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Temperature and Precipitation Explain Bee Diversity on Flowers Along an Elevation Gradient in the Mexican Transition Zone

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Abstract

Although ecologists have identified the key factors influencing species distribution along elevation gradients, each mountain's distinct characteristics, including its geology and biotic colonization processes, are often overlooked. The uniqueness of each mountain ecosystem implies that species distribution and the factors affecting them may vary across regions and taxonomic groups. The Mexican Transition Zone (MTZ) in central Mexico is a mountainous region of significant ecological and evolutionary importance, shaped by distinct biotic colonization and distribution patterns across its elevation gradient. However, most research in this region has focused on specific taxa, neglecting the vast diversity within the MTZ. In this study, we investigated the variations in flower-visiting bee diversity along an elevation gradient within the MTZ (10 sampling sites distributed from 4 to 3425 m a.s.l..), focusing on understanding the environmental factors influencing their distribution. Our findings reveal a declining bee diversity with increasing elevation, primarily driven by decreasing temperatures. However, when considering bee abundance, we identified precipitation as the predominant factor influencing bee diversity. Therefore, water and resource availability are critical in shaping bee diversity in this region. Furthermore, as elevation increased, we observed distinct and unique bee communities, highlighting the rarity and uniqueness of highland bee species as integral components of mountain ecosystems.

Introduction

The study of the distribution of biodiversity over natural gradients has been fundamental to understanding how and why species accumulate in tropical and mountainous regions of the Earth (Rahbek et al., 2019b). Accordingly, several hypotheses to explain why we find more species in the tropics and mountainous regions have been postulated (e.g., the temperature, water availability, productivity, and area hypotheses) (McCain & Grytnes, 2010; Brown, 2014). Although each hypothesis identifies the factors and provides a framework to explain species distribution along elevation gradients, generalizing such hypotheses and associated factors is not always ideal. This difficulty in generalization is because each taxon can be affected by environmental conditions in specific ways based on the ecophysiological adaptations that enable them to inhabit different mountain environments (Peters et al., 2016). Therefore, we must also acknowledge that each mountain has its unique geological and biotic colonization history, and it can be expected that species are not evenly distributed across different elevation gradients (McCain & Grytnes, 2010; Rahbek et al., 2019a, 2019b).

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In this sense, to better understand how species are distributed on Earth, ecological research requires evidence from different mountains and the testing of various predictions to more precisely determine how and why environmental conditions sort species along elevation gradients.

Elevation gradients offer ideal systems for testing different hypotheses postulated to explain the environmental factors that influence the distribution of a particular taxon. Over a single elevation gradient, we can observe substantial variations in temperature, precipitation, and primary productivity (McCain & Grytnes, 2010). In this context, the temperature hypothesis suggests that species richness increases with rising environmental temperatures since organisms' metabolic rates increase as the environmental temperature rises (Brown et al., 2004; Kaspari, 2005; Brown, 2014). Higher metabolic rates can, in turn, be associated with higher speciation rates, ultimately leading to greater species accumulation in warmer environments (i.e., lowlands). Regarding the water availability hypothesis, it predicts that species diversity is positively correlated with precipitation. This is because water availability directly affects resource availability, including primary productivity and nutrients, which, in turn, constrain the number of individuals and species that an environment can support (McCain & Grytnes, 2010). Furthermore, the productivity hypothesis posits that diversity is positively linked to primary productivity, as highly productive environments can sustain more species and higher population densities (McCain & Grytnes, 2010). In addition, the area hypothesis explains that larger areas can support more species than smaller areas, which is in line with the predictions of the neutral theory of biodiversity (Hubbell, 2001). Specifically, habitat area is expected to decrease with elevation, leading to lower species richness in higher elevations (Körner, 2007). Studies on species distribution along elevation gradients have supported one or more of these hypotheses, with variations observed across different mountains and taxonomic groups (Rahbek, 1995; Peters et al., 2016; Perillo et al., 2021). Therefore, testing different hypotheses when studying species gradients along elevation gradients is crucial. By doing so, we can identify which hypothesis best explains the spatial distribution of specific taxa and link our results to current ecological hypotheses and theories.

The Mexican Transition Zone (MTZ) is one of the most significant mountainous regions globally, harboring a rich diversity and endemism of animals, plants, and other taxa (Halffter & Morrone, 2017; Morrone, 2020). This region serves as the juncture where the Neotropical and Nearctic biotas intersect. Consequently, ecological communities in high, cold elevations originate in the Holarctic realm, while warm, lowland communities trace their roots to the Neotropical realm (Morrone, 2020). Despite our understanding of the colonization and speciation mechanisms that account for the MTZ's remarkable diversity, much of the existing evidence has focused on the study of individual taxa, such as dung beetles (Escobar et al., 2007; Joaqui et al., 2021). This approach has overlooked that this region hosts a wide array of animals, including insects, which the region's biogeographical makeup may have influenced. A particularly noteworthy group of insects includes bees, which exhibit both solitary and social behaviors, playing an essential role in pollinating numerous plant species. Indeed, evidence has shown that bee diversity in Mexico can be impacted by elevation. For instance, greater functional diversity has been observed in lowlands compared to highlands within Neotropical arid environments in Mexico, indicating that bees are responsive to environmental variations (Osorio-Canadas et al., 2022). However, within the specific context of the MTZ, our understanding of how bees are distributed and the environmental factors that explain their spatial distribution remains limited. Gaining insights into the distribution of bee diversity and how environmental conditions influence it is crucial, given the vital role bees play in plant reproduction and the persistence of plant populations. Additionally, their pollination services are essential for food production and the sustenance of human populations. Considering the backdrop of climate change, comprehending how bees are affected by environmental conditions becomes fundamental in predicting how climate changes may impact their diversity and, consequently, the interactions they establish with plants (Luna et al., 2023).

