



Temperature dissimilarity drives flower–visitor interaction turnover across elevation in the Mexican Transition Zone

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Abstract

Aim: Most biodiversity studies have considered species to be isolated entities, neglecting the fact that their biotic interactions and spatial variation are fundamental to their persistence across elevational gradients. Here, using a standardized sampling methodology, we evaluated how and why the composition of flower–visitor interactions (i.e. beta diversity) varies over an extensive elevational gradient. Specifically, we aimed to identify which biotic (species turnover) and abiotic factors (temperature, precipitation and primary productivity) inherent to elevational gradients can explain the distribution of floral visitor–plant interactions.

Location: Mexican Transition Zone.

Taxon: Angiosperms, Hymenoptera, Lepidoptera, Diptera, Hemiptera and Coleoptera.

Methods: We sampled ecological interactions between floral visitors and flowering plants at 10 sites along an elevational gradient from 4 to 3425 m.a.s.l. We measured the additive partitioning of the beta diversity of species interactions and used generalized dissimilarity modelling to assess how spatial and environmental factors can explain the observed dissimilarity.

Results: We found that the composition of interactions between floral visitors and plant species differs from lowlands to highlands mainly due to differences in temperature across the studied elevation gradient, rather than geographical distance or other environmental factors (i.e. mean annual precipitation and net primary productivity). We also observed that the main component of the beta diversity of interactions was

interaction turnover driven by the turnover of both plants and floral visitors along the elevation gradient studied, which may be influenced by both temperature and the biogeographical affinity of biotas.

Main Conclusions: We conclude that environmental filters play a crucial role in the establishment of novel interactions, as temperature can filter species and impact the behaviour and traits of floral visitors and plants across an elevational gradient. These findings underscore the importance of considering the role of abiotic factors in predicting and explaining the distribution of species interactions across different elevational gradients.

KEYWORDS

beta diversity, generalized dissimilarity models, interaction diversity, interaction networks, mountains, pollination

1 | INTRODUCTION

Traditionally, elevational gradients along mountains were used to understand how and why biodiversity is heterogeneously distributed on Earth (Brown, 2014; McCain & Grytnes, 2010; Peters et al., 2016). In the case of species richness, it is known that deterministic (e.g. temperature and net primary productivity), stochastic (e.g. area, connectivity and mid-domain effect) and evolutionary (e.g. higher diversity in areas of high speciation and/or low extinction) factors can explain gradients of species richness, which for many taxa is high in lowlands and decreases with elevation (Liu et al., 2018; McCain & Grytnes, 2010; Rahbek, Borregaard, Antonelli, et al., 2019; Rahbek, Borregaard, Colwell, et al., 2019). The factors that explain the variation in the distribution of biotas across different elevations are well known because mountains function as natural laboratories where one can test whether environmental and spatial variations explain particular components of diversity (e.g. taxonomic, functional or phylogenetic diversity). Therefore, elevational gradients allow one to test hypotheses and predictions, concerning, for example, how environmental conditions allow species to accumulate at certain elevations (e.g. Kraft et al., 2012; Peters et al., 2016). However, despite their heuristic properties, most studies on mountains regard species as isolated entities, neglecting the fact that all species on Earth are linked to others through their biotic interactions (Bascompte & Jordano, 2007; Dáttilo & Rico-Gray, 2018).

Given that biotic interactions are both a process and a component of biodiversity that contribute to its origin, maintenance and ecosystem functioning (Andresen et al., 2018), by studying elevational and latitudinal gradients it is possible to increase our understanding of how and why biodiversity varies across space (Luna et al., 2022; Schleuning et al., 2012). Current knowledge predicts that species interactions can vary across space due to ecological (e.g. species turnover, morphology and behaviour) and environmental (e.g. climate and productivity) filters. This implies that for an ecological interaction to occur, certain conditions must be met. These conditions may include the coexistence of the interacting species in

space or time, as well as their ability to overcome ecological filters such as environmental, morphological, disturbance or behavioural factors and even other types of interactions like predation or competition that may limit or facilitate the realization of an interaction (Luna & Dáttilo, 2021; Poisot et al., 2015; Tylianakis & Morris, 2017). For example, a floral visitor that is active in the morning can never interact with a plant that blooms at night, even though both co-occur (i.e. forbidden links, potential interactions between two species that are prevented or restricted by ecological or morphological filters; Olesen et al., 2011). This is similar to species environmental filtering, because, for example, a floral visitor can only live under a certain range of environmental and biotic conditions to which it is adapted (Classen et al., 2015; Ollerton, 2017; Soberón, 2007). Therefore, if the conditions in which the floral visitor lives are not met, the species will be filtered out and can no longer live there.

In the case of floral visitors and plants, their species richness decreases and their species composition changes with increasing elevation, a trend mainly explained by a reduction in temperature at high elevations and by variations in species abundance across space (Classen et al., 2015; Henriques et al., 2022; Peters et al., 2016). Moreover, when focusing on interactions between floral visitors and plants across elevational gradients, many studies have described how the local organization of their interaction networks vary without considering the environmental variation inherent to mountain systems (e.g. Lara-Romero et al., 2019; Minachilis et al., 2020; Ramos-Jiliberto et al., 2010). For instance, flower–visitor interactions can be either generalized (i.e. species establish a great number of interactions among them; Lara-Romero et al., 2019; Minachilis et al., 2020; Pitteloud et al., 2021) towards higher elevations, or show peaks in diversity at mid-elevations (Adedoja et al., 2018; Hoiss et al., 2015; Maglianesi et al., 2015; Minachilis et al., 2020). Additionally, flower–visitor interactions can show a consistent modular structure across different elevations (i.e. groups of species interacting more strongly with each other than with the species in the other groups in the network; Ramos-Jiliberto et al., 2010). Although there is growing evidence

showing how flower–visitor interactions are distributed over elevation gradients, we only know that temperature can reduce species' biotic specialization over elevation gradients (Classen et al., 2015, 2020; Pitteloud et al., 2021). Therefore, we still lack empirical and theoretical evidence that can be used to determine the extent to which stochastic and deterministic factors explain the observed variation of flower–visitor interaction networks through elevation gradients.

