Revista de Biología Tropical, ISSN: 2215-2075, Vol. 74: e2026278, enero-diciembre 2026 (Publicado May. 15, 2026)

REVISTA DE
Biología Tropical

https://doi.org/10.15517/wfnx9b94

Altitudinal gradients drive strong species turnover in epigeous ant communities of the Colombian Andes

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Received 07-VII-2025. Corrected 25-VIII-2025. Accepted 15-IV-2026.

ABSTRACT

Introduction: Epigeous ants are widely used as bioindicators to test ecological and biogeographic hypotheses. In tropical regions, elevation is a key driver of biodiversity patterns due to the rapid ecosystem shifts with increasing altitude.

Objective: To examine the distribution and turnover of epigeous ants along an altitudinal gradient (1 000-2 800 m asl) on the opposite slopes of the Western and Central Andean cordilleras in the tropical belt of Colombia, South America.

Methods: Intensive field sampling of ants was conducted, and Zeta diversity was used as an analytical metric to assess spatial diversity components within a multi-site partitioning framework, given its sensitivity to richness differences among habitat types.

Results: A total of 204 ant species were recorded: 128 on the Western Cordillera and 131 on the Central Cordillera. Myrmicinae was the most diverse subfamily, represented across all elevational bands. The mid elevation band (1 500 m asl) exhibited the highest diversity in both cordilleras, while the 2 800 m asl band showed the lowest. The 1 500 m band on the Central Cordillera harbored 71 species, in contrast, the 2 800 m band on the Western Cordillera had only two species. Ant community composition on opposite flanks of the Western and Central Cordilleras showed a high turnover, with only three species occurring across all five elevational bands in both ranges. The ant communities were dominated by rare species or those with low capture frequencies, likely reflecting the interaction of biotic and abiotic factors specific to each elevational life zone.

Conclusions: These findings confirm that each altitudinal gradient is home to specific ant communities that respond to the environmental, historical, and biogeographical conditions of each mountain range. Likewise, it is confirmed that environmental and spatial factors determine the composition of ants and the replacement rate of the community.

Key words: ant diversity; environmental filtration; distribution patterns; strategic ecosystems; tropical rainforest.

RESUMEN

Gradientes altitudinales impulsores del fuerte recambio de especies en las comunidades de hormigas epigeas de los Andes colombianos

Introducción: Las hormigas epigeas se utilizan ampliamente como bioindicadores para comprobar hipótesis ecológicas y biogeográficas. En las regiones tropicales, la altitud es un factor clave en los patrones de biodiversidad debido a los rápidos cambios en los ecosistemas a medida que aumenta la altitud.

Objetivo: Examinar la distribución y el recambio de las hormigas epigeas a lo largo de un gradiente altitudinal (1 000-2 800 m.s.n.m.) en las laderas opuestas de las cordilleras occidental y central de los Andes, en el cinturón tropical de Colombia, Sudamérica.

Métodos: Se llevó a cabo un muestreo intensivo de hormigas en el campo y se utilizó la diversidad Zeta como métrica analítica para evaluar los componentes de la diversidad espacial dentro de un marco de partición multisitio, dada su sensibilidad a las diferencias de riqueza entre los tipos de hábitat.

Resultados: Se registraron un total de 204 especies de hormigas: 128 en la cordillera occidental y 131 en la cordillera central. Myrmicinae fue la subfamilia más diversa, representada en todas las bandas altitudinales. La franja de altitud media (1 500 m.s.n.m.) presentó la mayor diversidad en ambas cordilleras, mientras que la franja de 2 800 m.s.n.m. mostró la menor. La franja de 1 500 m en la Cordillera Central albergaba 71 especies, en contraste, la franja de 2 800 m en la Cordillera Occidental sólo tenía dos especies. La composición de la comunidad de hormigas en los flancos opuestos de las cordilleras Occidental y Central mostró una alta rotación, con solo tres especies presentes en las cinco bandas altitudinales de ambas cordilleras. Las comunidades de hormigas estaban dominadas por especies raras o con bajas frecuencias de captura, lo que probablemente refleja la interacción de factores bióticos y abióticos específicos de cada zona de vida altitudinal.

Conclusiones: Estos hallazgos confirman que cada gradiente altitudinal alberga comunidades específicas de hormigas que responden a condiciones ambientales, históricas y biogeográficas de cada cordillera, así mismo, se confirma que los factores ambientales y los espaciales determinan la composición de hormigas y la tasa de reemplazo de la comunidad.

Palabras clave: diversidad de hormigas; filtración ambiental; patrones de distribución; ecosistemas estratégicos; bosque tropical.

INTRODUCTION

Colombia is located within the tropical belt and features a unique geographic position that harbors a remarkable diversity of ecosystems, ranging in elevation, from sea level to high Andean peaks (Pérez-Escobar et al., 2022; Rangel-Ch., 2015). This altitudinal complexity is shaped by the presence of the three Andean cordilleras (Western, Central, and Eastern) that traverse the country (Iriarte, 2006; Myers et al., 2000; Narváez-Vidal et al., 2024). The climatic shifts driven by this mountainous geomorphology pose adaptive challenges for ectothermic organisms, including ants, a highly diverse and ecologically dominant insect group in tropical ecosystems (Folgarait, 1998). Ants are highly sensitive to changes in temperature, humidity, precipitation, habitat transformation, and anthropogenic pressures (Guerrero & Sarmiento, 2010; Kaspari & Majer, 2000; Stuble et al., 2013).

Globally, ants inhabiting elevational gradients have been the subject of numerous studies, and Colombia is not the exception. Regional studies (v.g. Guerrero & Sarmiento, 2010) on the Northwestern slope of the Sierra Nevada de Santa Marta, and more localized efforts, such as those conducted in Tatamá National Natural Park (Idarrága-Giraldo, 2021) and Farallones de Cali National Natural Park (Narváez-Vidal et al., 2024), consistently report a decline in species richness with increasing elevation. These contributions are valuable not only for their findings but also for their spatial replicability and their capacity to reveal sharp environmental changes over relatively short distances (Kaspari & Majer, 2000; Longino & Branstetter, 2019; Longino & Colwell, 2011; Sanders, 2002). Beyond richness patterns, other ecological dimensions, such as the compositional turnover and the ecological mechanisms driving these changes, remain essential areas of inquiry, especially in the face of critical challenges like climate change (Ripple et al., 2024).

In ants, community richness is shaped by factors such as area, temperature, humidity, and soil nutrients, with temperature being a key predictor of assemblage composition, along with biotic interactions and historical factors (Longino & Colwell, 2011). In complex landscapes like the Andes, it becomes feasible to evaluate species turnover across elevations in different mountain ranges simultaneously, providing insights into their response to climatic variation. This is particularly important given the ongoing threat of habitat loss due to anthropogenic development, especially within certain altitudinal belts. Combined with climate change, such pressures could result in local, regional, or even global extinctions, especially among endemic species (Colwell et al., 2008; Hethcoat et al., 2019; Longino & Colwell, 2011; Parra-Sanchez et al., 2025). Understanding the patterns and drivers of species turnover across elevational belts is, therefore, essential to update conservation and restoration actions (e.g., connectivity) in a megadiverse country like Colombia, which is also dramatically affected by climatic global change.

