE had no effect on the observed richness pattern (Table 2).

3.3 | β -Diversity

β -Values within elevations displayed high values of total dissimilarity, turnover and nestedness. The turnover component had the major contribution to total dissimilarity with the highest values at the extremes of the mountain (see Figure S3a). When comparing only adjacent sites, total community dissimilarity and its components (i.e. turnover and nestedness) displayed strong variation with a multimodal pattern. Overall, sites along the elevational gradient exhibited a low proportion of shared species producing high values of total dissimilarity (mean: 0.67). The turnover component had a major

FIGURE 2 Relationship between standardized richness at $\hat{C}_n=88\%$ of leaf-litter ant richness and elevation along the eight sites of the western slope of Cofre de Perote mountain in Mexico. Differences in the standardized richness at each site is represented by different letters according to 95% confidence intervals computed through inter-extrapolation techniques. Regression line represents the predicted values based on the best explanatory variable (i.e. Temperature; see Table 2). Dot colour symbolizes the mean annual temperature at each site



Factors	AICc	Δ AICc	β	R^2
MAT	65.23	0	2.953	0.8656
MAP	81.01	15.77	-0.013	0.0345
MDE	81.18	15.94	4.025	0.0138
MAT + MAP	74.30	9.06	MAT (2.92) + MAP (-0.0049)	0.87

The Akaike information criteria with correction for small samples (AICc) was used to compare model performance. β represents the slope of the fitted regression line, whereas the R^2 is the proportion of the species richness variance explained by each model.

contribution to total dissimilarity, whereas the nestedness-resultant values were very low along the whole gradient (i.e. 0 and 3000 m; see Figure S3b).

The full models that tested the total effect of spatial and environmental distances on β -diversity accounted for 23.36% (β_{SOR}), 30.78% (β_{SIM}) and 0% (β_{NES}) of variation. According to MRM analysis, an increase of temperature distances was related to an increase in total dissimilarity (slope = 0.212, $p < 0.05$), and species turnover (slope = 0.223, $p < 0.05$). When the dissimilarity due to nestedness was regressed against climatic and geographic distances, we did not find significant relationships (Table 3; Figure 3).

4 | DISCUSSION

Over the last two decades, the intense study on large-scale patterns and drivers of species richness has shown that species richness varies considerably across elevational gradients both within and among taxa (Bhattarai et al., 2004; Brown, 2001; McCain, 2009; Rahbek, 1995). In this study, we found that leaf-litter ant richness exhibits a clear hump-shaped relationship across the eastern slope of Cofre de Perote, Mexico. This variation in species richness was accompanied by a nonlinear pattern in β -diversity pattern along the mountain with several peaks at the base (0–600), the middle (1000–1500) and top (2500–3000) of the mountain suggesting that most ant species experience important constraints to occupy adjacent elevations. Overall, turnover had a higher contribution to total dissimilarity in comparison with the nestedness component, therefore ant communities in the leaf litter along the mountain are structured by different species. Finally, temperature was the main factor explaining both species' richness and the variation in species composition across the mountain, suggesting high importance of temperature-driven mechanisms facilitating the origin and maintenance of the biodiversity of these insects (Allen et al., 2012; Zhou et al., 2016).

We found a hump-shaped pattern in leaf-litter ant richness in which the highest richness was located at 500–1000 m a.s.l. Such pattern of species richness has been widely documented in several ant elevational diversity studies (e.g. Bharti et al., 2013; Longino & Branstetter, 2019), though there are reports of linear decreasing patterns as well (e.g. Marathe et al., 2020; Sanders et al., 2007). Many studies have argued that variation in elevational patterns of species richness may depend on the regional factors of the mountain (Rahbek, 1995) or the taxa involved (McCain, 2009, 2010), but global

TABLE 2 Regression models evaluating the effect of temperature, precipitation and mid-domain effect (MDE) on standardized ant richness along the elevational gradient

TABLE 3 Results of multiple regressions on distance matrices (MRM) performed on total dissimilarity (β_{SOR}), turnover (β_{SIM}) and nestedness-resultant (β_{NES}) components