One framework that allows us to study how and why biotic interactions vary across space focuses on measuring the turnover of interactions (i.e. the beta diversity of interactions) (Poisot et al., 2012). This framework considers that the entities of variation are pairwise interactions and not the species per se, thereby allowing us to determine interaction composition by partitioning the dissimilarity of interactions into two additive components: interaction dissimilarity due to species turnover (i.e. interactions change as species assemblages change) and interaction rewiring (i.e. changes in pairwise interactions generated by the reassembly of interactions between the shared species in different sites/times) (Poisot et al., 2012). The beta diversity of interactions has proven to be useful in elucidating how and why species interactions vary by considering the dissimilarity between ecological networks (i.e. how pairwise interactions vary between networks by either of their components) (Carstensen et al., 2014; Kemp et al., 2017; Trojelsgaard et al., 2015). In other words, a beta diversity approach offers an alternative to studying flower–visitor interactions across elevational gradients beyond focusing on local network properties (e.g. network specialization or structure; Luna et al., 2020; Luna et al., 2022). For flower–visitor networks, the turnover of interactions driven by species turnover has been mainly explained by changes in plant composition, rather than by flower–visitor turnover (e.g. Carstensen et al., 2014; Trojelsgaard et al., 2015). Nonetheless, previous studies using an interaction beta diversity approach have neglected the fact that environmental conditions can influence how the composition of species interactions vary across space (but see Dáttilo & Vasconcelos, 2019).

The region where Neotropical and Nearctic biotas come into contact is known as the Mexican Transition Zone (MTZ). In this region, ecological communities at high elevations tend to be dominated by species with Holarctic affinity, while communities from lowlands are dominated by species with Neotropical affinities (Halffter & Morrone, 2017). The differential distribution of biotas across elevations in the MTZ is due to the contrasting colonization of biotas through a mosaic of habitats, ranging from tropical to alpine forests. The MTZ is of considerable ecological and evolutionary relevance because many hypotheses that explain how species colonize, live and evolve have arisen from studies in this region (Halffter & Morrone, 2017), and so it represents an ideal system to study how biotic interactions can be influenced by environmental filters and by the differential distribution of biotas over elevational gradients. Here, we evaluated how and why the composition of flower–visitor interactions varies over an elevational gradient, focusing on identifying their spatial variation (i.e. beta diversity) and their potential environmental drivers. We first assessed which component

of the beta diversity of interaction made the greater contribution to overall interaction beta diversity (β_{RW}), interaction turnover due to species turnover (β_{ST}) or interaction rewiring (β_{RW}). We expected that due to the high rates of floral visitor and plant turnover across elevations in the MTZ (Gómez-Díaz et al., 2017; Joaqui et al., 2021; Pérez-Toledo et al., 2021), the main component of interaction beta diversity would be flower–visitor interaction turnover due to species turnover. This is because, the presence of distinct species communities with varying geographical affinities along an elevation gradient can result in distinct species compositions and interactions at different elevations (Arroyo et al., 1982; Arroyo et al., 1985). Additionally, we tested how geographical and environmental distance (i.e. temperature, precipitation and productivity) explains the beta diversity of flower–visitor interactions across the studied elevational gradient. In this case, we expected that with increased geographical distance, flower–visitor interactions would be more different between sites due to neutral factors (e.g. dispersal limitations and random variation in species abundances) determining the composition of species assemblages and richness across space (Vellend, 2016). Moreover, we expected that temperature and precipitation would constrain the foraging behaviour of floral visitors (Albrecht et al., 2018; Classen et al., 2015, 2020; Luna et al., 2022), leading to different plant–floral visitor interactions between sites, mainly because in cooler temperatures, floral visitors reduce their activity (Arroyo et al., 1982; Arroyo et al., 1985) and tend to require more energy consumption, which affects how they forage on floral resources (Classen et al., 2020). Finally, we expected that primary productivity (i.e. resource availability) would influence the foraging behaviour of floral visitors, because resource availability can influence how many interactions a floral visitor can establish (i.e. optimal foraging theory) (MacArthur and Pianka, 1966).

2 | MATERIALS AND METHODS

2.1 | Study sites

We established 10 sampling sites separated by ~200–500 m in elevation on the eastern slope of Cofre de Perote, spanning an elevational gradient from 4 to 3425 m a.s.l. Cofre de Perote is an extant volcano in the eastern part of the MTZ (between 19° 25' 5.7" and 19° 36' 54" N, and 94° 44' 43.5" and 97° 09' 36.9" W), right at the confluence of the volcanic transversal belt and the Sierra Madre Oriental. Cofre de Perote has an elevation of 4282 m and its geological origin dates back to the Miocene (~20 million years ago, Figure 1). Our sampling sites were located in the Jamapa River basin, which encompasses the eastern slope of Cofre de Perote. Each of the sampling sites displayed different types of vegetation and were classified as coastal dunes (4–30 m elevation; temperature when the sampling was carried out ranging from 32 to 36°C), dry deciduous forest (30–1000 m; 23–31°C), cloudy mountain forest (1500–2500 m; 19–20°C), pine-oak forest (3000 m; 10–16°C) and fir forest (3500 m; 7–13°C); the tree line is located at approximately 3700 m of elevation.

