

Phylogenetic α - and β -Diversities Jointly Reveal Leaf-Litter Ant Community Assembly Mechanisms Along a Tropical Elevational Gradient

Gibran Renoy Pérez-Toledo

Instituto de Ecología, A. C., Red de Ecología Funcional.

Fabrizio Villalobos

Instituto de Ecología, A.C., Red de Biología Evolutiva

Rogério R. Silva

Museu Paraense Emílio Goeldi, Coordenação de Ciências da Terra e Ecologia

Claudia E. Moreno

Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo

Marcio Pie

Department of Biology, Edge Hill University, Ormskirk, Lancashire

Jorge. E. Valenzuela-González (✉ jorge.valenzuela@inecol.mx)

Instituto de Ecología, A. C., Red de Ecología Funcional.

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Abstract

Despite the long-standing interest in the organization of ant communities across elevational gradients, few studies have incorporated the evolutionary information to understand the historical processes that underlay such patterns. Through the evaluation of phylogenetic α and β -diversity, we analyzed the structure of leaf-litter ant communities along the Cofre de Perote mountain in Mexico and inferred its putative driving forces. Lowland and some highland sites showed phylogenetic clustering, whereas intermediate elevations and the highest site presented phylogenetic overdispersion. We infer that strong environmental constraints found at the bottom and the top elevations are favoring closely-related species to prevail at those elevations. Conversely, more benign conditions at intermediate elevations suggest interspecific interactions being more important in these environments. Total phylogenetic dissimilarity was driven by the turnover component, indicating that the turnover of ant species along the mountain is actually shifts of lineages adapted to particular locations resembling their ancestral niche. The greater phylogenetic dissimilarity between communities was related to greater temperature distances probably due to narrow thermal tolerances inherited to several ant lineages that evolved in more stable conditions. Our results suggest that the interplay between environmental filtering, interspecific competition and habitat specialization plays an important role in the assembly of leaf-litter ant communities along elevational gradients.

Introduction

Elucidating the mechanisms underlying the natural variation in species richness and composition across local communities has challenged ecologists for more than a century¹. Since the development of community phylogenetics, a vast number of studies have used the phylogenetic approach to disentangle the relative importance of both deterministic and stochastic processes involved in the coexistence of species within a community^{2,3}. The cornerstone of the phylogenetic approach is the assumption of phylogenetic niche conservatism, i.e., the tendency of species to conserve their niches over evolutionary history, with closely related species being ecologically more similar to each other than to distantly related species⁴. Based on this assumption, phylogenetically clustered communities (i.e., co-occurrence of closely related species) are typically thought to result from environmental filtering, where taxa are filtered by constraints imposed by the environment⁵. However, modern coexistence theory considers that phylogenetic clustering could also be driven by competitive exclusion where entire clades have higher competitive abilities leading to an exclusion of other lineages⁶. Conversely, phylogenetically overdispersed communities (i.e., co-occurrence of distantly related species) are thought to be structured by competition, which tends to select species with different ecological traits and thus low niche overlap⁷. Finally, a lack of phylogenetic structure suggests a predominance of neutral processes⁸ or the counteraction of both habitat filtering and interspecific competition⁹. Since these mechanisms can act simultaneously within communities¹⁰, the critical question is no longer which mechanism structures communities but rather which one plays a dominant role in community assembly along environmental gradients¹¹.

Community ecologists have expanded the community phylogenetics framework from α -(richness) to β -diversity (composition) patterns (phylogenetic beta diversity, hereafter PBD) into ecological contexts¹²⁻¹⁴. PBD explicitly adds phylogenetic information to evaluate how evolutionary relationships of component lineages change between communities or biomes across space¹². Furthermore, PBD links local processes (e.g. biotic interactions or environmental filtering) to more regional evolutionary processes (e.g. trait evolution, speciation and dispersal), hence providing further information about how current or historical environmental factors influence the variation in species compositions of communities across space^{12,15}. Environmental filtering and dispersal limitation have been suggested to largely determine patterns of community composition^{16,17}. Habitat filtering is expected to limit community members to habitats that resembles the ancestral niche where its lineage originated, i.e., habitat specialization¹⁸, resulting in closely-related species occupying similar portions of regional-scale climatic gradients. On the other hand, the dispersal limitation processes predicts that community dissimilarity between sites will be correlated to geographical distances separating those sites, regardless of the environmental gradients¹⁶. Since environmental filtering and dispersal limitation are not mutually exclusive, a greater variation in community dissimilarity predicted by geography reflects a greater importance of dispersal limitation, whereas greater variation explained by environmental distances indicates that habitat filtering is the structuring force¹⁹.

Recent methodological advances have improved our understanding of the origin and maintenance of geographic patterns of PBD through its decomposition into two antithetic components that account for the replacement of lineages between sites (the turnover-resultant component) and differences in the phylogenetic diversity between nested assemblages (the nestedness-resultant component;^{20,21}). Although the turnover and nestedness components both contribute to total dissimilarity, their relative importance depends on the processes structuring communities. For instance, if environmental conditions vary across space, and species are adapted to particular conditions, the turnover component of PBD is more likely to shape community composition under environmental filtering. Conversely, nestedness tends to be a more common component due to a number of processes as selective colonization, selective extinction, nestedness of habitats or passive sampling²¹. Analyzing the relationship between PBD (and its components) with climatic and geographic variables can provide a better understanding of community assembly along environmental gradients²².

Several studies have placed the phylogenetic α - and β -diversity into ecological and biogeographic contexts, such as the latitudinal pattern of phylogenetic diversity²³, the phylogenetic modification of native communities under species invasions²⁴ and the community structure along elevational gradients²⁵⁻²⁷. Particularly, ecological gradients occurring in mountains have successfully served to test community assembly processes given the strong dependence of species elevational distributions to the environmental conditions found at particular elevations^{28,29}. Particularly for thermophilic taxa, such as ants, deterministic processes related with both temperature³⁰⁻³² and precipitation^{26,33} have been shown to influence community membership at elevational gradients. In tropical mountains, as elevation

increases, temperature tends to decrease whereas precipitation increases³⁴ and, as a result, the abiotic conditions (cold and wet) at high-elevation sites become physiologically stressful for a majority of ant species in comparison with relative benign environments (warm and humid) at low elevations. This spatial structure created by the interplay of temperature and precipitation has been used to explain the changing phylogenetic structure from overdispersed ant communities at low elevations towards clustered communities at higher elevations²⁵⁻²⁷. Despite these findings, the relative importance of deterministic and stochastic processes driving ant community organization under the phylogenetic perspective is still incipient, particularly when tropical regions are considered.