In this study, we assessed bee diversity, both alpha and beta diversity, and examined how it is distributed and explained by environmental conditions along an elevation gradient within the MTZ. To achieve this, we conducted tests to investigate how the temperature, precipitation, and productivity hypotheses may elucidate bee diversity concerning flower foraging across an elevation gradient from 4 to 3425 m a.s.l. We expected that bee alpha diversity, encompassing richness and abundance, would decline with increasing elevation and that this decrease in diversity could be attributed to reductions in temperature and resource availability, specifically water availability and productivity. Furthermore, we also explored the variation in bee species composition, or beta diversity, across different elevation levels to identify sites that host distinct bee communities. In this context, we expected to observe significant turnover in bee species along the mountain, as the drastic shifts in environmental conditions would likely give rise to unique bee communities across various elevations, with only a limited number of species being shared between sites. Furthermore, we postulate that the differential colonization of mountains by Nearctic and Neotropical biotas will lead to variations in bee species composition along the elevation gradient studied.

Material and Methods

This study was conducted on the eastern slope of Cofre de Perote mountain, which has a maximum elevation of 4282 meters above sea level (m a.s.l.) in Mexico. We established ten sampling sites, each separated by approximately 200-500 meters in elevation, covering a wide elevation range from 4 to 3425 m a.s.l. (19° 25' 5.7" and 19° 36' 54" N, and 94° 44' 43.5" and 97° 09' 36.9" W) (see Figure 1). It is an inactive volcano at the confluence of the volcanic transversal belt and the Sierra Madre Oriental. The mountain's geological origins date back to the Miocene period, approximately 20 million years ago. Each of the sampling sites exhibited varying types of vegetation, ranging from dry coastal dunes (4–30 m a.s.l. elevation, with temperatures ranging from 26 to 36 °C during the sampling period), dry deciduous forest (30–1,000 m a.s.l.; 23–31 °C), cloudy mountain forest (1,500–2,500 m a.s.l.; 19–20 °C), pine-oak forest (3,000 m a.s.l.; 10–16 °C), to fir forest (3,500 m a.s.l.; 7–13 °C). Temperature ranges were assessed in situ by deploying 3 Hobos at each sampling site for 72 hours (Supplementary Material S1).

At each site, we collected bees during the rainy season, from May to August, corresponding to the flowering seasons of the understory vegetation. For this purpose, we established two plots measuring 250 × 10 meters at each elevational level. Two researchers walked through these plots, collecting all bees visiting flowers from 8:30 am to 14:30 hours for three consecutive days (Luna et al., 2023). We collected bees using entomological nets and entomological tweezers, and each collected bee was carefully placed in a plastic vial with alcohol and labeled for subsequent identification in the laboratory. Bees were taxonomically identified to the species level by Ismael Hinojosa-Díaz, who is also a co-author of the study. Specimens were deposited in the entomological collection (IEXA) at the Instituto de Ecología A.C. Xalapa, Mexico. Sampling was conducted under a scientific sampling license issued by Mexico's Secretariat of Environment and Natural Resources (SEMARNAT No. SGPA/DGVS/03940/19).

Environmental factors

To investigate the impact of temperature, precipitation, and productivity on bee diversity and its distribution across elevation gradients, we acquired three environmental datasets that characterize the conditions of the sampling sites. Mean annual temperature and precipitation data were sourced from Cuervo-Robayo et al. (2014) at a spatial resolution of 1 kilometer. Productivity was assessed using the Normalized Difference Vegetation Index (NDVI), computed from SENTINEL 2 satellite images (https://scihub.copernicus.eu/dhus/). To achieve this, we initially obtained cloud-free images of our specific sampling locations, corresponding to the timeframe during which our sampling was conducted. After obtaining the images, we utilized the near-infrared (NIR) and Red spectral reflectance bands and applied the following formula using ArcMap: NDVI=NIR-Red/NIR+Red. Then, the location of each sampling point was associated with each raster, and the environmental conditions related to each sampling point were extracted.

Data analysis

With the recorded bee abundance and richness, we estimated diversity profiles using the continuous Hill numbers curve (Jost, 2006; Chao et al., 2014). This measure characterizes the composition of an ecological community in