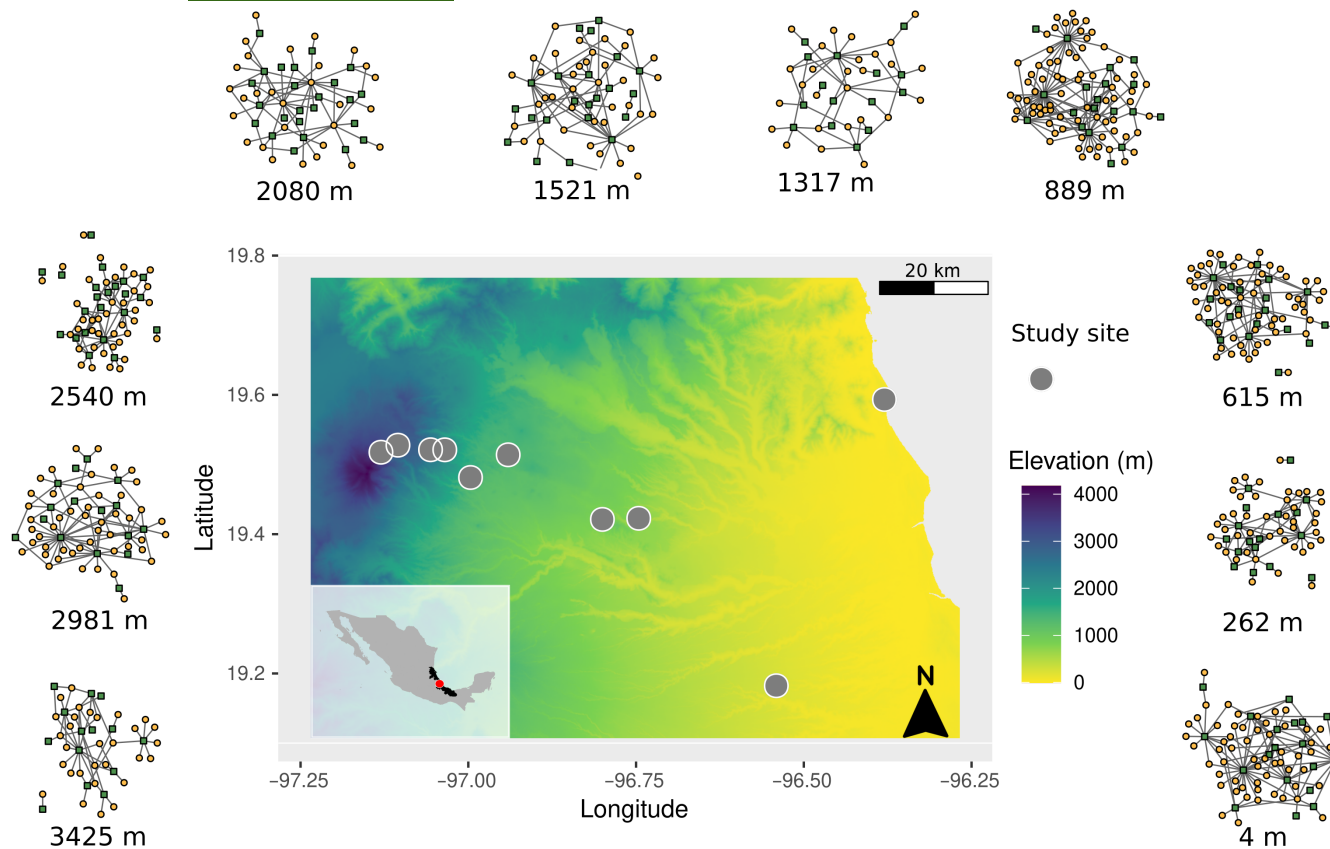


FIGURE 1 The red point in the inset map represents the region in Mexico in which this study was performed: the eastern slope of Cofre de Perote in the Mexican Transition Zone (datum WGS84), spanning an elevational gradient from 4 to 3425 m.a.s.l. Grey points denote the locations of the sampling sites where we sampled the interactions between plants and their floral visitors. The colour gradient denotes elevation; lighter colours denote low elevation and darker colours denote high elevation, from 0 to 4282 m.a.s.l. Plant–floral visitor networks surrounding the map are shown from high to low elevation (left to right). Green squares denote plant species and yellow circles denote floral visitor species; the lines are the interactions among them.

2.2 | Floral visitor–plant interactions and species identification

We performed our samplings from May to August 2019, corresponding to the rainy season when angiosperms bloom. To record the interactions between floral visitors (only arthropods) and plants, we placed three plots at each site with a size of ~250 m in length (depending on the topography of the site, the shape of the plot varied) and 10 m in width. We established the plots in areas where flowering plants were observed, with the common characteristic that they were open sites with little shade from trees (i.e. small gaps in the forest, or habitats free of trees like in coastal dunes). For interaction sampling, sessions were conducted only on days without rain, 6 h per day (8:30 a.m.–2:30 p.m.), and for 3 days per site. On each sampling day, one researcher moved slowly and without fixed corridors through the vegetation and captured all the arthropods that were observed visiting flowers. We only collected arthropods when they were observed in contact with the flower or any of its parts. Note that only one researcher conducted the sampling (P. Luna) and only recorded interactions in which potential floral visitors appeared to be actively engaged in foraging for floral nectar or pollen. Interactions where visitors did not seem to be interacting with the flowers were not recorded. However, we

acknowledge that our sampling might have included not only pollinators but also nectar and pollen robbers. We visited our sampling plots on consecutive days, and the collection of invertebrates was carried out with an entomological net and entomological tweezers. Each collected arthropod was placed in a plastic vial with 70% ethanol and labelled with the identity of the visited plant. A botanical sample was taken from each plant in which arthropods were captured, and plants were pressed in dry paper and later put to dry in the herbarium XAL of the Instituto de Ecología A.C. We identified plants in the herbarium XAL to the species level by PL and GCC. Arthropods were identified to the lowest possible taxonomic level. The species that we could not determine were identified as morphospecies and their family, subfamily or order was determined using taxonomic keys. Plants were deposited in the XAL herbarium and arthropods in the entomological collection IEXA of Instituto de Ecología A.C.