Ants may exhibit diverse patterns of richness and composition along elevational gradients, shaped by specific biological adaptations and ecological processes. Two main distribution patterns have been described: a mid-elevation peak in species richness (e.g., Sanders, 2002), and a monotonic decline with increasing altitude (Fisher, 1996; Stevens, 1992). The first pattern may result from factors such as higher productivity, larger available area, or the overlap of species' elevational ranges around the center of the gradient, leading to great richness, even in the absence of the productivity effects (Colwell & Lees, 2000). The second pattern aligns with Rapoport's rule, which suggests that species at higher elevations have broader elevational ranges due to greater environmental variability, although fewer species are able to tolerate such conditions. In contrast, lower elevations, with more stable climates, allow more species to coexist within narrower ranges (Stevens, 1992). Longino and Colwell (2011), suggest these patterns result from a combination of historical, evolutionary, and ecological factors, many of which are influenced by paleoclimatic events such as the current interglacial period, which has shifted species ranges in upslope. Furthermore, lowland species often experience a lack of competition at their lower range boundaries, enabling unique assemblages that occupy broad environmental niches. In contrast, highland species inhabit more restricted climatic zones and exhibit faster species replacement with elevation (Gaston, 2000; Gaston & Spicer, 2001; Janzen, 1967; Stevens, 1992).

Despite these general patterns, distribution of ants along elevational gradients remains controversial. While some studies show a monotonic decline in species richness with elevation (Fisher, 1996; Guerrero & Sarmiento, 2010; Longino & Colwell, 2011; Narváez-Vidal et al., 2024), others report richness peaks at mid-elevations, a pattern considered common in nature (Longino & Branstetter, 2019; Sanders, 2002). Even the interpretation of Rapoport's rule is debated: Rahbek (1995) argues that it describes a monotonic decline in diversity with elevation, whereas Sanders (2002) and Pérez-Escobar et al. (2022) contend it may also help explain mid-elevation richness peaks.

Given the ongoing controversy and the contrasting patterns of species diversity, examining compositional combinations along altitudinal gradients can be useful for understanding biodiversity responses to ecological changes and the availability of biodiversity resources. Parra-Sánchez et al. (2025), suggest the importance and urgency of understanding how community assembly occurs in natural habitats and how it is restructured under the influence of both natural and anthropogenic drivers across different spatial scales (local, landscape, and regional). At the landscape scale, anthropic transformation and subsequent land-use changes modify the structural and functional connectivity of natural habitats through habitat loss and fragmentation (Fahrig, 2003; Parra-Sanchez et al., 2025). The reduction in connectivity interrupts recolonization processes, hence favoring the replacement of species with restricted distribution ranges by those with wider distribution ranges (Fahrig, 2002; Fahrig, 2003; Fahrig, 2017).

Building on the previous discussion, our study employs zeta diversity as an analytical framework to quantify ant species distribution and turnover across multiple sites and spatial scales (McGeoch et al., 2019), incorporating the influence of natural drivers such as altitude and temperature. Zeta diversity allows a more detailed understanding of biodiversity change (Hui & McGeoch, 2014) by generating a series of values (ζ1, ζ2, ζ3, ..., ζN), where each value represents the number of species shared among different combination of sites, encompassing rare, intermediate, and common species that drive compositional turnover (Hui et al., 2018; Latombe et al., 2018; Parra-Sanchez et al., 2025).

Unlike pairwise beta diversity, equivalent to zeta diversity of order two (Magurran & Henderson, 2010; Shimadzu et al., 2015), which tends to be biased toward the contribution of rare species and may overestimate their influence (Jost, 2007), zeta diversity allows multi-site assessments of assemblage structure, less biased by rare species and providing insights into the rate and nature of compositional turnover. As zeta order increases, rare species are progressively excluded, enabling the detection of the differential contribution of the entire spectrum of species to compositional turnover across a range of orders (McGeoch et al., 2019; Parra-Sanchez et al., 2025).

In this context, the present study aims to understand how epigeous ant communities vary in species richness, composition and species turnover along an elevational gradient (1 000-2 800 masl) by examining two parallel mountain ranges adjacent to the Cauca River Valley in Colombia. Specifically, we assessed how environmental variation, particularly elevation and temperature, influences these patterns, and whether species with specialized habits and narrow environmental tolerances could be more vulnerable to climate change.

MATERIALS AND METHODS

Study area: The study area is in Southwestern Colombia, in the central region of the Valle del Cauca department. This inter-Andean valley separates two neighboring mountain ranges (hereafter referred to as "Cordilleras") involving an altitudinal gradient ranging from 1 000 masl (the elevation of the valley floor where the Cauca River flows South to North), up to 2 800 masl (the highest elevation involved in this study). The valley is flanked by the opposing slopes of the Central and Western cordilleras (Cordilleras "Central" and "Occidental" are the Spanish proper names of these two mountain ranges) (Fig. 1). The study area spans four ecosystem types (Table 1), from tropical dry forest (Bs-T) at the lowest elevations to lower montane very humid forest (Bmh-MB) at the highest based on the life zone classification system of Holdridge as adapted for Colombia by Espinal (1968). Using the Cauca River valley as a central reference, five altitudinal bands were selected along "mirror" slopes on each Cordillera, ranging from 1 000 to 2 800 masl. Consequently, five sampling sites were established on each slope at approximately 500 m intervals (Fig. 1). During sampling, temperature and relative humidity were recorded hourly for 15 consecutive days using data loggers (Elitech model RC-51H, Table 1). All reported data corresponds to ants collected in forested habitats or natural, unmanaged ecosystems specific to each elevation.

Epigeous ant sampling: Ants are highly conspicuous organisms in soil ecosystems, participating in a wide variety of ecological interactions (Del Toro et al., 2012; Donoso, 2017). Their role is crucial in key processes such as herbivory, predation, scavenging, the establishment of mutualistic relationships with other organisms and recirculation of nutrients in the soil (Urrego-Sánchez & Camero, 2020; Schultz & McGlynn, 2000). Because of their significant