In this study, we measured the phylogenetic α - and β -diversity to infer whether deterministic and stochastic processes are driving the organization of leaf-litter ant communities occurring along a tropical elevational gradient in Mexico. Leaf-litter ants have numerous attributes that make them an ideal system to explore assembly mechanisms. For instance, they exhibit high levels of local co-occurrence; with up to 35 species co-existing in only one square meter³⁵. Further, ant distributions are highly constrained by local and regional climate^{36,37}. They display a wide variety of both individual³⁸ and colony-level³⁹ thermoregulatory strategies to cope with cold and hot conditions. Lastly, molecular phylogenetic analyses of the major ant lineages are providing a stable framework to understand the evolutionary relationships of the group⁴⁰⁻⁴². Hinged on the assumption that ant species have retained their traits along their evolutionary history (i.e., phylogenetic niche conservatism^{23,43}), we expect that (1) ant communities inhabiting in more benign and stable habitats (warm and humid habitats) found at low elevations will show phylogenetic overdispersion since negative interspecific interactions might be more intense in these environments. Conversely, cold and wet conditions at high elevations would lead to phylogenetically clustered communities considering that only closely related species of a subset of lineages possess the physiological traits that allow them to persist in the harsh conditions present at those elevations. In terms of PBD, it is expected that (2) lineages would have high habitat specialization to the conditions where they originated and thus drastic environmental changes along the elevational gradient would lead to high lineage replacement. This will result in a greater importance of turnover on total phylogenetic dissimilarity along the elevational gradient. Finally, we can expect that (3) pairwise dissimilarity values for PBD and their components would be mainly explained by environmental filtering (i.e., climatic distances), following their ancestral climatic affinities rather than dispersal limitation.

Results

α -diversity

Overall, the tendency of SES.PD, SES.MPD and SES.MNTD was negative values at low and some high elevational sites, whereas positive values at mid-elevations and the highest site. Considering the SES.PD, this means that three intermediate-elevational sites (1000, 1500 and 3000) present high evolutionary history, whereas four sites (0, 500, 2000, 2500) have low phylogenetic diversity (Fig. 1a). This same trend was observed for the SES.MNTD (Fig. 1b), indicating that sites containing higher evolutionary history are

related to more distantly species (overdispersion), whereas sites with lower evolutionary history are inhabited by more closely-related species (clustering). For the SES.MPD, overdispersion was observed at three mid-elevation sites (1000, 1500, 2000) and the highest site (3000), whilst the rest of the sites (0, 500 and 2500) presented a clustering pattern (Fig. 1c). All those trends were consistent across the 1000 phylogenetic trees and remained the same when the MCC tree was used (Fig. 1). All these α -diversity trends were supported by a variable number of trees being statistically different from a null expectation at $\alpha = 0.05$, but most common at 2500 m for SES.PD and SES.MPD (Supplementary Table S4).

When we assessed the contribution of climatic variables on explaining the alpha metrics patterns, the additive effect of both $PC1_{\text{Temperature}}$ and $PC1_{\text{Precipitation}}$ explained a larger amount of variation in comparison with their individual effects (Table 1; Supplementary Fig. S2). Moreover, the additive model was considered the best statistically supported model in explaining SES.PD, SES.MPD and SES.MNTD patterns. However, in some instances, the individual effect of $PC1_{\text{Temperature}}$ and $PC1_{\text{Precipitation}}$ resulted as equally probable models (Table 1, Supplementary Fig. S4), suggesting that the main effect of both variables is biologically important, yet its combined effect refines model performance. Further, the general trend for both linear and multiple regressions was a positive relationship ($\beta > 0$) between $PC1_{\text{Temperature}}$ with all phylogenetic α -metrics, whereas $PC1_{\text{Precipitation}}$ related in a negative way ($\beta < 0$; Table 1).

β -diversity

We found that total phylogenetic dissimilarity derived from multiple-site calculations exhibited considerable high values ($PBD_{\text{multi.sor}}=0.73\pm 0.006$). Decomposition demonstrated that the turnover component ($PBD_{\text{multi.sim}}=0.52\pm 0.02$) had a greater contribution to total dissimilarity compared with the relatively low values of the nestedness-resultant component ($PBD_{\text{multi.nes}}=0.21\pm 0.01$). These patterns remained when the MCC tree was used (Supplementary Fig. S5). When assessing the patterns under the adjacent approach, we observed that the total dissimilarity ($PBD_{\text{adj.sor}}$) increased with elevation. For instance, lower values (<0.5) were observed at lowland sites (< 2000), whereas higher values (>0.5) at the highlands (>2000 ; Fig. 2a). In most cases, the β_{ratio} calculation displayed values higher than 0.5 indicating that total dissimilarity is determined dominantly by turnover. A deviation of this general trend was observed at 1500-2000 sites where the nestedness ($PBD_{\text{adj.nes}}$) dominated over the turnover component (Fig. 2b). Pairwise patterns of PBD showed that an increase of elevational distance results in greater total dissimilarity ($PBD_{\text{pair.sor}}$) and is produced by a mixture of turnover ($PBD_{\text{pair.sim}}$) and nestedness ($PBD_{\text{pair.nes}}$) values operating between different elevational ranges (Supplementary Fig. S6).

According to GDM analysis, the full model explained a considerably high variation of PBD pairwise patterns. For instance, 79.2% of deviance was explained for total dissimilarity ($PBD_{\text{pair.sor}}$), followed by 49.9% for nestedness ($PBD_{\text{pair.nes}}$) and in minor instance the turnover ($PBD_{\text{pair.sim}}$) with 26.4%. All models presented statistical significance for total dissimilarity, whereas turnover and nestedness were poorly supported with only three and seventy-two (out of 1,000) statistically significant models respectively (Table 2). These results are consistent when the MCC tree was used in the analysis (Supplementary Table

S4). In all PBD components, the variance explained by the $PC1_{\text{Temperature}}$ was much larger than explained by geographic distance or $PC1_{\text{Precipitation}}$, indicating that thermal affinity has played a much greater role than affinity to precipitation and dispersal limitation in shaping the phylogenetic composition of ant assemblages across our study area (Table 2).