2.3 | Predictor variables

To test how deterministic factors contribute to the dissimilarity of flower–visitor networks, we obtained three environmental variables describing the conditions of the sampling sites: mean annual

temperature, mean annual precipitation and primary productivity, which was measured using the Normalized Difference Vegetation Index (NDVI). Mean annual temperature and precipitation rasters were obtained from Cuervo-Robayo et al. (2014) with a resolution of 1 km. Note that these climatic rasters are the most updated climatic surfaces available for Mexico. The NDVI was calculated using satellite SENTINEL 2 images (<https://scihub.copernicus.eu/dhus/>). For this purpose, we first looked for images with no clouds corresponding to the location of Cofre de Perote in the period we conducted our samplings. Having obtained the images, we selected and used the bands corresponding to the near infrared (NIR) and red spectral reflectance, and then applied the map algebra functions in ArcMap using the following formula: $NDVI = \frac{(NIR - Red)}{(NIR + Red)}$. The NDVI is an index for estimating the quantity, quality and development of vegetation, and in this case, we used it as a proxy of primary productivity (Table S1).

2.4 | Data analysis

2.4.1 | Plant and floral visitor beta diversity

To understand the spatial variation in species interactions, we first measured how many floral visitors and plants were observed at each sampling point (i.e. number of floral visitors and visited plant species at each elevation). We then measured the spatial beta diversity (β -diversity) of floral visitors and plant communities, making pairwise comparisons of species dissimilarity between adjacent study sites from the lowest to the highest elevation (9 comparisons among 10 sites at different elevations, but located before or after one another along the gradient). We also made comparisons among all the sampling sites in order to obtain a dissimilarity matrix containing the beta diversity of all the possible combinations between sampling sites ($n=45$ paired comparisons). Furthermore, we used this matrix for our spatial analyses. For these measures, we used the beta diversity framework proposed by Baselga (2010, 2012) in which we partitioned the β_{jac} into two components, β_{sp} turnover (species change) and β_{ne} nestedness (species gain/loss), using the Jaccard dissimilarity index, because we used presence and absence data. Having obtained the values of β_{jac} and its components β_{sp} and β_{ne} , we tested whether there were differences between the components across the gradient using a linear mixed model where the fixed factor was the beta diversity components (β_{sp} and β_{ne}) and the random effect was the pairwise comparison; in total, we had 18 values (9 corresponding to β_{sp} and 9 to β_{ne}) from nine comparisons. We implemented a mixed-effects model because the components of beta diversity were derived from one measure and therefore were not independent (MacGregor-Fors et al., 2022). We obtained the significance of the mixed-effects models by Wald χ^2 tests.

2.4.2 | Interaction beta diversity

We used the data regarding the interaction between plants and floral visitors from each elevation to build 10 matrices A , where

A_{ij} = number of interactions between plant species i with floral visitor species j . We used these matrices to measure interaction beta diversity (β_{WN}). We calculated the turnover of plant-floral visitor networks using the framework proposed by Poisot et al. (2012) by calculating the dissimilarity or beta diversity of interactions (β_{WN}). The dissimilarity of interactions arises from changes in species composition (β_{ST}) and the rewiring of interactions (β_{RW}) between shared species of two communities. Therefore, since we require species shared species and its turnover to have interaction turnover; β_{RW} and β_{ST} are a subset of β_{WN} , leading to an additive partition of the beta diversity of interactions: $\beta_{WN} = \beta_{ST} + \beta_{RW}$ (for more details regarding these components, see Poisot et al., 2012). In this case, these measures were derived from beta diversity (β_W) (Whittaker, 1960), defined as: $\beta_W = \frac{a+b+c}{(2a+b+c)/2} - 1$ where a is the number of shared species between communities, b is the number of unique species of the first community, and c is the number of unique species of the second community. For the calculation of interaction beta diversity (β_{WN}), a represents shared interactions between communities, while b and c represent the interactions exclusively occurring within each community. This index provides values ranging from 0 to 1; values closer to 1 denote higher dissimilarity. We estimated the turnover of our 10 plant-floral visitor networks by doing pairwise comparisons between adjacent sites with a total of nine different combinations. We also measured the spatial variation of flower-visitor networks by comparing all the sampling sites, obtaining one dissimilarity matrix for β_{WN} ($n = 45$ paired comparisons). Having obtained the values of β_{WN} and its components β_{ST} and β_{RW} , we tested whether there were differences between the components across the gradient using a linear mixed model, where the fixed factor was the beta diversity of interaction components (β_{ST} and β_{RW}) and the random effect was the pairwise comparison (Table S2). We conducted our analysis of beta diversity in R version 4.2.2 (R Core Team, 2022), using the 'igraph' (Csardi & Nepusz, 2006) and 'bipartite' (Dormann et al., 2008) libraries for data manipulation. For the beta diversity analysis, we used the 'betapart' library for species dissimilarity (beta.multi and beta.pair functions; Baselga & Orme, 2012) and 'betalink' for interaction dissimilarity (betalink function; Poisot, 2016).