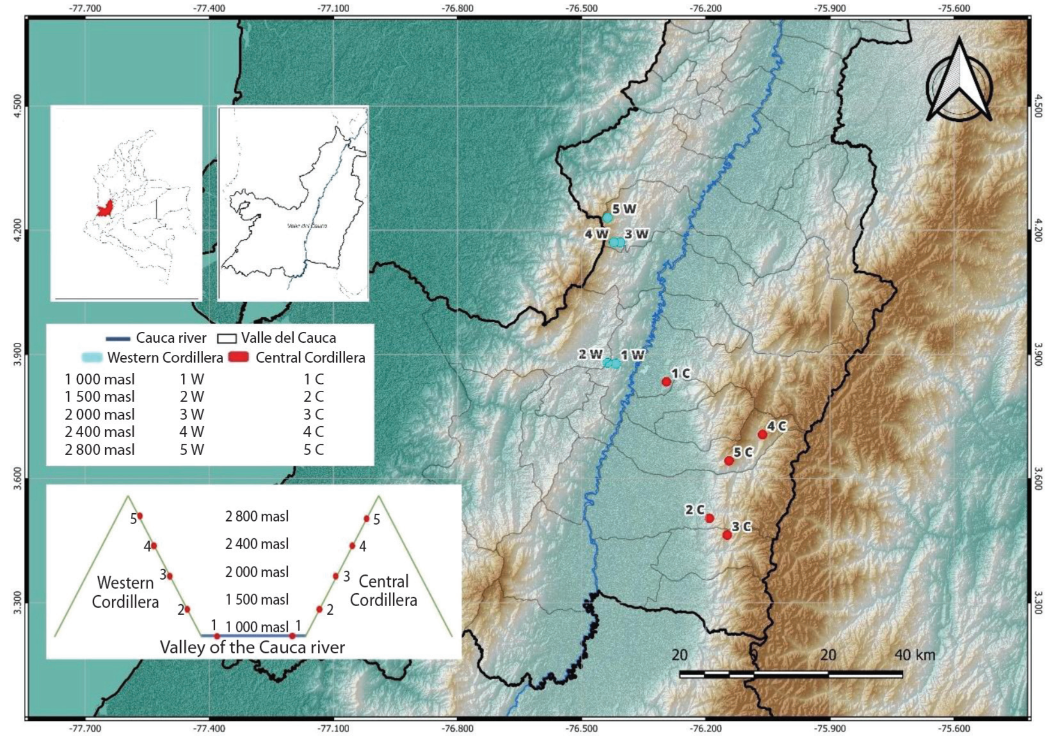

Fig. 1. Location of the study area: Colombia and Valle del Cauca Department (upper left corner), sampling sites along five elevational bands on the opposite slopes of the Western and Central Andes and the geographical valley of the Cauca River. The cordilleras profiles are shown at the lower left corner of the figure. **Note.** The map was created by the author based on a digital elevation model (DEM) obtained from *Colombia en mapas* (Instituto Geográfico Agustín Codazzi [IGAC], 2024).

Table 1

Environmental characterization of sampling localities.

Localities	Code	Cordillera	Coordinates		Altitude (m asl)	Landscape	Life zone	T °C Mean	% HR Mean
			Latitude	Longitude					
Fca. Monteloro	5W	Western	4.2297	-76.4364	2 800	Mountain	Bmh-MB	12.97	89.5
RNSC Madhú	5C	Central	3.6429	-76.1436	2 800	Mountain	Bmh-MB	14.92	97.3
Fca. Gratinianos	4W	Western	4.1716	-76.4237	2 400	Mountain	Bmh-T	16.27	89.69
RNSC El Pailón	4C	Central	3.7052	-76.0647	2 400	Mountain	Bmh-T	15.23	85.64
RNSC El Silencio	3W	Western	4.1704	-76.4064	2 000	Mountain	Bmh-T	18.29	88.43
RNSC El Triunfo	3C	Central	3.4632	-76.1479	2 000	Mountain	Bmh-T	17.45	88.03
RNF Bosque de Yotoco	2W	Western	3.8776	-76.4377	1 500	Mountain	Bh-T	21.91	89.29
Fca. El Canto ícaro	2C	Central	3.5037	-76.1912	1 500	Mountain	Bh-T	21.05	84.9
Rest. El Mirador	1W	Western	3.8782	-76.4143	1 000	Geographic valley	Bs-T	22.15	82.65
PNR. El Vínculo	1C	Central	3.8343	-76.2954	1 000	Geographic valley	Bs-T	25.11	73.82

All acronyms come from Spanish according to Espinal (1968): Bmh-MB = Very humid low montane forest, Bmh-T = Very humid tropical forest, Bh-T = Humid tropical forest, Bs-T = Dry tropical forest.

biomass, susceptibility to environmental stress, and crucial role in terrestrial ecosystems, epigeous ants are recognized by many researchers as a vital indicator group for assessing environmental changes (Andersen et al., 2002; Donoso, 2017; Fowler & Delabie, 1995; Urrego-Sánchez & Camero, 2020). Hence, we focused on this stratum thus pursuing the objectives of this study. At each elevation, three plots (10 m^2) were randomly established, with a minimum distance of 50 m between them. Within each plot, five pitfall traps were installed, each filled with a solution of 5 % acetic acid, one pound of salt per 20 l of solution, and 5 gr liquid soap. This solution was prepared once and used throughout the sampling period. Traps were operated for 15 days, buried at ground level, and camouflaged with surrounding vegetation. Sampling was complemented by manual collection (1 hour/person per plot), targeting all accessible substrates, including soil, leaf litter, understory vegetation, decomposing trunks, and hollow or dry twigs. Additionally, leaf litter was collected from 1 m^2 at four randomly selected points within each plot and processed by visual screening.

Each altitudinal band comprised 42 samples, totaling 420 samples across both gradients. All individuals were counted and identified to the highest possible taxonomic resolution using identification keys from Fernández-Castiblanco et al. (2019) and Feitosa and Dias (2024), as well as direct comparison with reference collection specimens from the Entomological Museum of the Universidad del Valle (MEUV), for its acronym in Spanish). Taxonomic verification was conducted with support from expert myrmecologists when needed. Species were functionally classified as forest specialists, generalists, or open-habitat specialists, following the Laboratório de Ecologia de Formigas (UFAC, 2023) application (SMT1). Forest specialists are defined in this study as species that depend exclusively on well-preserved forest habitats, while generalists are capable of inhabiting both forested and altered environments, and finally, open-habitat specialists are restricted to more open or disturbed vegetation types.

All specimens were preserved following standard entomological protocols and deposited in the MEUV collection under collecting permit No. 120, issued by Colombian Ministry of Environment and Sustainable Development (August 24, 2015). An incidence matrix (presence-absence) of samples was elaborated for each elevational band, incorporating environmental variables associated with each study plot.

Statistical analyses: All statistical analyses were conducted exclusively on worker ants. Rescaled zeta diversity was used to calculate diversity components at spatial scales under the same multi-site diversity partitioning framework (Hui et al., 2018; McGeoch et al., 2019), as this metric is more sensitive to richness differences inherent to each habitat types. Therefore, comparisons focused on zeta diversity differences between mountain ranges and forest zones along the altitudinal gradient (Hui & McGeoch, 2014; McGeoch et al., 2019). To complement the analyses, the effective number of species was calculated based on Hill numbers (Cultid-Medina & Escobar, 2019; Jost et al., 2010; Moreno, 2001), and Pearson correlation was used to verify whether diversity decreased or increased with altitude. Species composition and distribution patterns across the altitudinal gradient were explored through non-metric multidimensional scaling (NMDS) to detect structures or clusters in the data, followed by a PERMANOVA test with 999 permutations.

To account for spatial structure, we generated a matrix of spatial variables based on geographic distances using the Principal Coordinates of Neighbor Matrices (PCNM) method (Borcard & Legendre, 2002), incorporating spatial distances among altitudinal bands and between the flanks of the mountain ranges. This method extracts positive eigenvectors from a Euclidean distance matrix of sampling locations, based on multiple coefficients of determination (R^2). These eigenvectors were then used as covariates in a partial Redundancy Analysis (pRDA) following Blanchet et al. (2008). The pRDA was applied to a Hellinger-transformed community matrix (species per site), wich reduces the influence of double absences (Legendre, 2008). In this analysis, the matrix of environmental variables (Altitude, Leaf litter depth, PAP30, T mean, Tmax, Tmin, HR mean, HRmax, HRmin), previously centered and standardized using Z-scores, was used as the explanatory matrix. The significance of the pRDA was tested by ANOVA, and variable selection was performed using the forward selection method with a cut-off value of alpha = 0.05 and based on the R^2 coefficient.