Table 1

Summary statistics (mean \pm SD) of the coefficient of determination (R^2), bayesian information criterion (BIC) and beta coefficient (β) extracted from the set of linear models (1000 per alpha metric) adjusted independently against the standardized effect size of phylogenetic diversity (SES.PD), mean pairwise distance (SES.MPD) and mean nearest taxon distance (SES.MNTD) against the principal component of temperature ($PC1_{\text{Temperature}}$), precipitation ($PC1_{\text{Precipitation}}$) and the additive effect of both factors ($PC1_{\text{Temp}} + PC1_{\text{Prec}}$). Equally probable models were considered if the difference in BIC (Δ BIC) between the focal model and the model with the lowest BIC were < 2 . Value obtained from the MCC tree is expressed in the bold number within parenthesis.

	R^2	Δ BIC	β
SES.PD			
$PC1_{\text{Temperature}}$	0.06 \pm 0.09 – (0.31)	0.76 \pm 0.66 – (1.51)	0.04 \pm 0.10 – (0.26)
$PC1_{\text{Precipitation}}$	0.12 \pm 0.08 – (0.30)	0.20 \pm 0.73 – (1.79)	-0.02 \pm 0.07 – (-0.32)
$PC1_{\text{Temp}} + PC1_{\text{Prec}}$	0.20 \pm 0.15 – (0.58)	1.50 \pm 0.59 – (0.00)	$PC1_{\text{Temp}}$: 0.03 \pm 0.09 – (0.24) , $PC1_{\text{Prec}}$: -0.02 \pm 0.06 – (-0.31)
SES.MPD			
$PC1_{\text{Temperature}}$	0.009 \pm 0.008 – (0.01)	4.9 \pm 1.0 – (7.35)	-0.03 \pm 0.03 – (0.03)
$PC1_{\text{Precipitation}}$	0.50 \pm 0.06 – (0.65)	0 \pm 0 – (0.00)	-0.38 \pm 0.01 – (-0.35)
$PC1_{\text{Temp}} + PC1_{\text{Prec}}$	0.51 \pm 0.05 – (0.65)	1.74 \pm 0.16 – (1.83)	$PC1_{\text{Temp}}$: -0.04 \pm 0.03 – (0.01) , $PC1_{\text{Prec}}$: -0.038 \pm 0.02 – (-0.35)
SES.MNTD			
$PC1_{\text{Temperature}}$	0.04 \pm 0.07 – (0.12)	0.08 \pm 0.18 – (0.00)	0.02 \pm 0.08 – (0.15)
$PC1_{\text{Precipitation}}$	0.02 \pm 0.03 – (0.03)	0.27 \pm 0.69 – (0.79)	0.01 \pm 0.08 – (-0.10)
$PC1_{\text{Temp}} + PC1_{\text{Prec}}$	0.07 \pm 0.09 – (0.15)	1.84 \pm 0.17 – (1.77)	$PC1_{\text{Temp}}$: 0.02 \pm 0.08 – (0.14) , $PC1_{\text{Prec}}$: 0.01 \pm -0.08 – (-0.09)

Table 2

Summaries of the generalized dissimilarity models adjusted between total phylogenetic dissimilarity ($PBD_{pair.sor}$), the turnover ($PBD_{pair.sim}$) and the nestedness-resultant component ($PBD_{pair.nes}$) against the geographical and climate predictors. All values (except p-value ratio) are represented by the mean of the 1000 phylogenetic trees (\pm SD). P-value ratio is the proportion of significant models ($p < 0.05$) out of the 1000 phylogenetic trees.

	$PBD_{pair.sor}$	$PBD_{pair.sim}$	$PBD_{pair.nes}$
Model deviance	0.5 (\pm 0.06)	1.52 (\pm 0.2)	1.2 (\pm 0.15)
Deviance explained (%)	79.2 (\pm 2.5)	26.3 (\pm 7.6)	49.9 (\pm 5.1)
P-value ratio	1	0.003	0.072
Predictors	Predictor impact		
Geography	2.2 (\pm 0.84)	6.6 (\pm 8.3)	0.28 (\pm 0.5)
PC1 _{Temperature}	59.2 (\pm 3.07)	48.6 (\pm 12.4)	66.0 (\pm 9.0)
PC1 _{Precipitation}	23.2 (\pm 3.8)	20.7 (\pm 15.8)	18.3 (\pm 6.5)

Discussion

Over the last two decades since Webb et al.,⁷ developed the baseline of community phylogenetics, several studies in this field have been conducted to enhance our understanding of how deterministic and stochastic processes operate to assemble communities across space. In this study, we analyzed the phylogenetic α - and β - diversity to unravel the assembly of leaf-litter ant communities along a tropical mountain in Mexico. Overall, lowland and some highland sites contained communities with low evolutionary history and composed by closely-related species (phylogenetic clustering), whereas communities at intermediate elevations and at the highest site presented high evolutionary history and were composed by distantly-related species (phylogenetic overdispersion). All these patterns were highly supported not only across all the α -phylogenetic metrics (PD, MPD, MNTD) but also across 1000 hypothetical trees and the maximum clade credibility tree, thus patterns remained regardless of phylogenetic uncertainty. We found a positive relationship between all metrics and temperature, whereas a negative relationship with precipitation. Both the main and additive effect of precipitation with temperature were equally supported, yet the additive effect explained higher variation of phylogenetic α -diversity patterns for all metrics. Phylogenetic total dissimilarity was mainly driven by turnover, thus highland lineages are not subsets of lowland assemblages but instead they are communities with different lineage compositions. Finally, the temperature differences between sites emerged as the most important driver of total dissimilarity, turnover and nestedness components. In sum, our findings provide additional evidence that evolutionary processes mediated by climate-related (deterministic) mechanisms are strongly involved in the assembly of ant communities along elevational gradients.