Model	R^2	β
$\beta_{\text{SOR}} \sim \text{MATd} + \text{MAPd} + \text{GEOd}$	0.2336	
MATd	—	0.2121
MAPd	—	0.0090
GEOd	—	-0.0333
$\beta_{\text{SIM}} \sim \text{MATd} + \text{MAPd} + \text{GEOd}$	0.3078	
MATd	—	0.2233
MAPd	—	0.0080
GEOd	—	-0.0336
$\beta_{\text{NES}} \sim \text{MATd} + \text{MAPd} + \text{GEOd}$	0.0000	
MATd	—	-0.0112
MAPd	—	0.0009
GEOd	—	0.0002

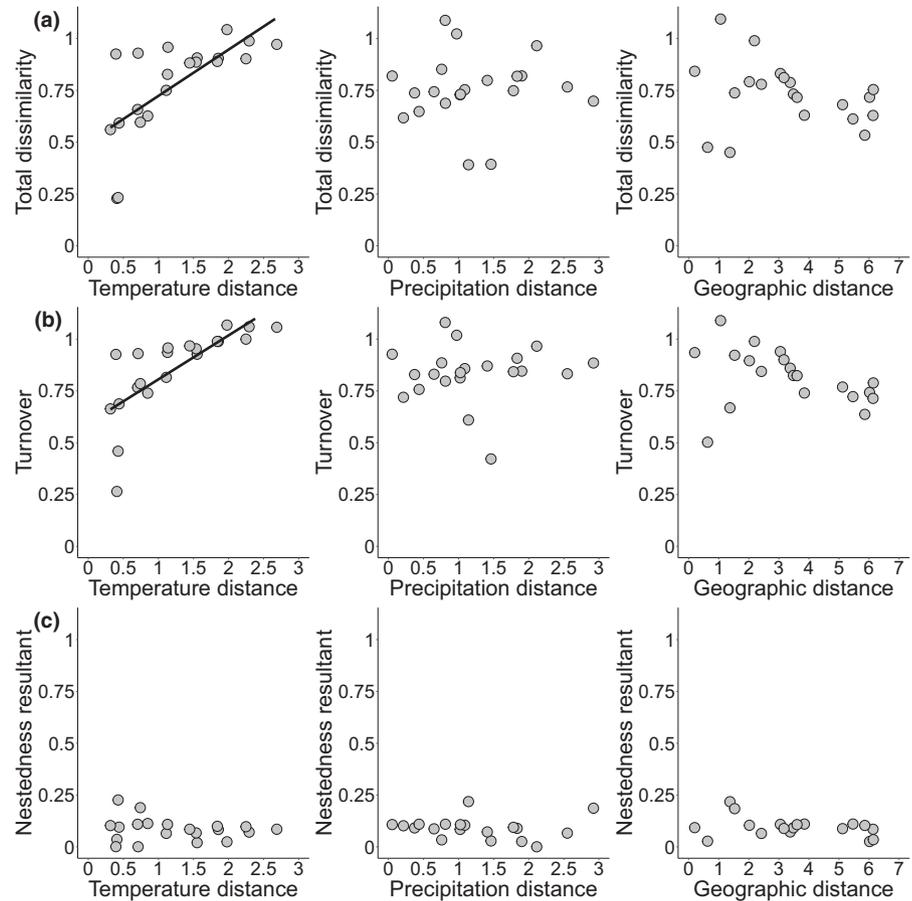
In each model, the variation explained of the full model (R^2) and the slope (β) of the regression line for each single predictor are expressed; bold = $p < 0.05$.

analyses have also pointed out that some inconsistency of patterns may be due to gradient truncation (McCain & Grytnes, 2010). In general, a truncated gradient occurs when only a portion of the mountain is sampled (Nogués-Bravo et al., 2008). In such cases, when the lower portion of the gradient is missing, a theoretical mid-domain pattern may instead exhibit a linear decreasing pattern (McCain & Grytnes, 2010). In this study, the elevational range extended from the lowest elevation (i.e. at sea level) to the highest point where no further leaf-litter ant species was found (~3500 m), therefore we assume that patterns reported here capture the whole gradient.