2.4.3 | Generalized dissimilarity modelling

To assess the relative influence of geographical and environmental distances on the species and interaction beta diversity among our sampling sites, we used generalized dissimilarity modelling (GDM, Ferrier et al., 2007). For this, we fitted a total of three GDMs, one model for each of the trophic levels (floral visitors and plants, two models) only considering the species turnover (β_{jac}), and another model for the turnover of interactions (β_{WN}). The predictor variables included in these models were geographical distance, mean annual temperature, mean annual precipitation and primary productivity. GDM offers an approach for comparing the biological distances between sites by transforming the distance between a pair of sites for different predictors. To fit the GDMs, we used the

dissimilarity matrices that were obtained by measuring the taxonomic and interaction beta diversity among all possible combinations between the 10 sampling sites ($n = 45$ possible combinations). Moreover, GDM can be used to assess the relationship between biological dissimilarity and environmental and/or spatial distance with a link function, $d_{ij} = 1 - e^{-\eta}$, where d_{ij} is the biological dissimilarity between sites i and j and η is the transformed environmental distance between those sites (i.e. predicted ecological distance). Therefore, model fitting is designed to generate the best estimate of predicted ecological distance by transforming each predictor variable p . Environmental distance η is derived as the sum across all predictor variables of the absolute differences in the model $f_p(x_p)$ between sites i and j : $\eta = b + \sum_{p=1}^m (f_p(x_{pi}) - f_p(x_{pj}))$. In GDM the model intercept is b and denotes the amount of dissimilarity expected between sites that have identical environments, and therefore its value is 0. To transform each predictor variable, GDM uses a combination of l-spline functions using non-negative least squares regression, making each spline flexible in shape, but constrained to increase monotonically. The constraints in spline values imply that dissimilarity can only increase as two sites become different in terms of the selected predictor variables (for more details, see Mokany et al., 2022). Here, we fitted GDMs to find the best fit between taxonomic beta diversity (plant β_{jac} and animals β_{jac}), interaction beta diversity (β_{WN}) and inter-site geographical-environmental distances. To obtain the relative importance of each predictor variable and associated p -values, we implemented a model to select the variables that best explained the observed biological dissimilarity with 50 iterations. GDM fitting was done using the *gdm* library in R. To further understand the relationship between species and interaction composition and geo-climatic variables, we performed Mantel correlations to test the correlation between the biological distances (beta diversity of plants, visitors and interactions) and geo-climatic variables (temperature, precipitation, productivity and geographical distances). In addition, as some environmental variables are expected to co-vary, we tested the correlation among all the geo-climatic variables (Table S3). We also performed partial Mantel tests to assess how biological distances were associated with environmental conditions by controlling their co-variation by geographical distance (Table S4).

3 | RESULTS

We recorded 876 independent interactions involving 151 plant species and 331 arthropod species (Tables S5 and S6). We collected plants from 37 families, of which the most abundant were Asteraceae (72 species, 47%), Fabaceae (33 species, 21%) and Malvaceae (21 species, 13%). We collected 331 arthropod species from eight orders, of which the most abundant were Hymenoptera (141 species, 34%), Lepidoptera (136 species, 33%), Diptera (91 species, 22%) and Coleoptera (43 species, 10%). We recorded different numbers of plant species and arthropods visited along the gradient: 4 m (18 plant species and 59 arthropod species), 262 m (17 and 44 species), 615 m (20 and 60 species), 889 m

(19 and 74 species), 1317 m (15 and 27 species), 1521 m (22 and 37 species), 2080 m (24 and 28 species), 2540 m (22 and 39 species), 2981 m (16 and 48 species) and 3425 (14 and 30 species; Figure S7).

3.1 | Taxonomic and interaction beta diversity

We observed that the main component of the taxonomic beta diversity (β_{jac}) for the pairwise comparison between sites was species turnover (β_{sp}) for both floral visitors (mean \pm SD: $\beta_{sp} = 0.89 \pm 0.5$; $\beta_{ne} = 0.018 \pm 0.01$, $\chi^2 = 2407.46$, $df = 1$, $p < 0.0001$; Figure 2a,d) and plants ($\beta_{sp} = 0.91 \pm 0.6$; $\beta_{ne} = 0.006 \pm 0.006$; $\chi^2 = 1652.14$, $df = 1$, $p < 0.0001$; Figure 2b,e). This indicates that each elevation tends to have unique floral visitor species visiting unique plant species. In the case of interaction beta diversity, we found that the main component of its dissimilarity was interaction turnover driven by species turnover ($\beta_{st} = 0.7 \pm 0.32$, $\beta_{RW} = 0.27 \pm 0.31$; $\chi^2 = 8.17$, $df = 1$, $p = 0.004$; Figure 2c,f). However, the dissimilarity of interactions driven by the rewiring of interactions was only detected between five adjacent elevations, reaching its highest value between high elevation comparisons (2500–3000: $\beta_{RW} = 0.75$ and 3000–3500: $\beta_{RW} = 0.73$) and its lowest values between low elevation comparisons (250–600: $\beta_{RW} = 0.5$; 600–1000: $\beta_{RW} = 0.17$; 1000–1300: $\beta_{RW} = 0.33$). Between adjacent sites where interaction rewiring was not detected, its contribution to overall interaction beta diversity was zero.

3.2 | Generalized dissimilarity modelling

Geo-climatic variables explained 76.5% of the compositional turnover of floral visitors (visitors β_{jac}). Temperature dissimilarity was the only predictor that explained the compositional turnover of floral visitors (78.9% of explained deviance) (Table 1). In the case of plant compositional turnover (plants β_{jac}), geo-climatic variables explained 60.9% of its dissimilarity and the only relevant predictor was also temperature dissimilarity (64.6%) (Table 1). For the turnover of interactions (β_{WN}), geo-climatic variables explained 62.5% of its compositional dissimilarity, and temperature dissimilarity was also the only predictor that explained its variation (83.1%) (Table 1; Figure 3). Regarding the Mantel tests, we observed that plant, visitor and interaction composition were positively correlated with temperature and geographical distances. For environmental variables, we observed that temperature distance was positively correlated with productivity and geographical distance (Table S2). However, when we controlled the correlations by geographical distance, we observed that plant, visitor and interaction composition were only positively correlated with temperature (Table S3).

