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Research Article

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Posted Date: November 25th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11637063/v1

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Additional Declarations: No competing interests reported.

Title page

Ithomiini butterfly assemblages and mimicry ring variation along an elevational gradient in the Atlantic Forest

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Abstract

Elevational gradients provide an opportunity to examine how insect communities and species associations vary over relatively short spatial distances. In mimetic butterflies, variation in species composition may also be accompanied by changes in the composition of local mimicry rings. This study investigates Ithomiini butterfly diversity and mimicry-ring composition across a short elevational gradient in the Atlantic Forest of southeastern Brazil. Communities were sampled at four locations spanning 850-1300 m elevation. Beta-diversity and its turnover component were used to assess variation in species composition, while mimicry-ring composition and relative abundance were evaluated among locations. A total of 1295 individuals belonging to 26 Ithomiini species were recorded. Community composition differed among locations, with beta-diversity driven primarily by species turnover, indicating that differences among communities resulted mainly from species replacement rather than nestedness. Species richness peaked at the intermediate elevation. Mimicry-ring composition also varied among locations, with communities separated by smaller elevational differences showing greater similarity in their mimetic composition. However, co-mimetic species did not co-occur more often than expected by chance across the gradient. Thus, variation in mimicry-ring composition appears to result primarily from the individual distributions of species, particularly the

dominant ones, rather than from co-occurrence of co-mimics. These results show that substantial differences in both taxonomic and mimicry composition can occur among Ithomiini communities distributed across a relatively short elevational gradient, while highlighting that mimicry rings do not necessarily represent ecological units with similar spatial distributions at a local scale.

Keywords: Altitudinal gradient, Atlantic Forest, Community composition, Environmental filtering, Müllerian mimicry.

Statements and Declarations

Data Availability Statement: All data and R scripts necessary to reproduce the analyses presented in this study are publicly available in the Zenodo repository https://doi.org/10.5281/zenodo.23929527.

Competing Interests: The authors have no conflicts of interest to declare. All co-authors have seen and agree with the contents of the manuscript.

Acknowledgments: We are grateful to all the staff members of Reserva Biológica da Serra do Japi for research permits and for providing us with accommodation. We are grateful to A Tacioli, L Murari, GB Evora, LM Pezzini, GPA Ancajima and LB Stadoan for their help in the fieldwork. We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for collection permits (10438-5 to 10438-8). The present study is registered in the SISGEN (A57211A).

Funding: This study was supported by CAPES (Finance Code 001) and the CAPES Doctoral Sandwich Program Abroad (PDSE) scholarship. A.V.L.F. was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grants 304291/2020-0, 408764/2024-4 and 317331/2025-6) and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; grants 2021/03868-8 and 2023/04393-9). M.E. was supported by the CAPES/PrInt_UNICAMP International Cooperation Project (88881.311261/2018-01).

Author contributions: Aline Vieira-Silva: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft. Marianne Elias: Methodology, Supervision, Writing - review and editing. André V. L. Freitas: Conceptualization, Methodology, Supervision, Funding acquisition, Writing - review and editing.

Introduction

Tropical forests are well known for hosting the world's most diverse ecosystems and a remarkable number of species. These species are not evenly distributed across space and often vary along environmental gradients, such as altitude. Altitudinal gradients create a mosaic of climates and habitats across short spatial scales, influencing species composition and providing natural conditions for investigating biodiversity patterns (Körner 2007; Peters et al. 2016). The elevational distribution of species is shaped by both long-term evolutionary processes, including speciation, dispersal, and extinction (Colwell & Rangel 2010; Larsen et al. 2011), and short-term ecological processes, such as competition, predation, mutualism, and responses to abiotic conditions (Jankowski et al. 2013; Early and Keith 2019). Because species interactions and environmental conditions may change rapidly across elevation, altitudinal gradients provide valuable systems for investigating how ecological communities are assembled and structured.

While elevational gradients are crucial for understanding biodiversity patterns, tropical montane forests are still not well-studied. Most research on altitudinal diversity gradients has focused on plants and in temperate regions, even though tropical arthropods account for the majority of terrestrial biodiversity. Among arthropods, butterflies are one of the best studied groups in the tropics and provide important models for investigating diversification, ecology, evolution, and conservation (Brown & Freitas 1999; Bonebrake et al. 2010). Most studies examining butterfly communities along elevational gradients have focused primarily on species richness and composition (e.g., Fleishman et al. 1998; Pyrcz & Wojtusiak 2002; Bhardwaj et al. 2012; Carneiro et al. 2014). However, less attention has been given to how elevational gradients influence ecological interactions, particularly mimicry systems in tropical butterflies, although some studies have addressed these questions (e.g., Chazot et al. 2014; Fougeray et al. 2026).

Because mimicry systems depend on the local coexistence and relative abundance of co-mimetic species (Elias et al. 2008; Chouteau et al. 2016), environmental gradients that alter species composition may also modify local mimicry assemblages. In aposematic Lepidoptera, mimicry rings, in which multiple species share similar warning color patterns, can vary along elevational gradients and across microhabitats (Beccaloni 1997; DeVries et al. 1999; Uehara-Prado & Freitas 2009; Chazot et al. 2014; Willmott et al. 2017; Fiedler & Brehm 2021), potentially reflecting the combined effects of environmental filtering, predator-mediated selection, and shared evolutionary history (Brown 1988; Elias & Joron 2015). Under these conditions, co-mimetic species may be expected to co-occur more frequently than predicted by random community assembly, leading to non-random mimicry structure within local communities (Elias et al. 2009; Chazot et al. 2014; Doré et al. 2023; Pérochon et al. 2025).