The linear decrease in temperature significantly explained the alpha diversity occurring along the mountain. This relationship has been widely documented in several studies across elevational gradients (e.g. Diamond et al., 2012; Dunn et al., 2009; Sanders et al., 2007) with several proposed mechanisms to explain this relationship. For instance, in ectothermic organisms like ants, the use of available resources requires first of the physiological activation that comes when temperatures reach a certain threshold (Willmer, 1983). Thus, considering that productivity is available enough along the mountain, it is expected that in warm environments, ants may reach higher community's abundance because temperature promotes longer foraging time activity (Azcárate & Peco, 2007; Brühl et al., 1999) leading



FIGURE 3 Partial regression plots from multiple regressions on distance matrices (MRM). (a) Total dissimilarity, (b) turnover and (c) nestedness-resultant components were modelled by temperature distance (left column), precipitation distance (centre column) and geographic distance (right column). Only regression lines of significant models at $\alpha = 0.05$ were plotted



to a higher net energetic intake (Classen et al., 2015). Additionally, higher temperatures hasten egg-to-worker development (Hölldobler & Wilson, 1990), enhancing both colony growth and survival. Those series of benefits promote taxon's abundance, consequently, reducing the local extinction risk (Seoane et al., 2017; Storch et al., 2018). This abundance-richness mechanism may convincingly explain why the species are numerically constrained at the higher and colder portion of the mountain than in the lowland. However, under this mechanism, a monotonic decrease of richness should emerge, mirroring the linear decline of temperature along the gradient (McCain & Grytnes, 2010; Szweczyk & McCain, 2016).

However, the decrease in species richness at the sea-level site suggests that additional factors may be acting to create the hump-shaped pattern observed in this study. A recent analysis considering the elevational patterns of leaf-litter ants through Middle America wet forests found a similar hump-shaped pattern where no environmental variables could explain the decline in diversity at the lowest elevations (Longino & Branstetter, 2019). The authors evoked the lowland biotic attrition (Colwell et al., 2008) as one plausible explanation. This phenomenon refers to the losses of species in the lowlands, where higher species richness would be expected otherwise, due to high rates of dispersion of lowland species to climatically suitable areas found at higher elevations as a response of sudden climate change. Given that a species pool from hotter areas is usually not available to replace those species that dispersed upslope, such

distributional shift results in an overall reduction of species richness at low elevations (Colwell et al., 2008). It has been proposed that lowland attrition had already occurred as a result of lowland range contractions during full glacial periods (Holloway et al., 1990) and that current climate around 500 m of elevation may represent the ancestral optimal climate for ants (Longino & Branstetter, 2019; Longino & Colwell, 2011). The fact that species richness peaked around the elevations where currently optimal conditions are expected suggests that our sea-level site could have experienced species losses due to lowland biotic attrition. However, further studies exploring the detailed distribution of species ranges at low elevations should lend insights about the consistency of lowland biotic attrition explaining the decrease of richness at those elevations.

The lack of correlation of species richness with precipitation may be explained by the absence of a strong precipitation gradient in this mountain. Although there are some marked variations in the precipitation regime across our elevational gradient, available data show there is plenty of water in our study sites (Table 1), potentially leading to a consistent humid climate along the studied area. While the importance of precipitation on ant physiology, such as reduction of desiccation risk (Kaspari & Weiser, 2000), or its indirect effect on habitat productivity (McCain & Grytnes, 2010) is undisputed, the rather homogenous distributions of precipitation across the areas may explain the insignificant effect of this factor. This result is straightforwardly related to the prediction of the elevational climate model, which

posits that on wet mountains where water is plentiful, temperature remains as the single variable determining species richness (McCain & Grytnes, 2010; Szewczyk & McCain, 2016).

Some studies have suggested that the MDE can account for most of the variation in species richness across space in general and elevation in particular (e.g. Kluge et al., 2006). But some other studies have shown that the MDE accounts for very little or no variation in species richness (e.g. Dunn et al., 2007; Sanders et al., 2007). In our studied elevational gradient, we did not find an effect of MDE on ant species richness. Instead, our findings showed a strong effect of environmental variables, namely temperature, in explaining the observed ant species richness pattern across our elevational gradient.