Ant communities at the lowland and highland sites (except for the 3000 site) displayed phylogenetic clustering. Such a pattern has been typically associated to the gradual loss of ant lineages due to abiotic constraints (i.e. environmental filtering) where only a subset of species possesses the necessary adaptations to persist under stressful conditions²⁵⁻²⁷. In our study area, the drastic reduction of temperature coupled with higher precipitation with increasing elevation may act as a strong filter on total diversity and the members of the regional species pool, such that the resultant high-elevation community would be phylogenetically clustered with taxa possessing wet and cold-resistant traits for dealing with this stress. Here, we found that >50% of species inhabiting phylogenetically clustered communities at high elevations belong mainly to two cold-specialist genus: *Stenamma* and *Temnothorax* (Supplementary Table S1). Strategies such as the hibernation of the ant colony during the winter season in *Stenamma* species⁴⁴ or the production of glycerol and another antifreeze substances in *Temnothorax*⁴⁵ may account as likely explanations for the ant persistence in this high, cold environments. Conversely, phylogenetic clustering at lowlands have never been reported for elevational ant studies. The reasons for this deviation require further study, but we propose two likely explanations. First, in comparison with the upper part of the mountain, lowlands of the Cofre de Perote are characterized by high temperatures and a marked precipitation seasonality. This means that all (or almost all) precipitation is concentrated in a relatively short time (3-months), leaving a prolonged drought season for the rest of the year. This drought period interacting with high temperatures may drastically prone ant species to desiccation⁴⁶, and as a result increase the importance of environmental filtering at those communities^{47,48}. The second explanation includes the competition displacement, in which native ants are locally excluded by tramp and alien ant species. The competition displacement may lead to phylogenetic clustering since it is expected that only closely-related taxa of the introduced species can subsist under these biological invasions²⁴. In fact, an observable characteristic of our lowland communities is the high dominance of three tramp and alien species: *Hypoponera opaciceps*, *Solenopsis geminata* and *Wasmannia auropunctata* (Supplementary Table S1). The well-known effects of these ant species in disrupting and displacing native ants⁴⁹⁻⁵¹ suggest that patterns of phylogenetic clustering observed at lowland communities may not be driven by contemporary climate alone, but is also a result of the invasion of these ant species.

We found intermediate elevations constituted by phylogenetically overdispersed communities. Typically, phylogenetic overdispersion is interpreted as evidence of interspecific competition since a long history of competitive interactions should cause evolutionary divergence in species niches⁵². Interspecific competition among ant species is intense and often involved in the configuration of ant communities⁵³, yet evidence suggest that the importance of competition may be higher in relatively benign, stable environments where abiotically stressful factors are absent^{27,54}. Intermediate elevations at Cofre de Perote reflect these conditions considering that at these elevations temperature is not too low to freeze available water nor too high to evaporate it (Supplementary Fig. S1). Besides, productivity, an ecological proxy of the amount of niches and resource heterogeneity in an ecosystem⁵⁵, is expected to peak at this point since productivity is limited by drought at lowlands and cold temperatures at highlands. Thus, if competition is the driving mechanism at these intermediate elevations, we should observed communities

containing a series of species with different evolutionary histories⁵⁶. Indeed, clades are well represented in these communities with seventeen tribes (out of eighteen) containing a mixture of species from both tropical and temperate origins distributed at low and high elevations respectively.

Whilst competitive interaction is congruent as a structuring force in phylogenetically overdispersed communities at more benign habitats found at intermediate elevations, it is unlikely that this hypothesis stands for the isolated overdispersed community at the highest stressful elevation (i.e., 3000 m). Particularly, we observed that the ant community at this elevation was composed by eight species, each one belonging to different genera dispersed across the phylogeny. Some studies have posited that geographic isolation for historical climatic variations has played a key role in the distribution of species at high-elevation habitats⁵⁷. Thus, the presence of species with contrasting evolutionary histories may suggest that communities at 3000 m could be acting as refugia, maintaining relict lineages that migrated from distant regions with temperate climate or were more widespread in the past but became geographically isolated as a consequence of habitat contractions in the last glaciations⁵⁸.

The complementary use of the multiple-site, adjacent, and pairwise approaches, coupled with the decomposition of total dissimilarity into the turnover and nestedness components, significantly contributed to unveil the underlying mechanisms influencing dissimilarity variation. For instance, all approaches showed a high dominance of the turnover component for total dissimilarity. This result indicates that the turnover of species is actually a turnover of entire lineages or clades¹². Besides, it suggests that ant lineages are established at specific elevations (habitat specialization) corresponding to the climatic conditions where they originated¹⁸. A deeper examination of the distribution of large clades along the Cofre de Perote may support this assumption. On one hand, several ant genera within the tribes Attini (e.g. *Octostruma*, *Pheidole* and *Strumigenys*) and Solenopsidini (e.g., *Solenopsis*, *Monomorium*, *Megalomyrmex*) belonging to the subfamily Myrmicinae are highly restricted to the warm conditions found at lowlands probably resembling their neotropical origin^{42,59}. On the other hand, middle elevations are highly dominated by *Adelomyrmex* species. This genus is considered as pantropically distributed but its dominance in cloud forests, such as those predominating in our sampled intermediate elevations, is well documented^{60,61}. Finally, lineages with more temperate origins such as *Stenammas*⁶² and *Temnothorax*⁶³ show a tendency to specialize at more high elevations and rarely spreading to lowlands (Supplementary Table S1). Taken together, our results bring evidence that habitat specialization is not only key driver of compositional dissimilarity of species (i.e.,^{22,25,32}), but also an important processes scaling up to entire lineages (i.e. phylogenetic niche conservatism), in such a way that evolutionary history strongly constraints the elevational distribution of ant species²⁵.

Despite adjacent turnover component having a preponderant impact on total dissimilarity, we observed a breakpoint between 1500 and 2000 where the phylogenetic nestedness prevailed over turnover. The possible reason for this dominant nestedness in PBD is that selective extinction, operating through environmental filtering, is playing an important role in shaping the patterns of phylogenetic dissimilarity at this particular elevation²¹. Because environmental filtering favors certain traits over others, a high

number of ant lineages are lost as a result of the temperature decrease and humidity increase occurring from 1500 to 2000 site⁶⁴. Indeed, we noticed that the distribution of certain ant species was restricted to low and intermediate elevations (Supplementary Table S2). Particularly, several well-known neotropical species belonging to *Brachymyrmex*, *Europhalothrix* and *Strumigenys* genera completely disappear at 2000 site (or higher elevation sites; Supplementary Table S1). These ant genera are mainly restricted to more tropical environments found in lowland areas, with one or few species within the same clade capable to cross to high elevations⁶¹. Therefore, we speculate that this point of the mountain can serve to broadly separate two well-distinguished ant fauna: low-montane fauna, distributed from sea level to below the 2000 m of elevation, and high-montane fauna habiting at 2000 elevation and greater.