4 | DISCUSSION

By standardizing our sampling effort over an elevational gradient in the MTZ, we found that flower–visitor interactions differ

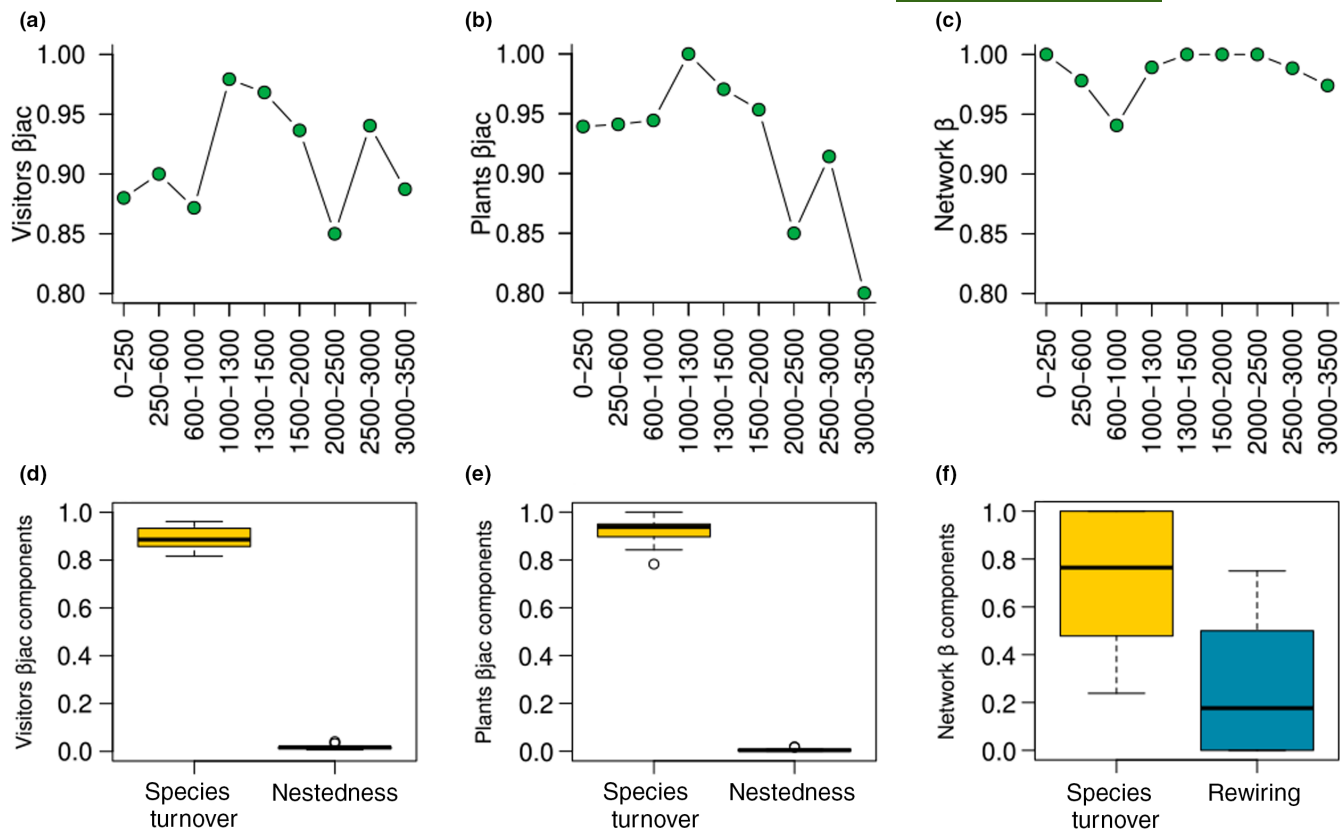


FIGURE 2 (a) Floral visitor pairwise beta diversity (β_{jac}) between adjacent study sites (i.e. neighbouring sites along the gradient but at different elevations), (b) plant pairwise beta diversity (β_{jac}) between adjacent study sites and (c) flower–visitor interaction pairwise beta diversity (β_{WN}) between adjacent study sites located on the eastern slope of Cofre de Perote in the Mexican Transition Zone. Each point denotes a beta diversity value obtained by comparing two adjacent sites from the lowest to the highest elevation combinations. (d) Partitioning of floral visitor beta diversity (species turnover β_{sp} and nestedness β_{ne}), (e) plant beta diversity and (f) interaction beta diversity (interaction turnover due to species turnover β_{ST} and interaction rewiring β_{RW}).

TABLE 1 Relative importance of geographical distance and environmental (mean annual temperature, mean annual precipitation and net primary productivity) predictors in explaining species beta diversity (floral visitors and plants) (β_{jac}) and interaction beta diversity (flower–visitor interactions) (β_{WN}) on the eastern slope of Cofre de Perote in the Mexican Transition Zone.

Predictor	Floral visitors (β_{jac})	Plants (β_{jac})	Flower–visitor interactions (β_{WN})
Mean annual temperature	42.35*	19.92*	56.12*
Geographical distance	0.32	3.86	6.41
Mean annual precipitation	10.64	5.94	1.91
Net primary productivity	0.30	1.07	3.40
Explained deviance (%)	76.5	60.91	62.52
p-value	<0.001	<0.001	<0.001

Note: Values denote the deviance explained by each factor obtained by fitting Generalized Dissimilarity Models. Asterisks denote statistical significance.

from lowlands to highlands mainly due to changes in temperature across elevation. Accordingly, we found that the main component of the beta diversity of flower–visitor interactions in the studied

elevational gradient was the turnover of interactions due to the spatial turnover of floral visitors and plants. Interaction rewiring was a component of the beta diversity of flower–visitor interactions only detected between certain elevations and not across all adjacent sites, which was contrary to our prediction. Our study revealed that changes in temperature across sites can account for the dissimilarity in the composition of interactions between floral visitors and plants. These findings have several explanations, ranging from how temperature filters species to how it can affect flower traits or floral visitors' behaviour.