As found in other studies (e.g. Bishop et al., 2015), and according to our expectations, we found that patterns of ant community dissimilarity primarily reflected species replacement among local communities. This indicates that highland assemblages are not subsets of lowland assemblages, but instead they are communities with different species compositions. Additionally, the prevalence of turnover over the nestedness component for total dissimilarity suggests that a considerable portion of ant species is restricted to certain elevations and does not colonize entire gradients. Whereas previous studies have related high rates of turnover with an increase in geographical distance (e.g. Fontana et al., 2020), we found strong support for habitat filtering, through temperature differences, modulating ant species replacement. These findings provide more support for the hypothesis that rather than geographical distance, ant community composition is mainly modulated by temperature-based processes in relation to environmental filtering (Fernandes et al., 2016; Wepfer et al., 2016), which selects species from the regional pool in terms of their physiological niche.

Understanding the drivers of both species richness and beta diversity is crucial to unveil the mechanisms structuring biological communities. As shown in this work, temperature emerged as the main driver of litter ant biodiversity, which suggests that physiological responses to the environment could be prevailing over geographical or dispersal constraints in our studied elevational gradient. Yet, the fact that the hump-shaped alpha pattern did not mirror the linear decrease in temperature suggests that additional factors, such as evolutionary and historical factors, could be interplaying with temperature to create the hump-shaped pattern observed in this mountain. Future research assessing how evolutionary and current environment interacts across elevational gradients will enhance our understanding of the mechanisms that govern biodiversity patterns, even from the most basic species-based approach.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The taxonomic matrix including the species list and their occurrences in each sampling site is available on the DRYAD digital repository (<https://doi.org/10.5061/dryad.573n5tb7s>).

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REFERENCES

- Allen, A. P., Gillooly, J. F., & Brown, J. H. (2012). Recasting the species-energy hypothesis: The different roles of kinetic and potential energy in regulating biodiversity. In *Scaling biodiversity* (pp. 283–299). Cambridge: Cambridge University Press. <https://doi.org/10.1017/cbo9780511814938.016>
- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, 14(1), 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Azcárate, M. F., & Peco, B. (2007). Harvester ants (*Messor barbarus*) as disturbance agents in Mediterranean grasslands. *Journal of Vegetation Science*, 18(1), 103. <https://doi.org/10.1111/j.1654-1103.2007.tb02520.x>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Bernadou, A., Espadaler, X., Le Goff, A., & Fourcassié, V. (2015). Ant community organization along elevational gradients in a temperate ecosystem. *Insectes Sociaux*, 62(1), 59–71. <https://doi.org/10.1007/s00040-014-0374-2>
- Bharti, H., Sharma, Y. P., Bharti, M., & Pfeiffer, M. (2013). Ant species richness, endemism and functional groups, along an elevational gradient in the Himalayas. *Asian Myrmecology*, 5(1), 79–101.
- Bhattarai, K. R., Vetaas, O. R., & Grytnes, J. A. (2004). Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31(3), 389–400. <https://doi.org/10.1046/j.0305-0270.2003.01013.x>
- Bishop, T. R., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2014). Elevation-diversity patterns through space and time: Ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*, 41(12), 2256–2268. <https://doi.org/10.1111/jbi.12368>