To assess whether the ant community follows a pattern of monotonic decline with altitude, we applied the approach proposed by Sanders (2002) and Longino and Colwell (2011). This involved estimating the altitudinal range for each species as the difference between its maximum and minimum recorded elevations, assuming continuous presence across that interval. All Statistical analysis were conducted in R version 4.3.3. (R Core Team, 2023), using the packages zetadiv (Latombe et al., 2018), vegan (Oksanen et al., 2022), and iNEXT (Hsieh et al., 2022).

RESULTS

A total of 32 321 individuals representing 204 species/morphospecies were recorded, from which 45 were identified as morphospecies given the extreme difficulty to reach the specific identity for being highly complex taxonomic genera groups. The genera with the highest number of morphospecies were *Pheidole* and *Camponotus*, which are megadiverse genera. Identification, mainly in *Pheidole*, is based on the soldier caste, and it is common to collect workers in the field (Fernández-Castiblanco et al., 2019). From the described total species, more than half were present in each of the mountain ranges, this is 128 were recorded in the Western Cordillera, while 131 in the Central Cordillera. Among all these, 51 species/morphospecies were shared between both ranges, and 80 and 77 were exclusive to the Central and Western cordilleras, respectively. Of all the species reported, *Linepithema neotropicum* (Wild, 2007) and *Linepithema piliferum* (Mayr, 1870) were found across all five altitudinal bands in both ranges. However, *Pheidole* sp. 9 is expected to occur along the full altitudinal gradient of the Central cordillera, as it was present in all bands except those at 2 000 and 2 400 masl.

Both elevation gradients exhibited truncated bell-shaped richness curves (SMF1), with peaks above 1 500 masl (with 59 and 71 species in the Western and Central Cordilleras, respectively), followed by the marked decrease in the valley zone at 1 000 masl (with 50 and 61 species in the Western and Central Cordilleras, respectively). At this mid-elevation belt, the most diverse subfamilies were, in order of richness: Myrmicinae, Ponerinae and Formicinae (consistent with patterns observed in other studies). In contrast, the lowest species richness occurred at 2 800 masl in both mountain flanks, with only two and six species recorded in the Western and Central Cordilleras, respectively. At this elevation, only five of the nine subfamilies reported in this study were present, with Dolichoderinae and Dorylinae being the most species-rich (five species each), and Formicinae the least diverse.

The subfamily Myrmicinae was the most diverse among both altitudinal gradients. It was present at all elevations and showed a great representation at 1 000 and 1 500 masl (lower elevations). In contrast, Agroecomyrmecinae and Amblyoponinae were the least represented, each with only one species, restricted to low elevations. Changes in the composition along the elevation gradient were mainly driven by species turnover within genera. The sampled ant species belonged to 59 genera, of which four (*Camponotus*, *Linepithema, Pheidole*, *Neoponera*) included species occurring both in lowlands and highlands sites. The most specious genera were *Pheidole* (40 spp.), *Camponotus* (18 spp.), *Pseudomyrmex* (11 spp.), *Linepithema* (11 spp.), *Strumigenys* (11 spp.), *Crematogaster* (9 spp.), *Solenopsis* (9 spp.), *Cyphomyrmex* (8 spp.) and *Hypoponera* (8 spp.). Conversely, only three genera, *Neivamyrmex*, *Parathrachymyrmex* and *Rophalotrix*, were found exclusively above 2 400 masl each with low diversity and abundance. At elevations between 1 000-1 500 masl, only 31 genera were recorded.

A total of 29 % of the species were forest specialists, 20 % generalists, and 2 % open-habitat specialists (SMT1). The remaining 49 % could be assigned to any category due to a lack available information, either because they are not catalogued or because of their taxonomic resolution at the morphospecies or family level. Similarly, SMF2 shows that forest specialists and generalists exhibited greater diversity at lower elevations, with richness decreasing above 2 400 masl.

Altitudinal variation in species richness: In both mountain ranges, ant diversity decreased with increasing elevation. The decline was steeper in the Western Cordillera than in the Central Cordillera, especially, for hill numbers at q = 0 (Fig. 2). Concerning order numbers q = 1, q = 2, which give more weight to the common and most abundant species, the slopes were less pronounced compared to q = 0 (Fig. 2).

Across both mountain ranges, the greatest number of shared ant species was found between the 1 000-1 500 masl bands, 17 for the Central and 11 for the Western range (Fig. 3). In contrast, the highest elevations (2 400 and 2 800 masl) showed no shared species in the Western Cordillera, and only one species, *Labidus spininodis* (Emery, 1890) was shared in the Central Cordillera. These results highlight strong compositional differentiation at high elevations, a pattern corroborated by the NMDS analyses (stress = 0.1159, Fig. 4) and pRDA ($R^2 = 26.42$, p-value = 0.001, Fig. 5).

At mid-elevation (2 000 masl), the Western Cordillera showed higher similarity in the composition between 2 000 and 2 400 masl (13 shared species), while similarity declined sharply below 2 000 m, with only six species shared between 1 500 and 2 000 masl: *Crematogaster nigropilosa* (Mayr, 1870), *Hypoponera* aff. *punctatissima* (Roger, 1859), *Myrmelachista zeledoni* (Emery, 1896), *Pheidole biconstricta* (Mayr, 1870), *Labidus coecus* (Latreille, 1802) and *Linepithema* sp. In the Central Cordillera no

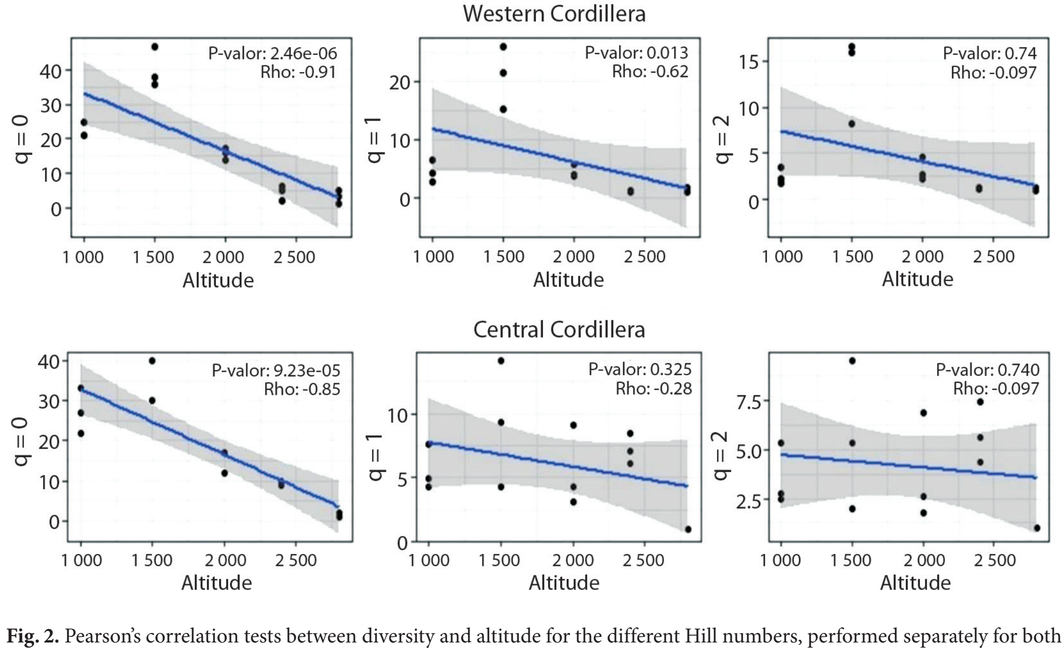

Fig. 2. Pearson's correlation tests between diversity and altitude for the different Hill numbers, performed separately for both mountain ranges: Western (top row) and Central (bottom row). In each case, response plots corresponding to values of q = 0, q = 1 and q = 2 are presented, arranged from left to right in that order.