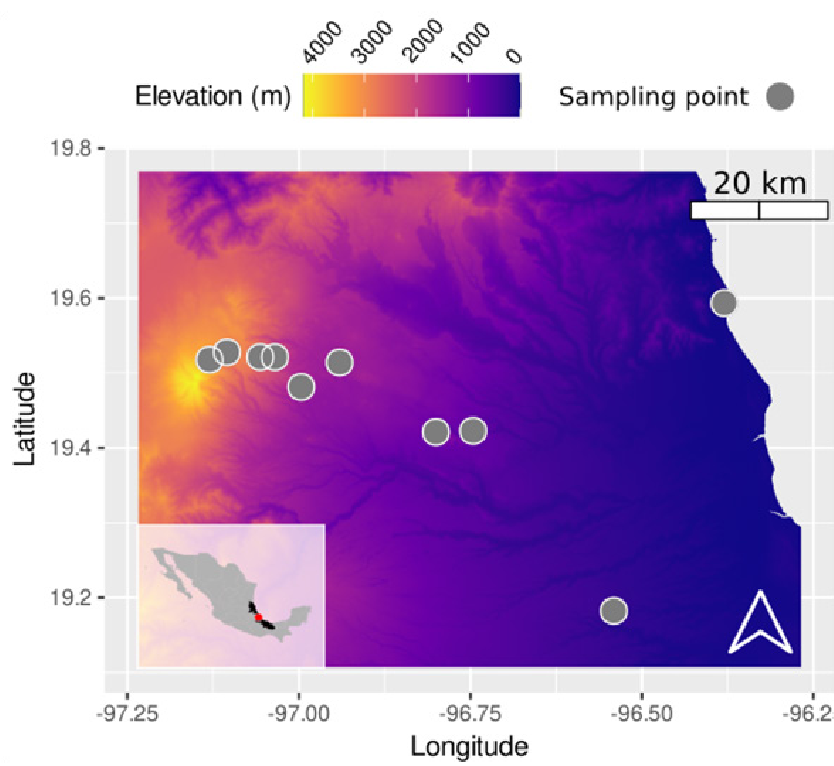

Fig 1. Map showing the eastern slope of Cofre de Perote and the location of the sampling points in Mexico. The color gradient denotes elevation; darker colors denote lower elevations, and lighter colors denote high elevations, from 0 to 4,282 m a.s.l.

terms of species richness (q0), the evenness of rare species (q1; equivalent to Shannon diversity), and the dominance of abundant species (q2; equivalent to Simpson diversity) (Jost, 2006; Chao et al., 2014). We computed q0, q1, and q2 diversity metrics for each elevation level. To investigate the distribution of bee diversity (q0) across elevational gradients, we employed a Generalized Additive Model (GAM). In this analysis, bee richness (q0) was the dependent variable, while elevation was the independent variable. We utilized a non-linear smoothing function to capture the non-linear relationship between bee richness and elevation. The GAM was fitted using the mgcv package in R version 4.3.1 (R Core Team, 2023).

Following the assessment of the relationship between elevation and bee richness, we employed Generalized Linear Models (GLMs) to examine the associations between climate variables and bee diversity. We utilized the diversity measures (q0, q1, and q2) as dependent variables and environmental factors (mean annual temperature, mean annual precipitation, and productivity) as independent variables. Three models were constructed, each corresponding to one of the diversity measures. In each model, we included all the environmental factors and the diversity measure as the response variable without any statistical interaction. We employed a Poisson error distribution with a log link for the model assessing