- Bishop, T. R., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2015). Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, 42(9), 1776–1786. <https://doi.org/10.1111/jbi.12537>
- Brehm, G., Colwell, R. K., & Kluge, J. (2007). The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography*, 16(2), 205–219. <https://doi.org/10.1111/j.1466-8238.2006.00281.x>
- Brown, J. H. (2001). Mammals on mountainsides: Elevational patterns of diversity. *Global Ecology and Biogeography*, 10(1), 101–109. <https://doi.org/10.1046/j.1466-822x.2001.00228.x>
- Brühl, C. A., Mohamed, M., & Linsenmair, K. E. (1999). Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, 15(3), 265–277. <https://doi.org/10.1017/S0266467499000802>
- Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533–2547. <https://doi.org/10.1890/11-1952.1>
- Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), 2351–2363. <https://doi.org/10.1098/rstb.2011.0063>
- Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., Hemp, A., Nauss, T., & Steffan-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Global Ecology and Biogeography*, 24(6), 642–652. <https://doi.org/10.1111/geb.12286>
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322(5899), 258–261. <https://doi.org/10.1126/science.1162547>
- Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, 144(4), 570–595. <https://doi.org/10.1086/285695>
- Colwell, R. K., Rahbek, C., & Gotelli, N. J. (2004). The mid-domain effect and species richness patterns: What have we learned so far? *The American Naturalist*, 163(3), <https://doi.org/10.1086/382056>
- CONABIO. (1998). Curvas de nivel para la República Mexicana. Escala 1:250000. En: *Modelo Digital del Terreno*. Instituto Nacional de Estadística, Geografía e Informática (INEGI). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Cuervo-Robayo, A. P., Téllez-Valdés, O., Gómez-Albores, M. A., Venegas-Barrera, C. S., Manjarrez, J., & Martínez-Meyer, E. (2014). An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology*, 34(7), 2427–2437. <https://doi.org/10.1002/joc.3848>
- Currie, D. J., & Kerr, J. T. (2008). Tests of the mid-domain hypothesis: A review of the evidence. *Ecological Monographs*, 78(1), 3–18. <https://doi.org/10.1890/06-1302.1>
- Delabie, J. H. C., Agosti, D., & do Nascimento, I. C. D. (2000). Litter ant communities of the Brazilian Atlantic rain forest region. In *Sampling ground-dwelling ants: Case studies from the world's rain forests*. (pp. 1–17).
- Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E., & Dunn, R. R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, 18(2), 448–456. <https://doi.org/10.1111/j.1365-2486.2011.02542.x>
- Dunn, R. R., Agosti, D., Andersen, A. N., Arnan, X., Bruhl, C. A., Cerdá, X., Ellison, A. M., Fisher, B. L., Fitzpatrick, M. C., Gibb, H., Gotelli, N. J., Gove, A. D., Guenard, B., Janda, M., Kaspari, M., Laurent, E. J., Lessard, J.-P., Longino, J. T., Majer, J. D., ... Sanders, N. J. (2009). Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, 12(4), 324–333. <https://doi.org/10.1111/j.1461-0248.2009.01291.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(3), 305–312. <https://doi.org/10.1111/j.1466-8238.2006.00284.x>