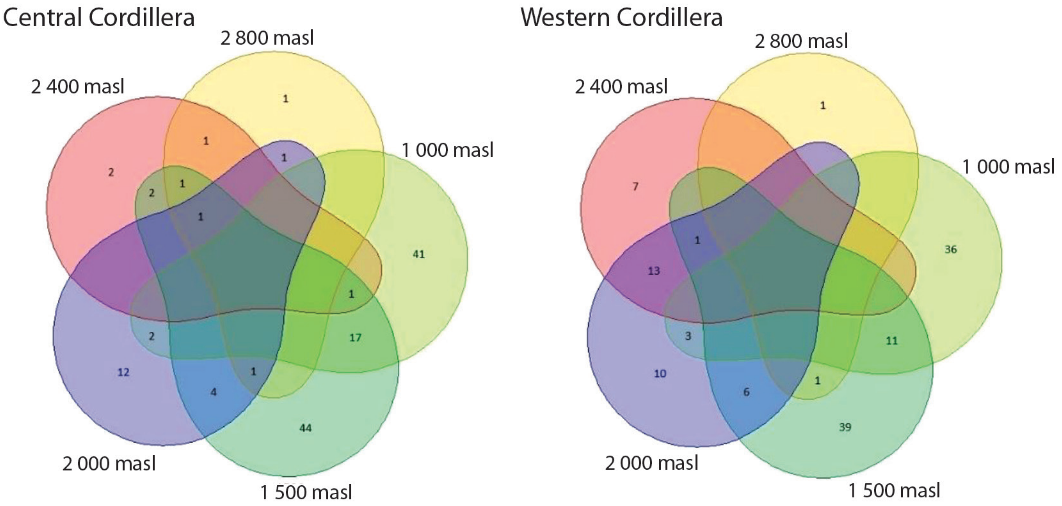

Fig. 3. Venn's diagram shows the similarity of the species community between the altitudinal gradient. **A.** The Eastern flank of the Central Cordillera. **B.** The Western flank of the Western Cordillera.

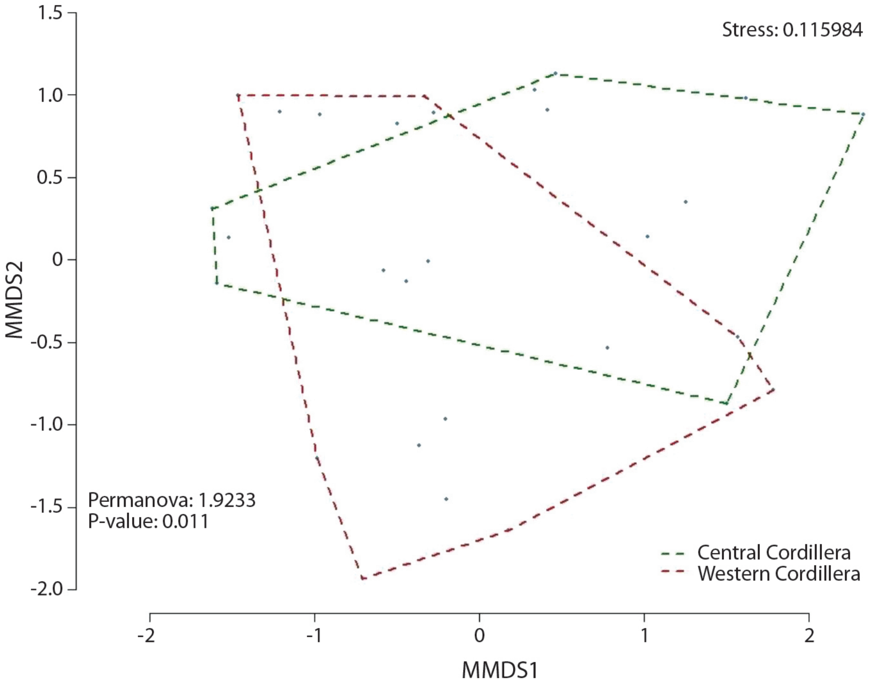

Fig. 4. Non-metric multidimensional scaling for the ant community of the Eastern flanks of the Western Cordillera and Western flanks of the Central Cordillera.

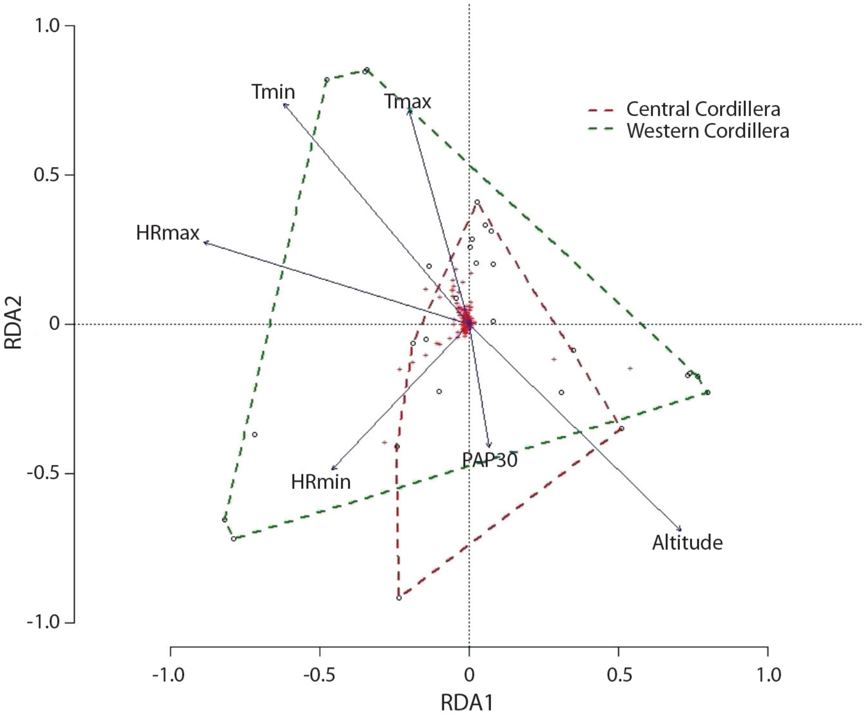

Fig. 5. pRDA analysis for the ant communities of two altitudinal gradients in the central and Western mountain ranges and the Cauca River geographic valley. Altitude is presented in meters above sea level. HRmax: Maximum values of relative humidity. HRmin: Minimum values of relative humidity. Tmax: Maximum temperature values in degrees Celsius. Tmin: Minimum temperature values in degrees Celsius. PAP30: Perimeter at chest height greater than 30.

species are shared between 2 000-2 400 m, and only four species, *C. nigropilosa*, *H.* aff. *punctatissima*, *M. zeledoni*, *P. biconstricta*, were found between elevations 1 500-2 000 masl. Notably, species composition was more similar between cordilleras at these mid-elevations (Fig. 3).