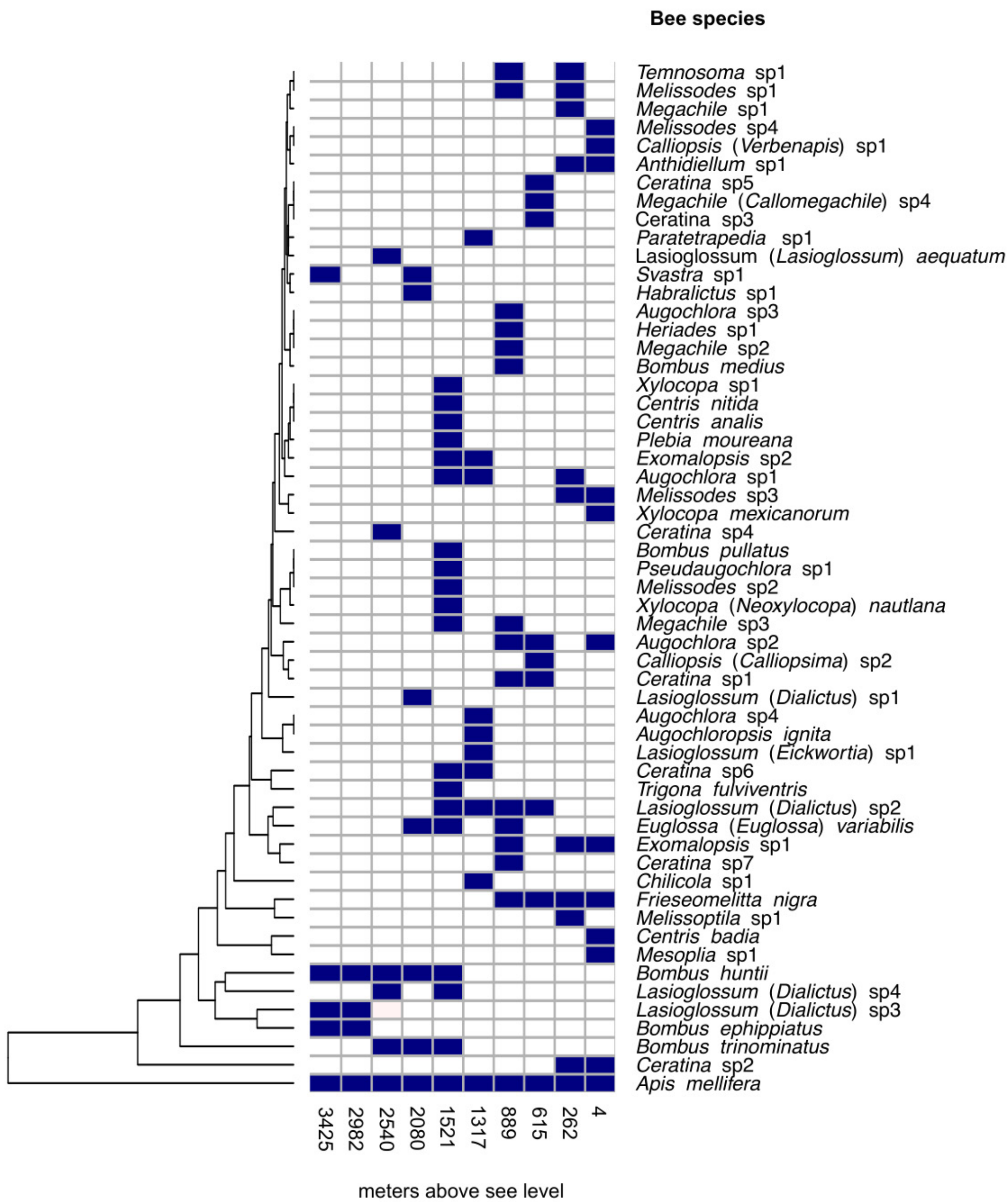

Fig 2. Dendrogram based on the Euclidean Distance method in which bee species are grouped based on their occurrence along an elevation gradient within the Mexican Transition Zone (from 4 to 3425 m a.s.l.).

species richness (q0) and a Gamma error distribution with an *inverse* link for the models evaluating Shannon diversity (q1) and Simpson diversity (q2). Before fitting the models, all variables (i.e., environmental factors) were centered by subtracting the mean of each factor from each observation of that factor. This centering process resulted in values with a mean of 0 and a standard deviation of 1. We did not include elevation as an explanatory variable in these models due to the observed negative correlation between mean annual temperature and elevation ($\rho = -1$, $P = 0.0001$).

We used beta diversity measures to assess the composition of bee communities along the elevation gradient. For this, we measured the spatial *β-diversity* of bee communities, making pairwise comparisons between adjacent elevational floors from the lowest to the highest elevation (9 comparisons among ten sites). 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 (i.e., species change) and β_{ne} nestedness (i.e., species gain or species loss) using the Jaccard dissimilarity index. We further explored the composition of bee communities by building a dendrogram showing how the different bee species were distributed in the studied elevation gradient.

Results

We recorded 597 bee individuals, representing 56 species (Supplementary Material S2) (Figure 2). Notably, we observed that the honey bee *Apis mellifera* was a dominant species across the studied elevation gradient, distributed from the lowest to the highest elevations (from 4 to 3425 m a.s.l.). On the other hand, we observed that *Bombus huntii* (from 1521 to 3425 m a.s.l.)*, B. trinominatus* (from 1521 to 2540 m a.s.l.)*, Lasioglossum* (*Dialictus*) sp3 (from 2982 to 3425 m a.s.l.) and sp4 (from 1521 to 2540 m a.s.l.) where bee species that had a constrained distribution towards high elevations (Figure 2). While *Anthidiellum* sp1, *Centris badia, Ceratina* sp2*, Melissodes* sp3 and sp4*, Mesoplia* sp., *Xylocopa mexicanorum* distribution was restricted to low lands (from 4 to 262 m a.s.l.). Moreover, some bee species were only observed at a specific elevation, like *Lasioglossum* (*Dialictus*) sp1, observed at 2080 m a.s.l., *Ceratina* sp4, which was observed at 2540 m a.s.l. or *Paratetrapedia* sp1 only observed at 1317 m a.s.l. (Figure 2). Overall, we observed that bee richness was higher in the lowlands and midlands (from 4 to 1521 m a.s.l.) but decreased at 2000 m a.s.l. reaching its lowest point in the highlands (3000 to 3425 m a.s.l.). The GAM had a single smooth term for elevation, with an estimated effective degree of freedom of 1.86. The model explained 68.1% of the deviance in the data. The intercept (t-value = 22.75, $p < 0.001$) and smooth term ($F = 6.261$, $p = 0.02$) for elevation were statistically significant (Figure 3).

Regarding the relationship between bee diversity and environmental factors, we observed that species richness (q0)

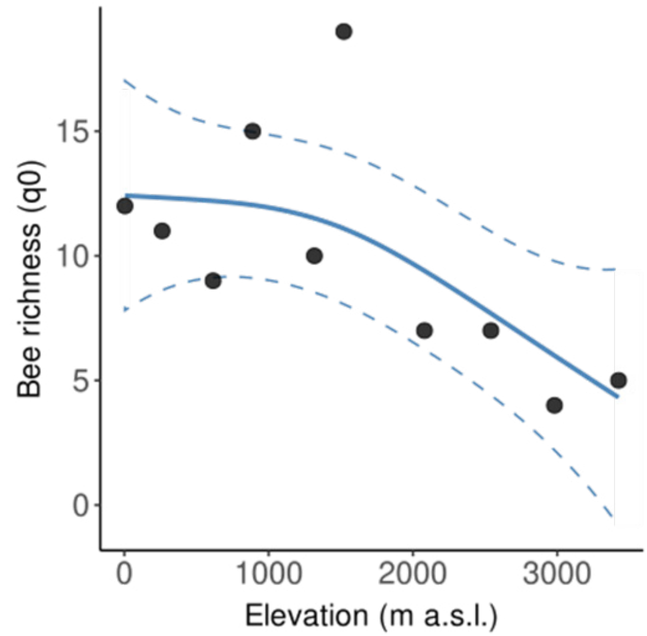

Fig 3. Relationship between elevation and bee richness, the dashed lines denote the standard error of the adjusted slope.