Our analysis revealed that the primary driver of beta diversity of interactions was interaction turnover resulting from species turnover (β_{ST}), rather than interaction rewiring (β_{RW}). This finding is consistent with previous studies conducted on Mount Olympus in Greece (Minachilis et al., 2023) and other spatial gradients (Carstensen et al., 2014; Trojelsgaard et al., 2015), which have shown that changes in plant composition and flower abundance, rather than changes in floral visitor composition, primarily influence the turnover of species interactions due to species turnover (β_{ST}). However, our study revealed that the turnover of interactions can be explained by the turnover of both floral visitors and plants, driven by temperature dissimilarity across

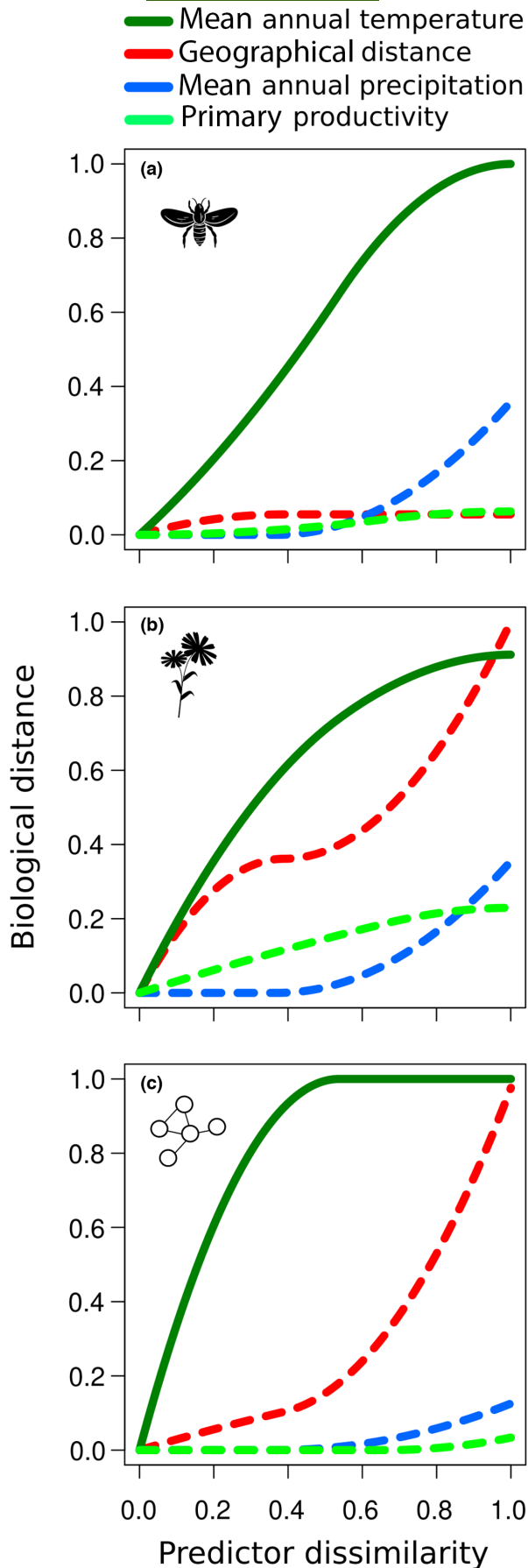


FIGURE 3 Plotted I-splines for the fitted generalized dissimilarity models analysing the relationship between geographical and environmental predictors with (a) visitors' (β_{sp}), (b) plants' (β_{sp}) and (c) flower–plant interactions' (β_{WN}) beta diversities on the eastern slope of Cofre de Perote in the Mexican Transition Zone. Each line represents a spline for each predictor variable: temperature dissimilarity (dark green), geographical distance (red), normalized difference, vegetation index dissimilarity (light green) and precipitation dissimilarity (blue). Spline height indicates the relative importance of the predictor variables, and the spline slope corresponds to the rate of change in a) floral visitor, b) plant and c) flower–visitor interaction compositional dissimilarity over the range of pairwise dissimilarities within the predictor. Continuous lines represent statistically significant predictors, and dashed lines represent predictors that were not statistically significant in the models.

different elevations. This finding differs from our prediction that only one trophic level (either plants or floral visitors) would be relevant in explaining the turnover of interactions. In the studied elevational gradient, a high turnover of plant species has already been reported, which is explained by the steep environmental changes found in this system (Carvajal-Hernández et al., 2017; Gómez-Díaz et al., 2017). However, in this case, we observed that such changes in plant diversity can contribute to one of the components of beta diversity of interactions, namely the turnover of interactions due to species turnover. The composition of floral visitors may change over the elevational gradient because animals can move between sites in search of resources (Vilela et al., 2014). Nonetheless, our findings suggest that floral visitors are limited to moving between nearby sites with comparable temperature conditions, indicating that temperature plays a crucial role in restricting floral visitors' movement, ultimately increasing the uniqueness of interactions at each elevation. It is important to note that our assessment only focused on how interacting plants and floral visitors drive interaction turnover. We did not investigate whether the turnover of entire plant and animal communities are responsible for the observed changes in interactions since our samplings were directed to only collect a subset of the whole flora and fauna.