Species at lower and mid elevations (1 000-2 000 masl) tended to have broader altitudinal ranges, while those at high elevations (2 000-2 800 masl), exhibited narrower distributions.

Differentiation and structure of the community: The NMDS ordination model for both mountain ranges yielded a stress of 0.1159, indicating congruence in the associations of the ant assemblages for the sampled flanks. The polygons delimit the composition related to each mountain range, thus the interaction between the mountain ranges largely explains the variation in the composition of the species (PERMANOVA: F = 1.92, $R^2 = 0.0665$, $p < 0.011$), and the differences between ant communities between the flanks of the mountain ranges (Fig. 4). However, the proportion of shared species is perhaps equal to or like that of dissimilar species between both flanks evaluated.

Environmental and spatial factors affecting community composition: The permutation test (F = 2.70, p = 0.001) confirmed a significant association between ant composition on the Western flanks of the Central Cordillera and the Eastern flank of the Western Cordillera ($R^2 = 0.2642$, $p < 0.05$, Fig. 5). The pRDA model explained 60.05 % of the variation in ant incidence between mountain ranges, with 24.08 % of the variance explained by covariates (spatial distances between sampling sites) and an additional 35.97 % corresponding to environmental variables (Altitude, PAP30, Tmax, Tmin, HRmax, HRmin). The Redundancy Analysis (RDA1 and RDA2 axes), accounted for 72.46 % of the variance explained (41.45 and 31.01 %, respectively). This indicates that the environmental gradients represented by these two axes are the main drivers of community structuring. The unexplained proportion of the model was 39.96 %, which is attributed to noise and/or unmeasured factors, such as biotic interactions and site history.

Zeta diversity pattern: In Fig. 6A, the zeta diversity decay curve illustrates high species turnover, as well as compositional heterogeneity along the elevation gradient. The sharp initial decrease indicates a high renewal and low species overlap between elevation bands, meaning that communities change rapidly as altitude increases. This decline reached zeta diversity of order 8 for both cordilleras (AIC = 5.699 for the Western and AIC = 9.558 for the Central). The Fig. 6B shows the species retention rate. In the Central Cordillera, the species retention increased to order 4-5, while in the

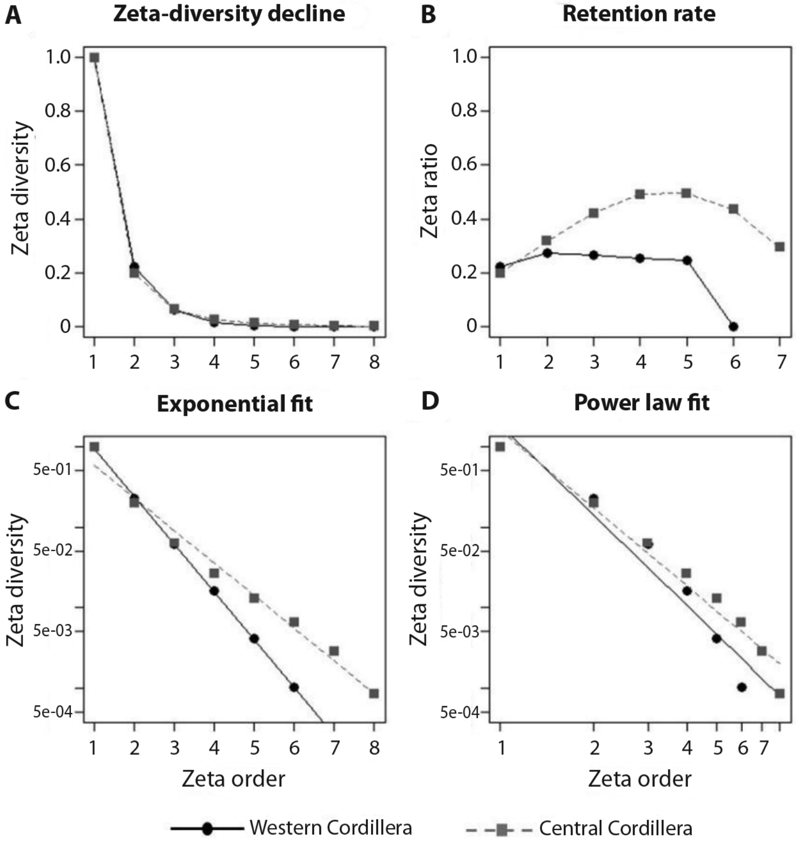

Fig. 6. Zeta diversity analysis for the ant community of the altitudinal gradient of two opposite flanks of the Western and central mountain range and the geographic valley of the Cauca River. **A.** Shows the decline in zeta diversity as a function of zeta order, showing the progressive decrease in the average number of shared species as the number of sites considered increases. **B.** Species retention rate (zeta ratio) across zeta orders, indicating the probability that species will remain shared as the number of sites increases. **C.** Exponential fit of zeta diversity (log scale) against zeta order, used to evaluate whether species turnover is dominated by stochastic processes or a constant probability of local extinction. **D.** Power-law fits zeta diversity (log scale) against zeta order, indicating the influence of deterministic processes, environmental structuring, or spatial constraints on species composition.

Western Cordillera it peaked at order two and decreased sharply by order five. This suggests that, above order five, the probability of species being retained across multiple sites decreases significantly, indicating an almost complete species renewal along the gradient. Since this strong compositional turnover can be partly explained by the low prevalence of many species in the samples, we used linear regression. Therefore, to evaluate whether this pattern followed a power law or an exponential decay, linear regression was used (Fig. 6C, Fig. 6D). The turnover fits a power law distribution, in turn showing a rapid exponential decline suggesting a non-linear turnover following a non-scale pattern of few shared species, which suggests that niche differentiation, rather than stochasticity, may underline the observed diversity patterns, a finding that was also observed in the NMDS results.

To compare different diversity metrics and assess how the species similarity changes with elevation, we evaluated ant richness across opposite flanks of the Cordilleras (SMF1). Both beta diversity (Jaccard) and normalized zeta diversity (equivalent to Jaccard n-site similarity) were considered (Fig. 7) Jaccard similarity showed steeper increase with elevation, indicating overestimation of shared species when only pairwise comparisons are considered. In contrast, normalized zeta diversity revealed a more gradual decline, suggesting that species heterogeneity across multiple elevation bands is lower than expected. This is because zeta diversity inherently includes all sites situated between the fixed point and a specified elevation band in its calculation, consequently leading to a lower count of shared species compared to direct comparisons between the fixed point and the specified band, as in Jaccard. This implies more complex patterns of species turnover, where different species dominate at different elevations, a pattern that corresponds with an increase in rare species at higher elevations and between mountain ranges.