increased with mean annual temperature and precipitation (temperature, $\chi^2 = 6.58$, df = 8, $P = 0.01$, Figure 4a; precipitation, $\chi^2 = 7.21$, df = 7, $P = 0.007$, Figure 4b). In this case, productivity was not associated with bee species richness ($\chi^2 = 0.46$, df = 6, $P = 0.49$). When we assessed the relationship between environmental factors and Shannon diversity (q^1), we found that bee diversity increased with mean annual precipitation ($\chi^2 = 1.13$, df = 7, $P = 0.0001$, Figure 4c). In contrast, mean annual temperature ($\chi^2 = 0.13$, df = 8, $P = 0.24$) and productivity were not associated with Shannon bee diversity ($\chi^2 = 0.01$, df = 6, P = 0.67). For Simpson diversity (q^2), we found that bee diversity increased with mean annual precipitation ($\chi^2 = 0.91$, df = 7, $P = 0.01$, Figure 4d). Mean annual temperature ($\chi^2 = 0.02$, df = 8, $P = 0.65$) and productivity ($\chi^2 = 0.003$, df = 6, $P = 0.85$) were unrelated to Simpson bee diversity.

We observed a high beta diversity of bee species across elevations ($\beta_{jac} = 0.93$), where species turnover ($\beta_{sp} = 0.90$) was the main component of the overall beta diversity. At the same time, nestedness had a lower contribution ($\beta_{ne} = 0.03$) to the overall variation of species composition. At the lower elevation, we observed that the main component of the beta diversity was species turnover (0-250 m a.s.l. comparison: $\beta_{sp} = 0.66$ and $\beta_{ne} = 0.01$). As elevation increased species turnover continued to be the primary driver of bee beta diversity (250-600 m a.s.l.: $\beta_{sp} = 0.82$; 600-1000 m a.s.l.: $\beta_{sp} = 0.57$; 1000-1300 m a.s.l.: $\beta_{sp} = 0.84$; 1300-1500 m a.s.l.: $\beta_{sp} = 0.62$; 1500-2000 m a.s.l.: $\beta_{sp} = 0.54$; 2000-2500 m a.s.l.: $\beta_{sp} = 0.66$). However, at higher elevations, nestedness became more relevant (2500-3000 m a.s.l.: $\beta_{ne} = 0.22$) being that in the higher elevations, nestedness was the only component of species beta diversity (3000-3500 m a.s.l.: $\beta_{ne} = 0.16$) (Figure 5).

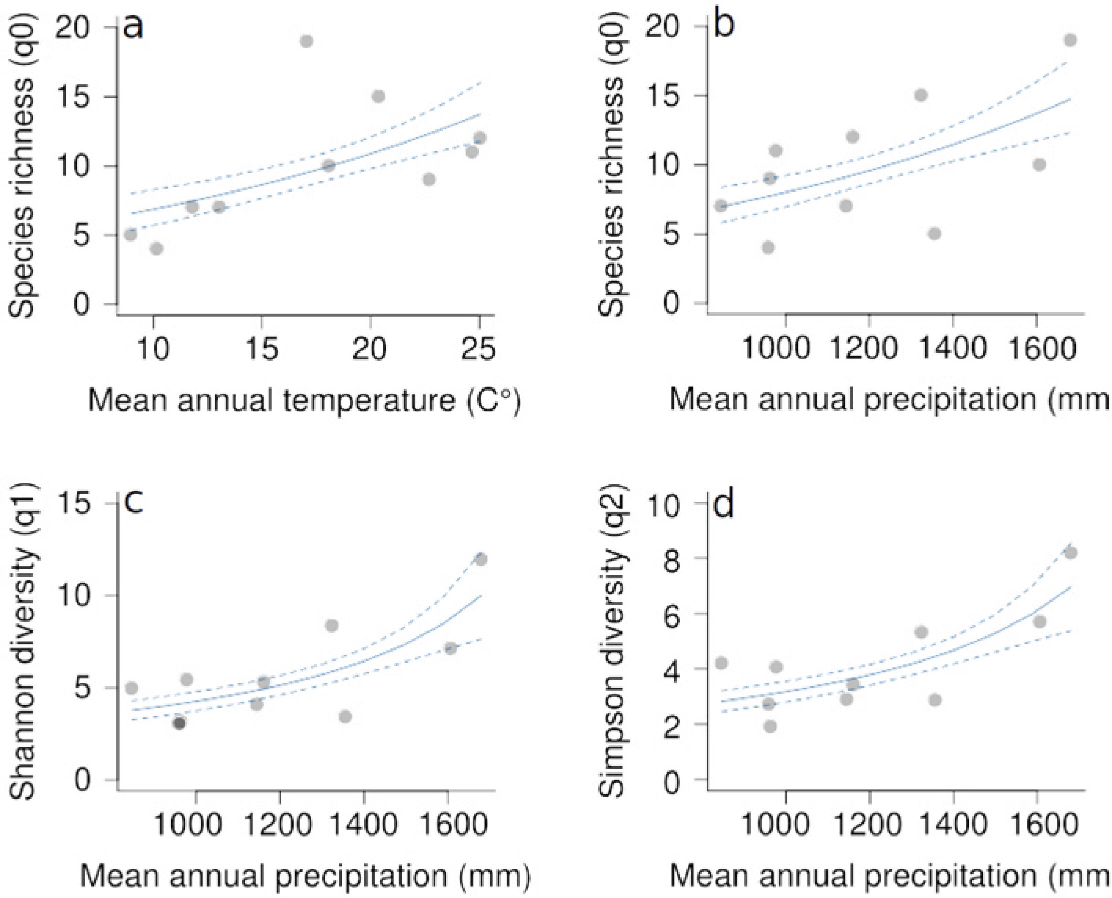

Fig 4. a) Relationship between bee species richness (q^0) and mean annual temperature. b) Relationship between bee species richness and mean annual precipitation. c) Relationship between bee Shannon diversity (q^1) and mean annual precipitation. d) Relationship between bee Simpson diversity and mean annual precipitation.