An additional aspect that can explain the observed turnover of floral visitors and plants is the biogeographical affinity of species across elevations in the MTZ. For instance, in another elevation gradient also located within the MTZ (Pico de Orizaba volcano, spanning 200–3450 m.a.s.l.), the biogeographical origin of dung beetles was one of the main factors explaining their species turnover as a result of biotas with Neotropical affinities not being found in cold highlands (Joaqui et al., 2021). The biogeographical origin explaining the observed beta diversity is not limited to animals because plants' composition in the MTZ can also be determined by their biogeographical affinity (Villaseñor et al., 2020). The assembly of biotas across the MTZ assumes that species coexisting at certain elevations share evolutionary history and, therefore, are adapted to the

environmental conditions where they live (Morrone, 2020). Indeed, biogeographical factors play a crucial role in explaining species turnover across elevations, and this phenomenon is not unique to the system we studied. In the Andes, for example, the distribution of vegetation and floral visitors can be explained by the upward migration of biotas with Mediterranean affinity (Arroyo et al., 1982), whereas in Brazil, the distribution of bees at high elevations is associated with the presence of plants with temperate affinity, which may have established in mountains during the cold periods of the Pleistocene (Silveira & Cure, 1993). Therefore, we contend that our observation of different floral visitors and plants along the studied elevational gradient is a result not only of current temperatures filtering species, but also of their biogeographical origin and evolutionary history. Given that we did not evaluate the biogeographical origin of the studied plants and floral visitors, this aspect warrants further research attention.

Beyond the turnover of interactions due to species turnover, our results showed that temperature dissimilarity across an elevational gradient is a factor that can explain the beta diversity of flower–visitor interactions (β_{WN}). Our findings diverge from previous research on the distance–decay relationship in biotic interactions due to two potential explanations. First, previous studies may have failed to consider the influence of environmental conditions on the turnover of interactions and therefore neglect the fact that the environment can play a role in explaining the distribution of biotic interactions (Carstensen et al., 2014; Trojelsgaard et al., 2015). Second, it is possible that other environmental factors, such as primary productivity rather than temperature, play a role in explaining the turnover of interactions in other environments (Dáttilo & Vasconcelos, 2019). The fact that our results show that temperature is a strong filter of flower–visitor interactions may have several non-mutually exclusive explanations. First, we must acknowledge that changes in temperature across a mountain can influence flower–visitor interactions by increasing foraging costs or by reducing the activity of floral visitors as temperature decreases with increasing elevation (Arroyo et al., 1985; Classen et al., 2020). We also have to consider that the groups of floral visitors can change from lower to higher elevations (e.g. higher bee richness at mid-elevations or higher fly richness at high elevations; Arroyo et al., 1982). These changes in the groups of floral visitors may provide additional dissimilarity to interactions across a mountain, because the number of interactions that each species can establish may vary according to its identity (e.g. bee, fly or butterfly), its location in terms of elevation and the ambient temperature (Arroyo et al., 1982; Arroyo et al., 1985). Moreover, floral visitors that live in cold environments can be functionally different from those found at warmer low elevations as they are adapted to fly under cold conditions (e.g. development of bigger wings; Henriques et al., 2022) which may also increase the observed interaction dissimilarity. In the case of plants, one study has shown that floral visitors change their feeding behaviours based on flower temperature, selecting cooler plants in high temperatures and warmer plants in cooler temperatures (Norgate et al., 2010). Given that both floral visitors and flowers are sensitive to temperature, we can predict that

species will likely interact in a similar way between two sites with the same temperature and similar species composition. However, species interactions may differ between environments as the temperature changes, as this study has shown. It is important to note that elevation gradients can reflect changes in environmental conditions similar to those found across latitudes, but on a smaller spatial extent. As a result, it is possible that temperature fluctuations across latitudes may also affect variations in biotic interactions. For example, evidence suggests that environmental factors, such as temperature, play a key role in determining the number of interactions between floral visitors and plants on a global scale, regardless of location in terms of latitude or elevation (Luna et al., 2022; Schleuning et al., 2012).

By studying flower–visitor interactions across an elevational gradient, we were able to identify how changes in temperature determine the dissimilarity of floral visitors and plants as well as their interactions in the MTZ. Specifically, we found that the considerable dissimilarity of plant–floral visitor interactions was explained by changes in temperature rather than by geographical distance and other environmental factors (i.e. mean annual precipitation and net primary productivity). These findings indicate that the way species interact can be predictable and be shaped by changes in temperature. While temperature has been recognized as a determinant of species distribution across elevational gradients (Peters et al., 2016), its impact on the distribution of species interactions remains poorly understood. Our findings highlight that temperature dissimilarity plays a crucial role in shaping the turnover of flower–visitor interactions, which could have significant implications for our empirical and theoretical understanding of the distribution of ecological functions such as pollination along elevational gradients (Andresen et al., 2018). Moreover, understanding how and why temperature shapes biotic interactions is critical for predicting how climate change will affect the ways in which species interact. By recognizing the influence of temperature on biotic interactions and by studying the uniqueness of such interactions across different elevations, we can better anticipate the consequences of climate change and comprehend why tropical mountains and their biodiversity are at risk of environmental disturbances. In summary, our study represents an effort to integrate species interactions with biodiversity theory, using mountains as natural laboratories to understand how biotic interactions are distributed on Earth.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Supporting data are available in the Supporting information while raw data are available at: doi: [10.6084/m9.figshare.23504907](https://doi.org/10.6084/m9.figshare.23504907)

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BIOSKETCH

Pedro Luna is an early career scientist interested in understanding the geographical distribution and predictability of biotic interactions. The research team of this article is comprised of ecologists and taxonomists interested in understanding the factors affecting the distribution of biodiversity, in this case, biotic interactions.

Authors' contributions: PL and WD conceived the original idea. PL, FE, FV and WD selected sampling sites. PL did the field work. PL and IHD identified arthropod species. PL and GCC identified plant species. PL and WD discussed and performed statistical models. PL wrote the first draft of the manuscript under the supervision of FE, FV, FN and WD. All authors contributed substantially to revisions.

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