We show here that phylogenetic total dissimilarity was best explained by temperature distance among pairwise sites regardless of the precipitation or geographical distance among them. More specifically, the further two elevational sites are in terms of their temperature, higher total dissimilarity between them is expected in comparison with two sites sharing similar temperatures. This result agrees with those found by Liu et al.,²⁵ who documented that PBD in ant composition dissimilarity of the Hengduan mountain was mainly driven by climatic distance (in which a set of temperature-related variables were included). This high importance of temperature distance shaping PBD may be explained by the climate variability hypothesis proposed by Janzen⁶⁵. The climate variability hypothesis proposes that species exposed to variable climates (such that occurring at higher elevations) evolve broad thermal tolerances, allowing those species to traverse climatic gradients found across elevations, resulting in a wider geographic distribution than thermal specialists from stable climates (generally found at lower elevations). Therefore, we should expect lineages which originated in more tropical regions (e.g., neotropical) to be characterized by narrower thermal tolerances resulting in more restricted distribution in comparison with lineages originated in more variable climates (e.g., nearctic). This consistent effect of thermal adaptations constraining not only species distributions^{32,66} but those of entire lineages support that climatic niches are conserved over evolutionary history of the ant clade (^{25,43}). Taken together, these results highlight the role of species sorting processes⁶⁷, where the phylogenetic composition is mainly driven by deterministic process (i.e. habitat filtering) in response to local environmental conditions rather than stochastic processes (i.e. dispersal limitation). The simultaneous examination of the phylogenetic α - and β - diversity (and its components of turnover and nestedness) enhances our understanding of the relative importance of deterministic and stochastic processes in structuring patterns of ant diversity.

Here, we showed that environmental filtering, interspecific competition and habitat specialization jointly structure the leaf-litter ant communities along the Cofre de Perote. These results highlight the importance of deterministic (niche-based) processes over stochastic processes. Further, our results provide insights about phylogenetic niche conservatism since some ant lineages have retained the necessary traits to colonize harsher environments (the colder habitats at the summit). Additionally, the large evolutionary history accumulated in the lineages inhabiting each elevational site along with the remarkable rates of phylogenetic turnover contributing to total phylogenetic dissimilarity confirms the importance of mountains not only as centers of species diversity but crucial reservoirs of unique evolutionary

history^{68,69}. Altogether, this work builds up on the theory that not only contemporary but historical factors also influence the structure of leaf-litter ant assemblages along environmental gradients and this can be detected by integrating α - and β -phylogenetic diversities.

Methods

Study area and ant sampling

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 meters of altitude (Fig. 3). Regardless of the geographical distance, all sites were systematically separated with an elevational difference of 500 meters 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 discrete units (i.e. 0, 600, 1000, 1500, 2100, 2500, 3100, 3500 m).

We obtained 320 m² leaf-litter samples in 8 study sites (see ³² for a complete description of sampling design). 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 and identified at the species level or assigned to a morphospecies number.

Ethics approvals

All applicable international, national and institutional guidelines for the collection of ant specimens and leaf-litter material were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the studies were conducted. The material was collected in accordance with the permits issued by SEMARNAT (license number: FAUT-0312).

Phylogenetic tree constructions

Ideally, one would use a complete, species-level phylogeny of all ant species present in your study area to calculate phylogenetic diversity, yet our current understanding of ant relationships is still limited. As an alternative, we built a genus-level phylogeny based on the tree by Moreau & Bell⁷⁰, but using the phylogenetic relationships and divergence times within Myrmicinae from Ward⁴². This phylogeny was then pruned to keep only a single species per genus to generate a genus-level phylogeny. To maximize taxonomic coverage, we replaced genera that were missing from those studies by closely-related lineages that were not present in our dataset using other phylogenetic studies⁷¹⁻⁷³. We then used the list of species (Supplementary Table S1) in our dataset to simulate a species-level phylogeny in which the

relationships within genera were obtained from a Yule (pure-birth) process using the *genus.to.species.tree* function in the “phytools” package⁷⁴. A total of 1000 simulated trees were obtained to account for phylogenetic uncertainty [see ⁷⁵ and ⁷⁶ for similar approach]. Additionally, we constructed a maximum clade credibility tree (hereafter MCC tree) which was used to summarize the uncertainty of the 1000 simulated trees. The MCC tree was constructed from the sample of the 1000 trees with the *maxCladeCred* function incorporated in the “ape” package⁷⁷. Both the 1000 hypothetical trees and the MCC tree were used in downstream analyses (Supplementary Fig. S1).

Alpha and beta phylogenetic diversity

Phylogenetic alpha diversity patterns of leaf-litter ant assemblages at each site was estimated using three metrics: Faith’s PD⁷⁸, mean pairwise distance (MPD) and mean neighbor taxon distance (MNTD). PD measures the total phylogenetic branch length that joins the basal node to the tips of all the species in the sample⁷⁸, and is used as a measure of absolute phylogenetic diversity⁷⁹. MPD and MNTD are two phylogenetic divergence metrics^{7,80}, with the former being an estimate of the average phylogenetic relatedness between all possible pairs of taxa in a local community, whereas the latter is an estimate of the mean phylogenetic relatedness between each taxon in a local community and its nearest relatives.

To investigate which processes may be influencing the patterns of phylogenetic alpha diversity, we calculated the standardized effect sizes (SES) for each α -diversity metric (i.e., SES.PD, SES.MPD, SES.MNTD). SES values were calculated by taking the difference between the observed value of PD, MPD and MNTD and their corresponding mean random values derived from null communities, then dividing these differences by the standard deviation across randomizations⁸¹. The null communities were generated by randomizing the community data matrix using the “independentswap” algorithm with 1000 iterations. Positive and negative SES.PD values indicate species in a community accumulated more or less evolutionary history than expected by null communities, respectively⁸². Whereas for MPD and MNTD, positive SES values suggest phylogenetic overdispersion, whereas clustering is inferred by negative values⁷. Statistical significance is inferred if SES values are greater than 1.96 or less than -1.96. All these analyses were conducted using the *ses.pd*, *ses.mpd* and *ses.mntd* functions incorporated in the “picante” package⁸³ of the R software⁸⁴.