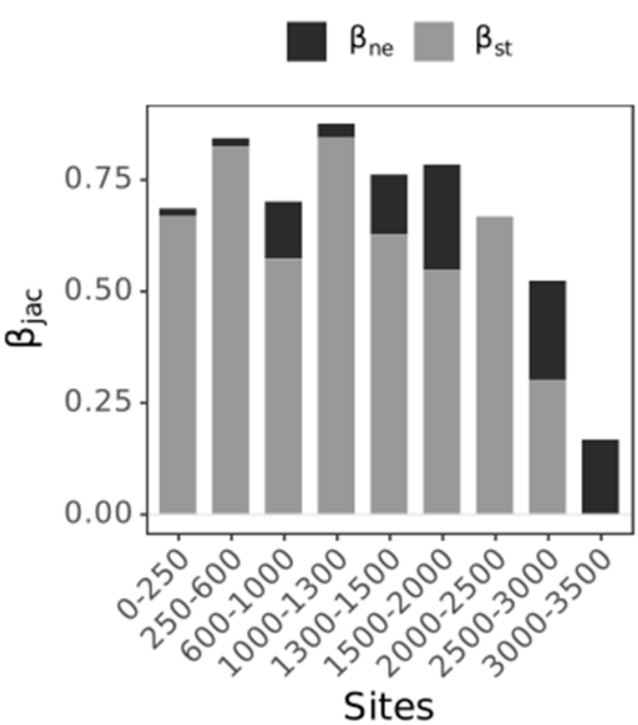

Fig 5. Partition of the beta diversity of bees in the studied elevation gradient. Gray colors denote species turnover, and black denotes nestedness (species gain or loss). Each bar represents the comparison between two adjacent sites in the elevation gradient.

Discussion

In this study, we observed that both precipitation and temperature influenced the variation in bee diversity along an elevation gradient within the MTZ. Specifically, we found higher bee diversity in sites with higher precipitation at mid-elevations. As for species richness, it peaked at low and mid elevations and decreased gradually towards higher elevations, which can be attributed to the decrease in temperature with increasing elevation. While temperature and precipitation are known factors that can directly influence ecosystem primary productivity, in this case, productivity did not appear to explain bee richness, Shannon diversity, and Simpson diversity. Instead, we found that water availability emerged as the primary factor determining high bee diversity. Precipitation accounted for bee richness and influenced diversity measures, particularly when considering bee abundance (Shannon and Simpson diversity). As anticipated, lower elevations exhibited greater bee richness, with the number of individuals and species progressively declining as elevation increased. This pattern aligns with previous ecological evidence, consistently showing increased species diversity in lowland and midland regions and a corresponding decline in diversity with higher elevations (McCain & Grytnes, 2010; Rahbek et al., 2019b). Notably, our study revealed a peak in species richness at intermediate elevations, around 1,521 m a.s.l, underscoring the significance of the cloud forest within the studied elevation gradient. These unique environmental conditions, along with the plant community characteristic of cloud forests, are likely conducive to drive a higher diversity of bee species, a pattern previously observed for other insect taxa in the MTZ, such as ants and dung beetles (Joaqui et al., 2021; Pérez-Toledo et al., 2021). Another aspect to consider is that mid-elevation areas represent a unique convergence zone for Neotropical and Nearctic biotas, as Halffter & Morrone (2017) noted. This overlap can increase species diversity in these mid-elevation regions compared to other parts of the elevation gradient.

The influence of mean annual temperature and precipitation on bee richness underscores the significance of these climatic variables in shaping species composition. The positive association between species richness and these environmental factors aligns with the temperature and water availability hypotheses (McCain & Grytnes, 2010). These findings also correspond with research conducted in other mountainous regions worldwide. For instance, on Mount Kilimanjaro, temperature and resource availability are the primary factors explaining bee diversity (Classen et al., 2015). While we do not have direct evidence of a relationship between bee diversity and resource availability, we have evidence indicating that water availability may be a constraining factor for bee diversity within the MTZ. Similar patterns were observed across the Atlantic forest in Brazil, where factors such as temperature, seasonality, and precipitation were found to explain bee diversity. In contrast, temperature primarily accounted for species richness (Faria & Gonçalves, 2013). On the other hand, in Brazilian mountains, bee diversity has been attributed to temperature, as species tend to accumulate in areas where the risk of extinction is lower due to increased resource availability (Perillo et al., 2021). Indeed, warmer temperatures and increased precipitation create more favorable conditions for bee diversity, as both factors enhance plant diversity (Ewel, 1980), serving as the primary food source for most bee species (Ollerton, 2021). Although evidence suggests that resource availability (specifically, productivity) is a critical factor in determining bee diversity in other mountainous regions (McCain & Grytnes, 2010; Rahbek et al., 2019b), we did not find a clear relationship between productivity and bee species richness in our study. This discrepancy may reflect the complexity of interactions among productivity, resource availability, temperature, and precipitation in shaping bee community composition. It is possible that other factors not considered in this study, such as habitat heterogeneity and plant diversity, also play a role in shaping bee richness and productivity.