- Escalante, T., Rodríguez, G., & Morrone, J. J. (2004). The diversification of Nearctic mammals in the Mexican transition zone. *Biological Journal of the Linnean Society*, 83(3), 327–339. <https://doi.org/10.1111/j.1095-8312.2004.00386.x>
- Evans, K. L., Greenwood, J. J. D., & Gaston, K. J. (2005). Relative contribution of abundant and rare species to species-energy relationships. *Biology Letters*, 1(1), 87–90. <https://doi.org/10.1098/rsbl.2004.0251>
- Fernandes, G. W., Almeida, H. A., Nunes, C. A., Xavier, J. H. A., Cobb, N. S., Carneiro, M. A. A., Cornelissen, T., Neves, F. S., Ribeiro, S. P., Nunes, Y. R. F., & Pires, A. C. V., Beirão, M. V. (2016). Cerrado to rupestrian grasslands: Patterns of species distribution and the forces shaping them along an altitudinal gradient. In *Ecology and conservation of mountaintop grasslands in Brazil* (pp. 345–378). Springer International Publishing. https://doi.org/10.1007/978-3-319-29808-5_15
- Fichaux, M., Vleminckx, J., Courtois, E. A., Delabie, J., Galli, J., Tao, S., Labrière, N., Chave, J., Baraloto, C., & Orivel, J. (2021). Environmental determinants of leaf litter ant community composition along an elevational gradient. *Biotropica*, 53(1), 97–109. <https://doi.org/10.1111/btp.12849>
- Fisher, B. L. (1995). Ant diversity patterns along an elevational gradient in eastern Madagascar. In *Environmental change in Madagascar* (pp. 84–85).
- Fontana, V., Guariento, E., Hilpold, A., Niedrist, G., Steinwandter, M., Spitaler, D., Nascimbene, J., Tappeiner, U., & Seeber, J. (2020). Species richness and beta diversity patterns of multiple taxa along an elevational gradient in pastured grasslands in the European Alps. *Scientific Reports*, 10(1), <https://doi.org/10.1038/s41598-020-69569-9>
- Fontanilla, A. M., Nakamura, A., Xu, Z., Cao, M., Kitching, R. L., Tang, Y., & Burwell, C. J. (2019). Taxonomic and functional ant diversity along tropical, subtropical, and subalpine elevational transects in southwest china. *Insects*, 10(5), 1–15. <https://doi.org/10.3390/insects10050128>
- Fu, C., Hua, X., Li, J., Chang, Z., Pu, Z., & Chen, J. (2006). Elevational patterns of frog species richness and endemic richness in the Hengduan Mountains, China: Geometric constraints, area and climate effects. *Ecography*, 29(6), 919–927. <https://doi.org/10.1111/j.2006.0906-7590.04802.x>
- Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.
- Goslee, S., & Urban, D. (2007). The ecodist Package: Dissimilarity-based functions for ecological analysis. *Journal of Statistical Software*, 22, 1–19.
- Halffter, G. (1987). Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology*, 32, 95–114. <https://doi.org/10.1146/annurev.ento.32.1.95>
- Halffter, G., & Morrone, J. J. (2017). An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa*, 4226(1), 1–46. <https://doi.org/10.11646/zootaxa.4226.1.1>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105–3117. <https://doi.org/10.1890/03-8006>
- HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>

- Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. Springer.
- Holloway, J. D., Robinson, G. S., & Tuck, K. R. (1990). Zonation in the Lepidoptera of Northern Sulawesi. In W. J. Knight, & J. D. Holloway (Eds.), *Insects and the rain forest of South East Asia (Wallacea)* (pp. 153–166). Royal Entomological Society of London.
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7(12), 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Hubbel, S.P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Kaspari, M., Donnell, S., & Kercher, J. R. (2000). Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *American Naturalist*, 155(2), 280–293. <https://doi.org/10.1086/303313>
- Kaspari, M., & Weiser, M. D. (2000). Ant activity along moisture gradients in a Neotropical forest. *Biotropica*, 32(4), 703–711. <https://doi.org/10.1111/j.1744-7429.2000.tb00518.x>
- Kluge, J., Kessler, M., & Dunn, R. R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for peridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, 15(4), 358–371. <https://doi.org/10.1111/j.1466-822X.2006.00223.x>
- Körner, C. (2007). The use of “altitude” in ecological research. *Trends in Ecology and Evolution*, 22(11), 569–574. <https://doi.org/10.1016/j.tree.2007.09.006>
- Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L., Inouye, B. D., Harrison, S. P., & Myers, J. A. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, 333(6050), 1755–1758. <https://doi.org/10.1126/science.1208584>
- Kwon, T. S., Kim, S. S., & Chun, J. H. (2014). Pattern of ant diversity in Korea: An empirical test of Rapoport’s altitudinal rule. *Journal of Asia-Pacific Entomology*, 17(2), 161–167. <https://doi.org/10.1016/j.aspen.2013.12.006>
- Lapolla, J. S., Suman, T., Sosa-Calvo, J., & Schultz, T. R. (2007). Leaf litter ant diversity in Guyana. *Biodiversity and Conservation*, 16(2), 491–510. <https://doi.org/10.1007/s10531-005-6229-4>
- Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., Grytnes, J.-A., Virtanen, R., & Svenning, J.-C. (2010). Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. *PLoS One*, 5(12), <https://doi.org/10.1371/journal.pone.0015734>
- Leprieux, F., Tedesco, P. A., Hugué, B., Beauchard, O., Dürr, H. H., Brosse, S., & Oberdorff, T. (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, 14(4), 325–334. <https://doi.org/10.1111/j.1461-0248.2011.01589.x>
- Lichstein, J. W. (2007). Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology*, 188(2), 117–131. <https://doi.org/10.1007/s11258-006-9126-3>
- Liu, C., Dudley, K. L., Xu, Z. H., & Economo, E. P. (2018). Mountain meta-communities: Climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*, 41(1), 101–112. <https://doi.org/10.1111/ecog.03067>
- Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, 10(1), 3–13. <https://doi.org/10.1046/j.1466-822x.2001.00229.x>
- Longino, J. T., & Branstetter, M. G. (2019). The truncated bell: An enigmatic but pervasive elevational diversity pattern in Middle American ants. *Ecography*, 42(2), 272–283. <https://doi.org/10.1111/ecog.03871>
- Longino, J. T., & Colwell, R. K. (2011). Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere*, 2(3), 1–20. <https://doi.org/10.1890/ES10-00200.1>
- Longino, J. T., & Nadkarni, N. M. (1990). A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane Forest. *Psyche (New York)*, 97(1–2), 81–93. <https://doi.org/10.1155/1990/36505>
- Machac, A., Janda, M., Dunn, R. R., & Sanders, N. J. (2011). Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography*, 34(3), 364–371. <https://doi.org/10.1111/j.1600-0587.2010.06629.x>
- Marathe, A., Priyadarsanan, D. R., Krishnaswamy, J., & Shanker, K. (2020). Spatial and climatic variables independently drive elevational gradients in ant species richness in the Eastern Himalaya. *PLoS One*, 15(1), <https://doi.org/10.1371/journal.pone.0227628>
- Mazerolle, M. J. (2006). Improving data analysis in herpetology: Using Akaike’s information criterion (AIC) to assess the strength of biological hypotheses. *Amphibia Reptilia*, 27(2), 169–180. <https://doi.org/10.1163/15685380677239922>
- McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, 31(1), 19–31. <https://doi.org/10.1046/j.0305-0270.2003.00992.x>
- McCain, C. M. (2007). Area and mammalian elevational diversity. *Ecology*, 88(1), 76–86. [https://doi.org/10.1890/0012-9658\(2007\)88\[76:AA MED\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[76:AA MED]2.0.CO;2)
- McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18(3), 346–360. <https://doi.org/10.1111/j.1466-8238.2008.00443.x>
- McCain, C. M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*, 19(4), 541–553. <https://doi.org/10.1111/j.1466-8238.2010.00528.x>
- McCain, C. M., & Grytnes, J.-A. (2010). Elevational gradients in species richness. In J. Wiley (Ed.), *Encyclopedia of Life Sciences*. John Wiley & Sons Ltd. <https://doi.org/10.1002/9780470015902.a0022548>
- Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R., & Green, J. L. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters*, 11(9), 904–917. <https://doi.org/10.1111/j.1461-0248.2008.01202.x>
- Morrone, J. J. (2015). Halffter’s Mexican transition zone (1962–2014), cenocrons and evolutionary biogeography. *Journal of Zoological Systematics and Evolutionary Research*, 53(3), 249–257. <https://doi.org/10.1111/jzs.12098>
- Myers, J. A., Chase, J. M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters*, 16(2), 151–157. <https://doi.org/10.1111/ele.12021>
- Nogués-Bravo, D., Araújo, M. B., Romdal, T., & Rahbek, C. (2008). Scale effects and human impact on the elevational species richness gradients. *Nature*, 453(7192), 216–219. <https://doi.org/10.1038/nature06812>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., & O’Hara, R. B. (2013). Package vegan. *R Packag Ver*, 254.
- Olson, D. M. (1994). The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology*, 10(2), 129–150. <https://doi.org/10.1017/S0266467400007793>
- Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Mwangomo, E., Ngereza, C., Otte, I., Röder, J., Rutten, G., ... Steffan-Dewenter, I. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, 7, <https://doi.org/10.1038/ncomms13736>
- Qian, H. (2009). Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, 18(3), 327–332. <https://doi.org/10.1111/j.1466-8238.2009.00450.x>