We investigated the patterns of β -diversity through three complementary approaches: (i) the multiple-site approach (PBD_{multi}), used to summarize in one value the overall dissimilarity in the mountain, (ii) the adjacent approach (PBD_{adj}), used to investigate the unidirectional β -diversity variation focusing only on adjacent sites towards the summit, and (iii) the pairwise approach (PBD_{pair}), used to investigate how β -diversity patterns were related to the environmental and geographical distance between all pairwise sites. For all approaches, we calculated the total dissimilarity through the PhyloSor distance (multiple-site: $PBD_{\text{multi.sor}}$, adjacent: $PBD_{\text{adj.sor}}$; pairwise: $PBD_{\text{pair.sor}}$) and further decomposed it into the turnover (multiple-site: $PBD_{\text{multi.sim}}$, adjacent: $PBD_{\text{adj.sim}}$; pairwise: $PBD_{\text{pair.sim}}$) and the nestedness (multiple-site: $PBD_{\text{multi.nes}}$, adjacent: $PBD_{\text{adj.nes}}$; pairwise: $PBD_{\text{pair.nes}}$) components. Under the phylogenetic

framework, total dissimilarity captures the proportion of shared and exclusive branch lengths among assemblages, turnover measures 'true' lineage turnover and nestedness considers the differences in Faith's PD between assemblages²¹. Multiple-site calculations were obtained using the *multi.phylo* function, whereas pairwise and adjacent values with the *phylo.beta.pair* function incorporated in the "betapart" package⁸⁵ of the R software⁸⁴.

To assess the relative contribution of the spatial turnover component to the total dissimilarity between adjacent sites, we calculated the ratio of turnover over total dissimilarity (hereafter β_{ratio}) following Dobrovolski et al.⁸⁶: $\text{PBDadj.sim} / \text{PBDadj.sor}$. Thus, $\beta_{\text{ratio}} > 0.5$ indicates that total dissimilarity is determined dominantly by the turnover, and $\beta_{\text{ratio}} < 0.5$ indicates nestedness is the dominant component^{86,87}. We did not conduct such analyses for the pairwise approach since the raw-unconverted data is necessary for GDM analyses (see statistical analyses section).

Climatic predictors

To evaluate whether local climate may account for the observed phylogenetic diversity patterns, we extracted the 19 climatic variables from the bioclimatic raster available for Mexico at 3 arc-second resolution (~90 m;⁸⁸) coincident with the coordinates of our forty sampling points (Supplementary Fig. S1). For practical purposes, each site was characterized by averaging these forty values. We first divided those 19 variables into temperature- and precipitation-related subsets. Then, we used separate principal components analyses (PCA) to generate a synthetic uncorrelated climatic variable that represents the original variables contained in each climatic subset. Before PCA analyses all variables were standardized to remove the unit and were centered (mean=0, SD=1). Since the first principal component accounted for a high variation contained in each subset of temperature (PC1_{Temperature}:85.3%) and precipitation (PC1_{Precipitation}:67.5%), we conducted the consecutive analyses using only these vectors.

The examination of variable loading in each principal component revealed that almost all variables included in the analysis (75% of the total) highly contributed (i.e., large weights) to each first component (Supplementary Table S2). Therefore, any interpretation using PC1_{Temperature} and PC1_{Precipitation} should largely reflect the broad variation in terms of temperature and precipitation occurring along the Cofre de Perote mountain.

Statistical analyses

To evaluate which climatic variables (i.e., temperature and precipitation) better explained the phylogenetic alpha diversity, we implemented simple linear models where the 1000 SES values of each alpha metric (SES.PD, SES.MPD, SES.MNTD) were regressed individually with the first principal component of each climatic subset (PC1_{Temperature} and PC1_{Precipitation}). Simultaneously, we constructed a multiple regression model with the same response variables but now modeled against the additive effect of both climatic factors (PC1_{Temperature} + PC1_{Precipitation}). Normality assumption was checked in the residuals of all the adjusted models using the Shapiro test at $\alpha=0.05$. To avoid spurious interpretation, a second run of

regression models was conducted including only models which met the normality assumption (models syntaxis and number of trees included in final analyses are condensed in Supplementary Table S3).

We selected the best simple or multiple regression model explaining the phylogenetic α -diversity patterns. For this purpose, all linear and multiple regression models were evaluated and the model with the lowest Bayesian Information Criterion (BIC) was chosen as the best model⁸⁹. We selected BIC over the Akaike information criterion (AIC) since BIC is based on the assumption that a true model exists among the set of candidate models⁹⁰. We considered this scenario true since temperature and precipitation (and their interaction) have been documented as the most important predictors of ant diversity (e.g.,^{30,33,61}). We considered a model equally probable to the best fit model if the difference in BIC (Δ BIC) between the focal model and the model with the lowest BIC were < 2 . Further, we extracted the coefficients of determination (R^2) and the slope coefficient (β) to evaluate the proportion of variance explained by each model and the relationship between each phylogenetic alpha metric with the climatic predictors respectively. Regression models and normality tests were conducted through the *lm* and *shapiro.test* functions respectively, whereas model performance was conducted using the *bicTab* function incorporated in the “AICmodavg” package⁹¹. All functions are incorporated in the R project software⁸⁴.

To assess whether environmental filtering (climate distances) or dispersal limitation (geographical distances) better explained pairwise PBD patterns, we used Generalized Dissimilarity Modelling (GDM; ⁹²). GDM uses a nonlinear matrix regression technique for analyzing spatial patterns in compositional dissimilarity, providing fitted I-splines to describe the relationships between a dissimilarity matrix (response) and both climatic and geographical predictors, coupled with the partial deviance explained by each predictor ⁹³. Moreover, GDM standardize variables so they can be directly compared with one another and is highly robust to multicollinearity among predictors⁹². To conduct GDM, we first converted the observed pairwise dissimilarity matrices ($PBD_{pair.sor}$, $PBD_{pair.sim}$, $PBD_{pair.nes}$) into a GDM site-pair table using the *formatsitepair* function setting the type 3 in the “bioFormat” argument. The *gdm* function was used to fit the model which included the climatic variables ($PC1_{Temperature}$ and $PC1_{Precipitation}$) and the geographical coordinates corresponding to the centroid of the total sampling points located at each site. Finally, the function *gdm.varImp* was used to extract the total deviance explained by each model, the significance of the full model and the importance of each predictor. Predictor importance is quantified as the percent change in deviance explained by the full model and the deviance explained by a model fit with that variable permuted⁹⁴. We used 1000 permutations to estimate predictor importance and full model significance. Since this complete procedure was ran across the 1000 matrices of each PDB component, we thus calculated the ratio between the number of significant values ($p < 0.05$) out of the 1000 phylogenetic trees. GDM analyses were conducted using the functions incorporated in the “gdm” package⁹⁴ of the R-project software⁸⁴.