To further explain bee diversity, the historical contingency of the mountain must be considered. This is because the colonization of biota along the studied elevation gradient may differ from that in other biogeographical regions worldwide (Lomolino, 2001). Thus, it is crucial to account for the biogeographical origin of bees within the MTZ. In fact, in this region, the biogeographical origins of biotas play a significant role (Halffter & Morrone, 2017). For example, in the case of dung beetles, it is well-documented that beetle species inhabiting lowlands have a Neotropical origin, while those in highlands have a Nearctic origin (e.g., Joaqui et al., 2021). However, there is limited supporting evidence for this idea for bees and ants (Pérez-Toledo et al., 2021). Nevertheless, it should be considered in future studies within the MTZ, as in other mountainous regions worldwide, biogeographical origins seem to be relevant in shaping bee diversity. In Brazil, for instance, the distribution of bees at high elevations is associated with the upward migration of plants during the Pleistocene (Silveira & Cure, 1993).

Concerning bee beta diversity, we observed that across the studied elevation gradient, species turnover was the primary factor driving variation in the composition of bee communities, with nestedness playing a lesser but still significant role. The prevalence of species turnover in shaping beta diversity along the elevation gradient underscores the importance of species replacement in response to changing environmental conditions, aligning with expectations that shifting conditions lead to changes in species assemblages (Perillo et al., 2021). In this case, the turnover of bee species can be explained by corresponding changes in plant communities and their interactions with floral visitors. As the elevation increases within the studied gradient, plant communities and their interactions with floral visitors undergo drastic changes, leading to unique species assemblages at different elevations (Gómez-Díaz et al., 2017; Luna et al., 2023). Moreover, the increasing contribution of nestedness at higher elevations suggests a different ecological dynamic. At these altitudes, the relatively harsher environmental conditions might restrict the number of species capable of persisting, resulting in unique species assemblages. This finding underscores the potential vulnerability of high-elevation bee communities to the effects of ongoing climate change, as the loss of certain species could lead to decreased rare species and homogenization of these communities.

In addition to the effects of climate and the biogeographical affinity of bees, it is important to recognize that bee species exhibit distinct distribution trends with specific explanations. For instance, we observed that the honeybee (*Apis mellifera*) was distributed throughout the entire elevation gradient. Such a broad distribution range could be attributed to the eusocial behavior and broad thermal tolerance observed for *A. mellifera* within the MTZ, which can thrive from lowlands to highlands due to its adaptability to varying temperatures (Barreiro et al., 2024). On the other hand, species like *Bombus huntii* and *B. trinominatus* were found predominantly at cold, high elevations, likely reflecting their biogeographical origins within this genus. The evolutionary history of *Bombus* dates to the Eocene-

Oligocene boundary (34 million years ago), a period marked by significant global cooling, suggesting an affinity of the genus for colder environments (Hines, 2008). Although *Bombus* bees can be found in warmer tropical regions, their origins in colder climates are well-documented (Hines, 2008). We also observed that species like *Anthidiellum* sp1, *Centris badia, Ceratina* sp2*, Melissodes* sp3 and sp4*, Mesoplia* sp., and *Xylocopa mexicanorum* were only observed in warm lowlands. The restricted distribution of these species may reflect their Neotropical affinity. For example, the distribution of the bee genus *Centris* has been associated with the warm Tropics (i.e., the Amazonian jungle and Atlantic forest) or to dry environments like the Neotropical Savanna (i.e., Cerrado biome) (Gianninini et al., 2013; Velez et al., 2016). Indeed, the Neotropical savanna is recognized as an essential center of biodiversity for the genus *Centris* (Alves-dos-Santos, 2009). In this case, *C. badia* was observed in warm coastal dunes, which present an exuberant tropical vegetation, owing to the high diversity and possible Tropical origin of the *Centris* genus, which might explain why *C. badia* distribution was restricted to lowlands. Therefore, such affinity to either low, mid, or highlands may reflect species' affinity to specific environments where they live. Such affinity can be related to temperature changes along the elevation gradient, which strongly influence the distribution of pollinators and their associated plant resources due to high environmental filtering (Luna et al., 2023). Therefore, bees restricted to particular elevations can persist only where suitable food sources are available and where they have developed adaptations to thrive.

The relationship between bee diversity and climatic variables underscores the potential consequences of climate change on bee populations. As temperatures increase and precipitation patterns shift, bee communities may alter their composition and abundance, potentially disrupting their essential roles in pollination and ecosystem functioning. We found that bee richness and diversity (Shannon and Simpson diversity) within the MTZ vary significantly with changes in elevation, primarily due to higher precipitation at mid-elevations, which is congruent with the highest bee richness which was observed at mid-elevations, which can be attributed to increased water availability, primarily driven by precipitation. This, in turn, likely enhances the abundance of plant-derived resources in the cloud forest at such elevations. Moreover, our observations indicate that bee communities become more distinct and unique as elevation increases, sharing fewer species with habitats at lower elevations. This trend suggests that bee populations at higher elevations are particularly susceptible to ongoing climate change impacts, as they face a greater risk of isolation and habitat loss. This study contributes to understanding how bee diversity is distributed across elevation gradients in the MTZ. The findings offer valuable insights into the ecological mechanisms that shape bee communities, with implications for biodiversity conservation, ecosystem services, and our ability to predict and mitigate the impacts of climate change on these crucial pollinators.