- Rahbek, C. (1995). The elevational gradient of species richness: A uniform pattern? *Ecography*, 18(2), 200–205. <https://doi.org/10.1111/j.1600-0587.1995.tb00341.x>
- Reymond, A., Purcell, J., Cherix, D., Guisan, A., & Pellissier, L. (2013). Functional diversity decreases with temperature in high elevation ant fauna. *Ecological Entomology*, 38(4), 364–373. <https://doi.org/10.1111/een.12027>
- Robertson, H. G. (2002). Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodiversity and Conservation*, 11(9), 1637–1652. <https://doi.org/10.1023/A:1016883901065>
- Sabatini, F. M., Jiménez-Alfaro, B., Burrascano, S., Lora, A., & Chytrý, M. (2018). Beta-diversity of central European forests decreases along an elevational gradient due to the variation in local community assembly processes. *Ecography*, 41(6), 1038–1048. <https://doi.org/10.1111/ecog.02809>
- Sabu, T. K., Vineesh, P. J., & Vinod, K. V. (2008). Diversity of forest litter-inhabiting ants along elevations in the Wayanad region of the Western Ghats. *Journal of Insect Science*, 8(69), 1–14. <https://doi.org/10.1673/031.008.6901>
- Sanders, N. J. (2002). Elevational gradients in ant species richness: Area, geometry, and Rapoport's rule. *Ecography*, 25(1), 25–32. <https://doi.org/10.1034/j.1600-0587.2002.250104.x>
- 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(5), 640–649. <https://doi.org/10.1111/j.1466-8238.2007.00316.x>
- Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, 35(1), 1–3. <https://doi.org/10.1111/j.1600-0587.2011.07338.x>
- Seoane, J., Laiolo, P., & Obeso, J. R. (2017). Abundance leads to more species, particularly in complex habitats: A test of the increased population size hypotheses in bird communities. *Journal of Biogeography*, 44(3), 556–566. <https://doi.org/10.1111/jbi.12877>
- Smith, M. A., Hallwachs, W., & Janzen, D. H. (2014). Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography*, 37(8), 720–731. <https://doi.org/10.1111/j.1600-0587.2013.00631.x>
- Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist*, 152(4), 510–529. <https://doi.org/10.1086/286187>
- Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, 21(6), 920–937. <https://doi.org/10.1111/ele.12941>
- Sundqvist, M. K., Sanders, N. J., & Wardle, D. A. (2013). Community and ecosystem responses to elevational gradients: Processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics*, 44, 261–280. <https://doi.org/10.1146/annurev-ecolsys-110512-135750>
- Swenson, N. G. (2014). *Functional and phylogenetic ecology in R* (pp. 64–75). New York, NY: Springer.
- Szewczyk, T., & McCain, C. M. (2016). A systematic review of global drivers of ant elevational diversity. *PLoS One*, 11(5), <https://doi.org/10.1371/journal.pone.0155404>
- R Core Team. (2019). A language and environment for statistical computing. R Foundation for Statistical Computing, 2. Retrieved from <http://www.r-project.org>
- Tello, J. S., Myers, J. A., Macía, M. J., Fuentes, A. F., Cayola, L., Arellano, G., Loza, M. I., Torrez, V., Cornejo, M., Miranda, T. B., & Jørgensen, P. M. (2015). Elevational gradients in β -diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS ONE*, 10(3), <https://doi.org/10.1371/journal.pone.0121458>
- Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33(1), 2–22. <https://doi.org/10.1111/j.1600-0587.2009.05880.x>
- Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of Western Amazonian forests. *Science*, 299(5604), 241–244. <https://doi.org/10.1126/science.1078037>
- Vavrek, M. J. (2011). fossil: Palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica*, 14(1).
- Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S. J., & Hao, Z. (2011). Spatial patterns of tree species richness in two temperate forests. *Journal of Ecology*, 99(6), 1382–1393. <https://doi.org/10.1111/j.1365-2745.2011.01857.x>
- Warren, R. J., & Chick, L. (2013). Upward ant distribution shift corresponds with minimum, not maximum, temperature tolerance. *Global Change Biology*, 19(7), 2082–2088. <https://doi.org/10.1111/gcb.12169>
- Wepfer, P. H., Guénard, B., & Economo, E. P. (2016). Influences of climate and historical land connectivity on ant beta diversity in East Asia. *Journal of Biogeography*, 43(12), 2311–2321. <https://doi.org/10.1111/jbi.12762>
- Willmer, P. (1983). Thermal constraints on activity patterns in nectar-feeding insects. *Ecological Entomology*, 8(4), 455–469. <https://doi.org/10.1111/j.1365-2311.1983.tb00524.x>
- Zhou, J., Deng, Y. E., Shen, L., Wen, C., Yan, Q., Ning, D., Qin, Y., Xue, K., Wu, L., He, Z., Voordeckers, J. W., Nostrand, J. D. V., Buzzard, V., Michaletz, S. T., Enquist, B. J., Weiser, M. D., Kaspari, M., Waide, R., Yang, Y., & Brown, J. H. (2016). Temperature mediates continental-scale diversity of microbes in forest soils. *Nature Communications*, 7, <https://doi.org/10.1038/ncomms12083>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Statistics for biology and health, mixed effects models and extensions in ecology with R. In *Genetics*, <https://doi.org/10.1007/978-0-387-87458-6>

BIOSKETCH

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SUPPORTING INFORMATION

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

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