Declarations

Data availability

The taxonomic matrix along with the 1000 simulated trees and the Maximum Clade Credibility tree constructed in each elevational site are available on the Zenodo digital repository (doi: 10.5281/zenodo.5646220).

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Author contributions

G.R.P.-T., J.V.-G and F.V conceived the ideas; G.R.P.-T conducted all statistical analyses assisted by F.V., R.R.S. and C.E.M.; M.P. constructed phylogenetic trees used in all analyses; F.V., R.R.S and C.E.M suggested several methodological improvements. G.R.P.T. led the writing of the manuscript with input from all authors.

Competing Interests Statement

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

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Figures

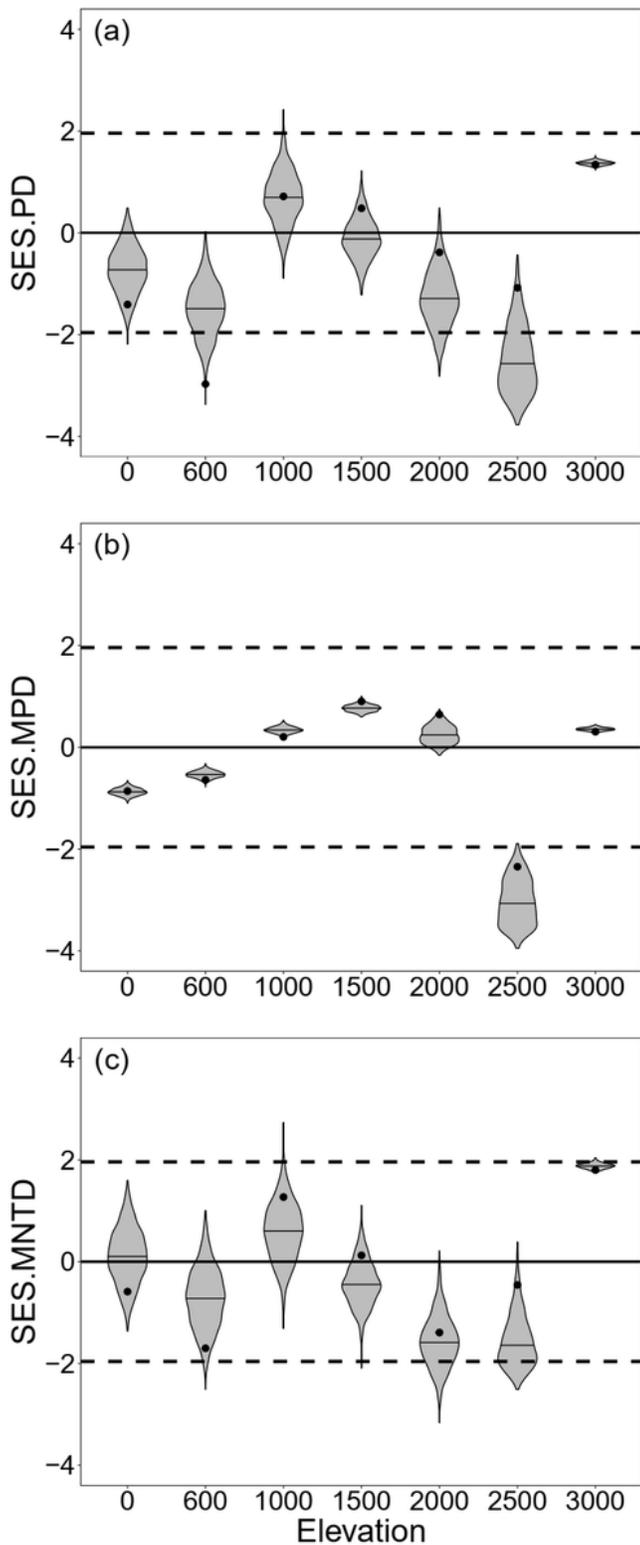


Figure 1

Standardized effect sizes of (a) phylogenetic diversity, PD; (b) mean pairwise distance, MPD; and (c) mean nearest taxon distance, MNTD of the leaf-litter ant assemblages at seven elevations along the Cofre de Perote mountain. The inner horizontal line in each violin represents the mean of the 1000 SES values per elevation. Black point represents the SES values from the MCC tree. Statistical support is inferred in values laying on areas beyond 1.96 and -1.96.