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Supplementary Material

Table S1. Temperature range across the sampling sites. Data was Taken with Hobos that where place din the sampling sites for three days.

Elevation (m a.s.l.)	Temperature (C°)	Standard deviation (±)
4	31.9	6.41
262	25.6	4.41
615	26.32	5.52
889	23.7	4.01
1317	19.5	4.33
1521	21.73	4.71
2080	18.66	5.4
2540	20.18	5.72
2981	14.05	6.32
3425	10.37	6.2

Table S2. Distribution of bee species along an elevation gradient in the Mexican Transition Zone (MTZ) in central Mexico.

Bee species	4 m a.s.l.	262 m a.s.l.	615 m a.s.l.	889 m a.s.l.	1317 m a.s.l.	1521 m a.s.l.	2080 m a.s.l.	2540 m a.s.l.	2981 m a.s.l.	3425 m a.s.l.
Anthidiellum sp1	1	1	0	0	0	0	0	0	0	0
Apis mellifera	45	17	40	24	17	24	5	9	19	1
Augochlora sp1	0	1	0	0	2	1	0	0	0	0
Augochlora sp2	2	0	4	1	0	0	0	0	0	0
Augochlora sp3	0	0	0	2	0	0	0	0	0	0
Augochlora sp4	0	0	0	0	4	0	0	0	0	0
Augochloropsis ignita	0	0	0	0	4	0	0	0	0	0
Bombus ephippiatus	0	0	0	0	0	0	0	0	7	3
Bombus huntii	0	0	0	0	0	17	3	5	1	9
Bombus medius	0	0	0	1	0	0	0	0	0	0
Bombus pullatus	0	0	0	0	0	3	0	0	0	0
Bombus trinominatus	0	0	0	0	0	1	19	18	0	0
Calliopsis (Calliopsima) sp2	0	0	3	0	0	0	0	0	0	0
Calliopsis (Verbenapis) sp1	1	0	0	0	0	0	0	0	0	0
Centris analis	0	0	0	0	0	2	0	0	0	0
Centris badia	16	0	0	0	0	0	0	0	0	0
Centris nitida	0	0	0	0	0	2	0	0	0	0
Ceratina sp1	0	0	2	1	0	0	0	0	0	0
Ceratina sp2	8	32	0	0	0	0	0	0	0	0
Ceratina sp3	0	0	1	0	0	0	0	0	0	0
Ceratina sp4	0	0	0	0	0	0	0	4	0	0
Ceratina sp5	0	0	1	0	0	0	0	0	0	0
Ceratina sp6	0	0	0	0	6	8	0	0	0	0
Ceratina sp7	0	0	0	6	0	0	0	0	0	0
Chilicola sp1	0	0	0	0	13	0	0	0	0	0
Euglossa (*Euglossa*) *variabilis*	0	0	0	9	0	3	1	0	0	0
Exomalopsis sp1	2	3	0	5	0	0	0	0	0	0
Exomalopsis sp2	0	0	0	0	1	2	0	0	0	0
Frieseomelitta nigra	1	9	3	1	0	0	0	0	0	0
Habralictus sp1	0	0	0	0	0	0	1	0	0	0
Heriades sp1	0	0	0	2	0	0	0	0	0	0
Lasioglossum (*Dialictus*) sp1	0	0	0	0	0	0	5	0	0	0
Lasioglossum (*Dialictus*) sp2	0	0	1	5	3	5	0	0	0	0
Lasioglossum (Dialictus) sp3	0	0	0	0	0	0	0	1	11	12
Lasioglossum (*Dialictus*) sp4	0	0	0	0	0	4	0	14	0	0
Lasioglossum (Eickwortia) sp1	0	0	0	0	7	0	0	0	0	0
Lasioglossum (Lasioglossum) aequatum	0	0	0	0	0	0	0	1	0	0
Megachile (Callomegachile) sp4	0	0	1	0	0	0	0	0	0	0
Megachile sp1	0	1	0	0	0	0	0	0	0	0
Megachile sp2	0	0	0	2	0	0	0	0	0	0
Megachile sp3	0	0	0	3	0	2	0	0	0	0
Melissodes sp1	0	1	0	1	0	0	0	0	0	0
Melissodes sp2	0	0	0	0	0	3	0	0	0	0
Melissodes sp3	3	1	0	0	0	0	0	0	0	0
Melissodes sp4	1	0	0	0	0	0	0	0	0	0
Melissoptila sp1	0	13	0	0	0	0	0	0	0	0
Mesoplia sp1	10	0	0	0	0	0	0	0	0	0
Paratetrapedia sp1	0	0	0	0	1	0	0	0	0	0
Plebia moureana	0	0	0	0	0	1	0	0	0	0
Pseudaugochlora sp1	0	0	0	0	0	3	0	0	0	0
Svastra sp1	0	0	0	0	0	0	1	0	0	1
Temnosoma sp1	0	1	0	1	0	0	0	0	0	0
Trigona fulviventris	0	0	0	0	0	9	0	0	0	0
Xylocopa (*Neoxylocopa*) *nautlana*	0	0	0	0	0	4	0	0	0	0
Xylocopa mexicanorum	2	0	0	0	0	0	0	0	0	0
Xylocopa sp1	0	0	0	0	0	2	0	0	0	0