DISCUSSION

Altitudinal variation in species richness: In Colombia, ants inhabit nearly all ecosystems,

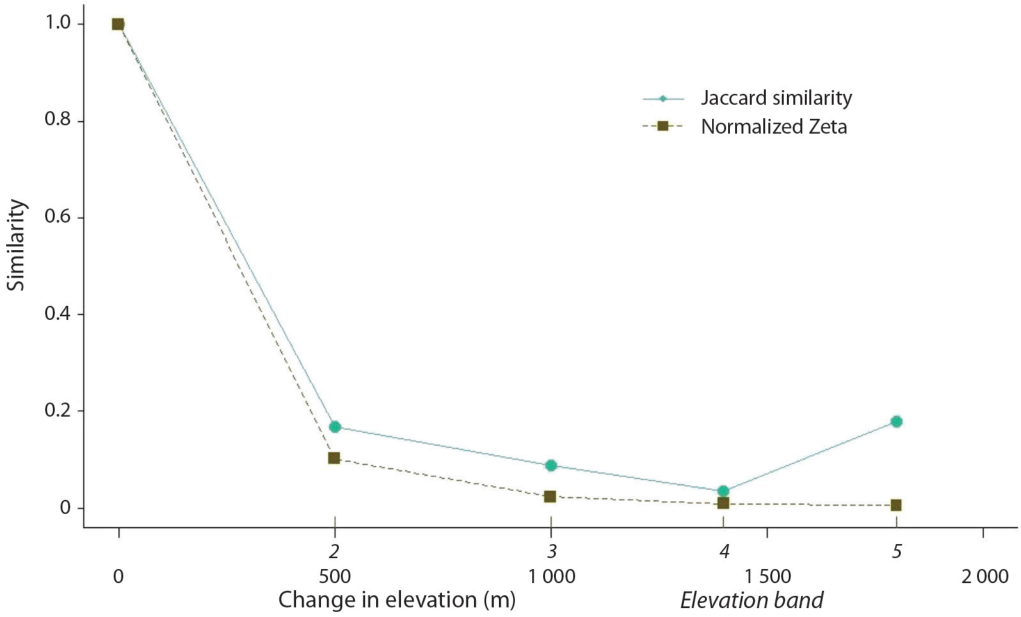

Fig. 7. Decline of ant diversity of the altitudinal gradient of two opposite flanks of the Western and Central cordillera and the geographic valley of the Cauca River, using two similarity metrics: normalized zeta and Jaccard similarity.

ranging from sea level to elevations above 3 000 masl. Although this study did not include sites above 3 000 masl, Narváez-Vidal et al. (2024) reported three ant species at elevations up to 3 200 masl in the Farallones de Cali National Natural Park (Western Cordillera), but none at 3 800 masl. This pattern was confirmed in our study, where no ants were found in some sampling units at 2 800 masl. Although our study covered a wide altitudinal gradient, it did not include sites below 1 000 masl, as such elevations are absent from the inter-Andean valley of the upper Cauca River basin, and it was not possible to sample lower elevations for topographic reasons.

There is consistent evidence supporting a pattern of declining species richness with increasing altitude in tropical mountains. In this context, our findings align with those of Narváez-Vidal et al. (2024) and other studies (Guerrero & Sarmiento, 2010; Longino & Colwell, 2011; Rodríguez & Lattke, 2012), which report a decrease in richness at higher elevations. In the Western Cordillera, this decline was more pronounced than in the Central Cordillera (q = 0, Fig. 2). The declining pattern likely reflects a combination of ecological traits, evolutionary history, and biogeographic processes that shape ant communities because life zones sharply change in tropical regions.

For abundant species (q = 1), the most frequent species in the Western Cordillera followed the altitudinal gradient, whereas in the Central Cordillera, no clear pattern of decline with altitude was observed (Fig. 2). This behavior may be explained by the hypothesis proposed by Longino and Colwell (2011), who argue that temperature is a key factor in predicting ant presence, linking local patterns to broader global biodiversity trends.

Differentiation and structure of the community: Anthropogenic disturbance is believed to be a key factor influencing ant composition along altitudinal gradients, although it was not directly measured in this study. While our sampling focused on forest remnants within each altitudinal belt, none of the sites represented pristine conditions. The sampled forests were structurally intact but disturbed, an expected scenario in a region with a long history of human settlement.

As a result of prolonged anthropogenic transformation, this study reports the widespread presence of two generalist species (*L. neotropicum* and *L. piliferum*), recorded throughout the entire gradient in both mountain ranges. Their ecological plasticity enables them to persist in both natural and human-modified habitats. Escárraga & Guerrero (2016) also documented a broad altitudinal distribution for these species: from 0 to 2 600 masl for *L. neotropicum*, and up to 2 800 masl for *L. piliferum*.

Parra-Sánchez et al. (2025) found that anthropic tensors shape the composition of bird, beetle, and orchid communities, effectively nullifying the influence of altitude on their composition. In contrast, our study found that, while the epigeous ant community responded to altitudinal variation, geographical and environmental factors, habitat transformation also played a role in shaping community composition and structure.

Consequently, the number of habitat-based groups decreased with altitude. This pattern may be related to the fact that seven of the ten sites evaluated were reserves dedicated exclusively to conservation, each under different protection categories (Table 1). These categories appeared to influence forest structure: protected reserves differed from forests located on private farms, some of which were civil society reserves maintained by landowners. However, this distinction was not considered in the diversity analyses, as all sampled habitats were classified as forested and structurally mature.

The high dominance of rare species (low-frequency) and the low similarity of shared species along altitudinal gradients suggest that each elevation band harbours distinct ant assemblages (Fig. 3, Fig. 4). These differences reflect a combination of ecological, landscape, historical, and environmental factors that vary both with altitude and between mountain ranges. NMDS ordination (stress 0.1159) and

PERMANOVA analyses ($F = 1.92$, $R^2 = 0.0665$, $p < 0.011$) confirm this pattern, revealing a significant separation in species composition between the Western and Central Cordilleras.

From an ecological theory perspective, this pattern can be interpreted through the lens of island biogeography (MacArthur & Wilson, 1967), wherein each mountain range functions as an isolated unit that fosters rare species assemblages due to limited dispersal and environmental heterogeneity, a pattern observed in pRDA (Fig. 5) and the Zeta diversity analysis (Fig. 6). Similarly, the theory of environmental filters helps explain how altitudinal gradients and local conditions selectively shape community composition (Kraft et al., 2015; Longino & Colwell, 2011; Rahbek, 1995).

The observed overlap is likely attributable to shared species with broad ecological niches, eurytopic, or neutral responses to environmental variation, while the distinct groupings reflect habitat selection processes and the influence of geographical isolation. This suggests that altitudinal gradients in each mountain range are not equivalent, and that regional diversity is maintained through their ecological complementarity. Therefore, the generalized prediction of decreasing ant diversity pattern with altitude in tropical mountains is reinforced in this study. A similar pattern was reported by Narváez-Vidal et al. (2024) along an altitudinal gradient in the Western Cordillera, underscoring the importance of conservation strategies that account for metacommunity structure and the biogeographic uniqueness of the Andes (Baselga, 2010; Leibold et al., 2004).

Environmental and spatial factors affecting community composition: Using pRDA with appropriate environmental and spatial covariate showed that decline in species diversity and the high turnover of ant communities observed along both altitudinal gradients can be attributed to temperature and spatial distance, as illustrated in Fig. 7 and supported by Longino & Colwell (2011). These factors are key drivers of ant community composition. Temperature variation is closely linked to altitude, which in turn shapes life zones, vegetation structure, and habitat heterogeneity along the gradient.