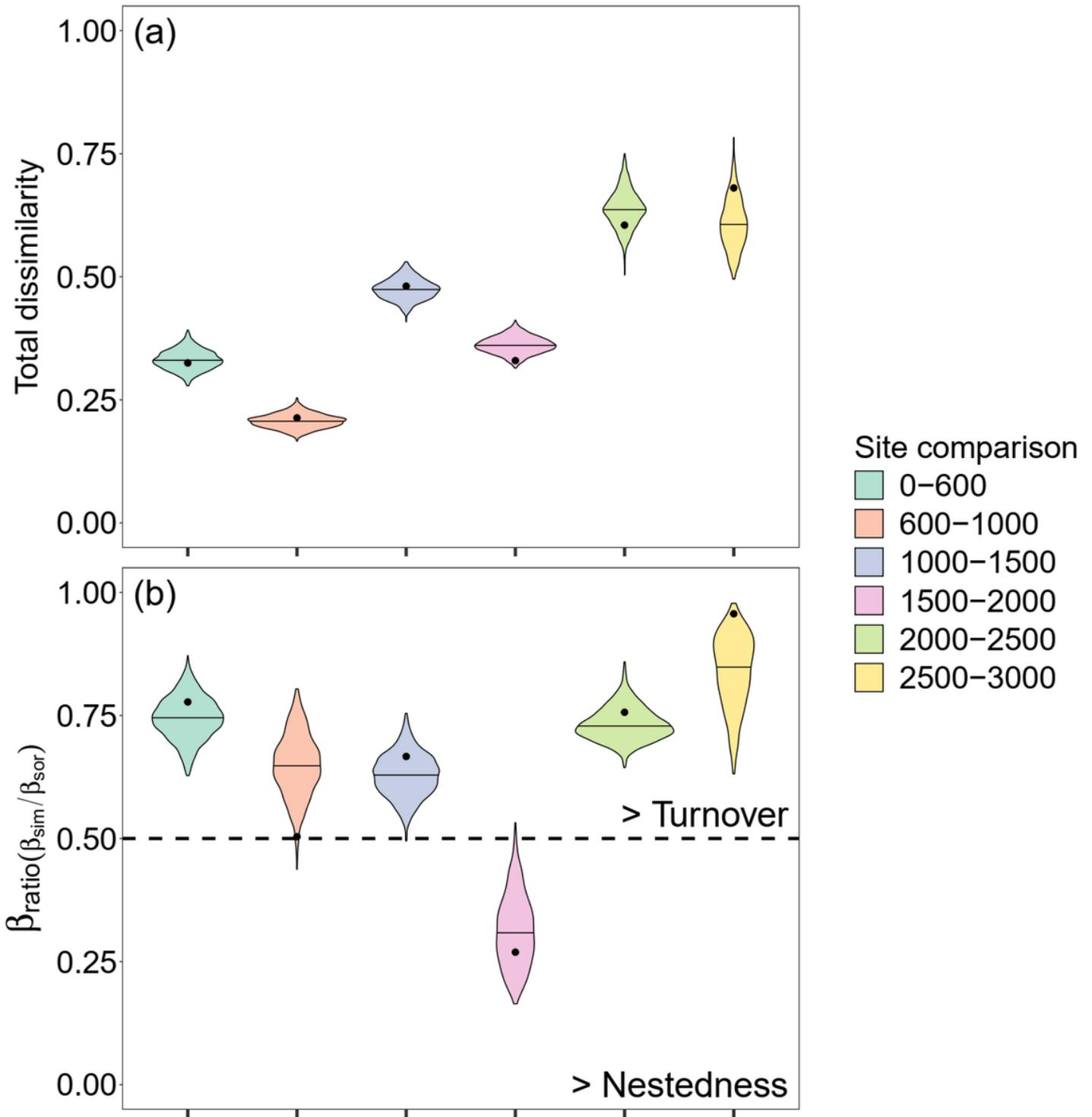


Figure 2

Patterns in the (a) phylogenetic total dissimilarity and (b) the relative contribution of the turnover over the total dissimilarity (i.e., $\beta_{ratio} = \text{PBD}_{adj.sim} / \text{PBD}_{adj.sor}$) between adjacent sites along the tropical mountain of Cofre de Perote, Mexico. $\beta_{ratio} > 0.5$ indicates that beta diversity is determined dominantly by species turnover, whereas $\beta_{ratio} < 0.5$ indicates the predominance of the nestedness component. The inner horizontal line in each violin represents the mean of the 1000 PBD values per site comparison. Black point represents the SES values from the MCC tree.

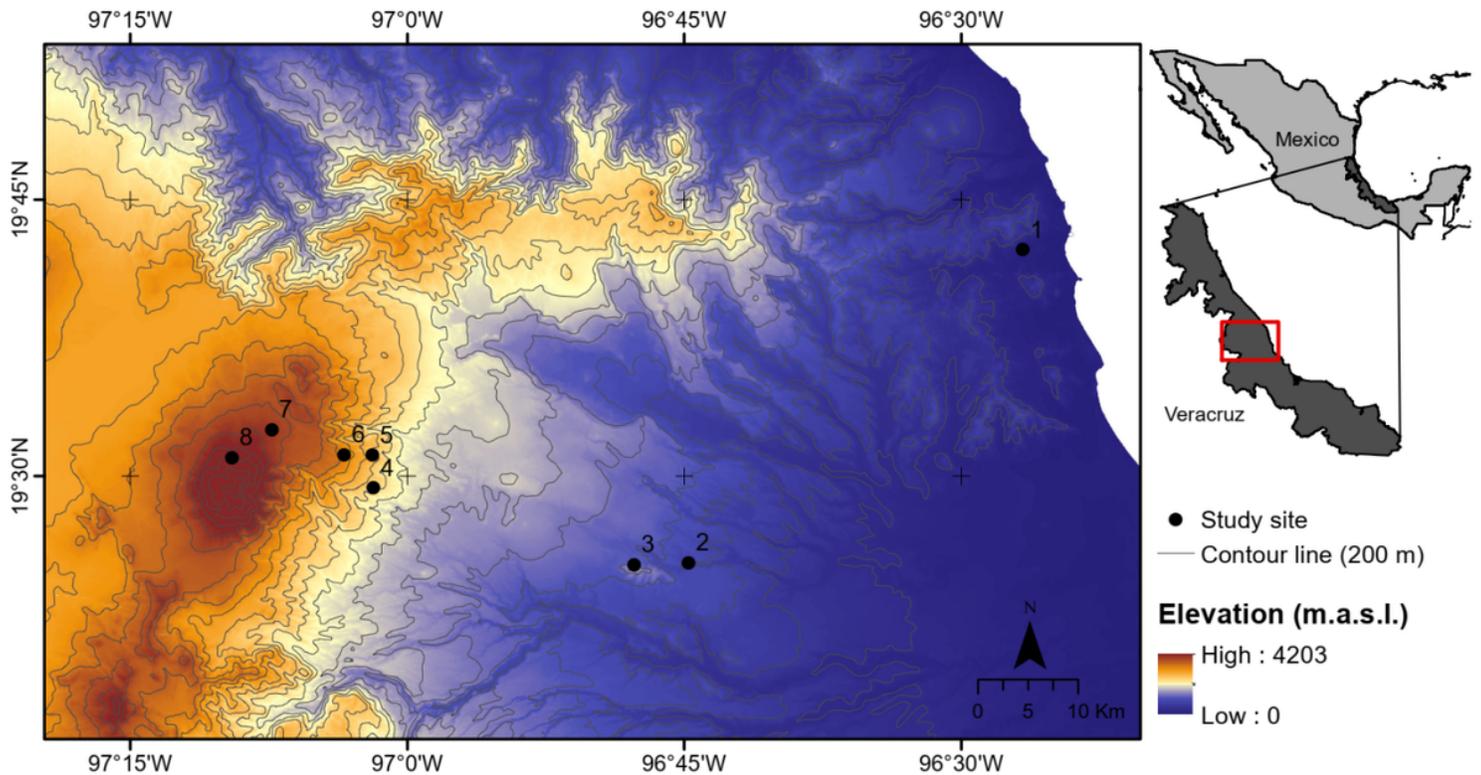


Figure 3

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 World Mercator projection (Datum: WGS 1984).

Supplementary Files

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- [SupplementaryMaterialPhylogeneticsSciRep.pdf](#)