In tropical regions, such as Colombia, temperature decreases at an average rate of approximately 0.65 °C per 100 m increase in altitude, with greater thermal variability at higher altitudes. However, unlike temperate zones, tropical mountains experience little seasonal variation in temperature, which removes an important ecological filter affecting organisms elsewhere (Colwell et al., 2008; Janzen, 1967; Longino & Branstetter, 2019).

In addition, lowland species are usually stenothermic, adapted to more restrictive environmental conditions and limited by their tolerance to cold. For instance, the pRDA test for *Atta cephalotes*¸ indicated that this species was associated with conditions of lower altitude and higher temperature. This physiological limitation makes lowland species more vulnerable to climate change (Longino & Branstetter, 2019; Sanders, 2002; Stevens, 1992). Conversely, higher altitude species are usually eurythermic and can tolerate warmer temperatures than they usually experience. This is the case of *L. spininodis* and *Neoponera carbonaria*, both with a high positive score on axis 1 and negative on axis 2. These two species were associated with higher elevation and lower temperature units. Although this issue is still under debate and it is accepted that temperature is strongly correlated with ant distribution, some studies argue that low temperatures (such as those found in paramo ecosystems) are the ones who most determines the pattern since this condition reduce ant metabolic activity, larval development, and their ability to colonize or persist in unsuitable environments (Kunene et al., 2022). From a macroecological perspective, these patterns are explained as the result of temperature and precipitation variation along the altitudinal gradient (Kaspari & Majer, 2000).

Our results suggest that ant communities and/or composition are influenced by predictor variables such as geographic distances, which in turn reflect a multi-scale process of species turnover. For both mountain ranges, environmental factors (altitude, for Western and temperature and humidity, for Central) were determinant in driving turnover along each gradient, because the community structure was adjusted according to the ecological tolerances of each species and each community was structured according to environmental filters specific to each mountain range, as well as dispersal limitations (Kraft et al., 2015). Our grouping analyses coincided in supporting that each mountain range functions as a unit semi-isolated by a geographic barrier, such as the inter-Andean valley; however, the composition of myrmecofauna and the turnover of species within (and between) each mountain range give structure to the regional diversity (gamma diversity). On the other hand, although not measured here, factors such as climatic changes during the current interglacial period, could also be influenced by potentially causing altitudinal changes in species distribution through interspecific competition at ecological boundaries (Longino & Colwell, 2011).

Zeta diversity pattern: The steep drop shows that few species are shared, suggesting a high turnover in species (Parra-Sanchez et al., 2025). This is consistent with niche theory, where species respond to environmental filtering by deterministic mechanisms (Kraft et al., 2015; Leibold et al., 2004). Geographic distances also influence community composition, especially when assessing turnover between locations. This was evident in our zeta diversity analyses: as comparisons between multiple locations increased, species overlap decreased and rare species became more dominant (Fig. 6) (Hui & McGeoch, 2014; McGeoch et al., 2019; Parra-Sanchez et al., 2025).

Regarding species retention, it was observed that the Central Cordillera harbors more generalist or widely distributed species, resulting in a more stable community with greater species fidelity across all elevations. In contrast, the Western Cordillera exhibits a marked decline in species retention. This difference between the communities of both gradients reinforces the findings from other analyses, which indicate that community composition is shaped by environmental filtering specific to each mountain range (Hui & McGeoch, 2014; Kraft et al., 2015; Leibold et al., 2004; Longino & Colwell, 2011; McGeoch et al., 2019).

The power-law fit reflects that community structuring in the Central Cordillera obeys more deterministic niche-based assemblage processes, possibly reflecting stronger environmental filtering, habitat continuity, or historical stability. In contrast, the exponential fit in the Western Cordillera is consistent with a more stochastic turnover, which could result from greater fragmentation, reduced dispersal, or more irregular microhabitats.

Thus, Zeta diversity analyses revealed that as the number of sites compared in this study increases, the ant communities in both gradients are strongly influenced by rare or habitat-restricted species. This finding supports and reinforces the patterns observed in other analyses regarding species turnover. The zeta diversity results show marked species turnover across the two mountain ranges, albeit with contrasting patterns. In the Western Cordillera, the steep decline in zeta diversity and low species retention suggest highly differentiated communities dominated by species with restricted distributions and low frequencies, indicating a more stochastic assemblage shaped by limited dispersal and high environmental heterogeneity. In contrast, in the Central Cordillera, the greater persistence of species across zeta orders and the better fit to a power-law model reflect a more deterministic pattern, where environmental filtering allows the presence of generalist species with broad distributions. These differences align with metacommunity theory (Leibold et al., 2004), in which the Western range approximates a “dispersal-limited” model, while the Central range exhibits characteristics of species with broad ecological niches that tolerate environmental variation and are distributed across multiple sites along the gradient.

In conclusion, our findings confirm that species turnover along each gradient is influenced by environmental, spatial, biogeographic, historical, and demographic factors specific to each mountain range. These factors shape the composition and structure of ant communities, which may be dominated by rare, unique, or limited-dispersal species. Such species tend to be more sensitive to environmental variation, which, in turn, leads to the high species replacement observed in this study. Alternatively, communities could have been dominated by common, generalist, and widely distributed species, resulting in greater stability and promoting biotic homogenization, something that did not occur in this study.

Therefore, we emphasize the need for conservation and restoration strategies in all the altitudinal floors of tropical mountains, in order to enhance landscape connectivity along altitudinal gradients. Although not directly measured in this study, fieldwork observations suggest that species within elevation bands may experience population declines due to accelerated habitat loss and fragmentation. These findings highlight the urgency of applying the precautionary principle to prevent local and regional extinctions. Protecting Andean natural forests and restoring connectivity across elevations would facilitate rescue effects and help maintain metapopulation dynamics in these highly fragmented landscapes.

In this context, adopting a preventive and proactive approach to preserve Andean ecosystems is imperative. Protecting natural forests and restoring connectivity between them are essential actions to mitigate the effects of fragmentation and ensure the long-term persistence of metapopulations. Preserving forests in all altitudinal gradients and promoting ecological connectivity will be crucial for safeguarding ant diversity and, by extension, the integrity of Andean ecosystems in the face of accelerating climate change and increasing human pressure. These measures would not only protect endemic and vulnerable species but also enhance ecosystem resilience to future environmental and anthropogenic disturbances.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

The authors thank Minciencias and Univalle for funding the program “Multiscale relationships of biodiversity in altitudinal gradients of the tropical forest”, Code: 1106-852-70306, Contract No. 491-2020. We also express special thanks to the communities and administrators of the different properties that were sampled for their hospitality during the field days. We also thank the biology students from Universidad del Valle and Universidad del Quindío, as well as biologists Nataly Forero, Diana Urcuqui, Sebastián Forero, Javier Cuervo, Nicolás Montero and Anderson Arenas for their valuable collaboration in the sampling. Finally, we extend our thanks to the expert myrmecologists Roberto José Guerrero, Emira García, Maria Alejandra Bautista, Sabrina Amador, Adrián Troya and Francisco Serna for their support and corroboration in the taxonomic identification of the collected ants.

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