Most studies addressing these patterns in tropical butterflies have focused on Andean systems, which are characterized by broad elevational ranges and strong environmental turnover (Pyrcz et al. 2009; Chazot et al. 2014). By contrast, there is relatively little information about how species composition and mimicry rings vary along narrower altitudinal gradients, such as those found in the Atlantic Forest, where elevational differences are less pronounced. Consequently, it remains unclear whether these relatively small elevational differences are sufficient to reshape butterfly communities and mimicry assemblages at local spatial scales.

Among Neotropical butterflies, the tribe Ithomiini (Nymphalidae: Danainae) represents an ideal model group for investigating these questions. This tribe comprises almost 400 species distributed from lowlands to elevations above 3000 m throughout the Neotropics (Brown 1979; Willmott & Freitas 2006; Doré et al. 2022). Ithomiini butterflies are chemically defended and constitute the principal models in Neotropical mimicry rings (Brown & Benson 1974; Brown 1992), often dominating these both in species richness and abundance (Brown & Benson 1974; Willmott et al. 2017). Furthermore, many Ithomiini species exhibit marked habitat specificity and sensitivity to environmental conditions (Uehara-Prado & Freitas 2009; Willmott et al. 2017), making them particularly suitable for investigating how habitat and climatic variation shape the organization of tropical butterfly communities and mimicry systems.

Here, we investigated the patterns of Ithomiini butterfly diversity and mimicry ring composition along a local altitudinal gradient in an Atlantic Forest reserve in southeastern Brazil. Specifically, we asked whether: (1) Ithomiini community composition and mimicry ring structure vary along a short elevational gradient; (2) community dissimilarity along the gradient is driven primarily by species turnover rather than nestedness; and (3) local communities are non-randomly structured according to mimicry rings. We predicted that even relatively small elevational differences would be enough to restructure both species and mimicry ring composition, leading to communities that are characterized primarily by species replacement rather than by nested subsets along the gradient.

Materials and Methods

Study Area

Fieldwork was conducted in the Biological Reserve of Serra do Japi, located in the state of São Paulo, southeastern Brazil (23°14'S, 46°58'W) (Fig. 1A). The reserve covers an area of 354 km² and is situated within a continuous forest block of about 10,000 ha, which has varying degrees of regeneration, being one of the largest areas of continuous Atlantic Forest in the interior of the state of São Paulo (Morellato and Leitão-Filho 1992). The altitude ranges from 700 to 1300 m, and the predominant vegetation is a Semi-deciduous Seasonal Forest with fragments of montane forest and

vegetation typical of rocky outcrops (Morellato and Leitão-Filho 1992; Ballerini et al. 2021). The area presents a cold-dry season between April and September (average temperature 11-15 °C) and a warm-wet season between October and March (average temperature 18-22 °C), with mean annual rainfall of 1500 mm (Pinto 1992). The reserve features several trails that range from 2 to 6 m wide, commonly used by forest guards, tour guides, and researchers. These trails are periodically maintained, resulting in relatively open canopy conditions along the trails (Gueratto et al. 2020). The highest site sampled in this study (1300 m) exhibited even more open vegetation in some sections, including regenerating forest patches and trails exposed to more frequent maintenance due to access to a transmission tower.



Fig. 1 Study area and sampling sites along an elevational gradient in the Serra do Japi, southeastern Brazil. **(A)** Geographic location of the study area with sampling points indicated across four elevations (850 m, 1000 m, 1180 m, and 1300 m). **(B-E)** Representative views of the habitat at each elevation: (B) 850 m, (C) 1000 m, (D) 1180 m, and (E) 1300 m. Colored circles correspond to the sites indicated in panel A

Study Design and Sampling Constraints

To measure the distribution and abundance of butterflies, four locations with different altitudes were selected (850 m, 1000 m, 1180 m, and 1300 m; Fig. 1). Despite the relatively small elevational range, previous studies in the area have shown that this altitudinal difference is sufficient to influence community composition and abundance in frogs and small mammals (Giaretta et al. 1997, Sakane et al. 2019). Moreover, the floristic and phytosociological study by Rodrigues et al. (1989) demonstrated that the vegetation of Serra do Japi exhibits a well-defined variation in soil, vegetation structure, and floristic composition along this altitudinal gradient.

At each elevation, a transect was established consisting of 7 to 14 sampling units of 50 m each (hereafter SU). The transects at 850 m and 1000 m each included 10 SUs, the one at 1180 m contained 7 SUs, and the one at 1300 m contained 14 SUs. The variation in the number of SUs among elevations resulted from the need to maintain a constant altitude along each transect, which in some areas prevented the establishment of at least 10 SUs. Each transect was surveyed three times per month, except at 1300 m, where logistical constraints limited sampling to two surveys per month. Field work was carried out between January and May 2024, which corresponds to the peak of Ithomiini abundance period at the study site (A.V.L.F., personal observations).

Butterflies were sampled by a single collector who walked each linear transect at a slow, constant pace for 4 h between 07:00 and 12:30 h, preferably under sunny conditions. Each transect was repeatedly surveyed until the total sampling time was completed. A schematic representation of the sampling design is provided in Online Resource 1. Following the protocol of Freitas (1993, 1996), all observed butterflies were captured with a 1-3 m entomological net whenever possible, individually marked with a sequential number, identified, and released. For each captured individual, sex, forewing length, and age class based on wing wear were recorded.

As there are no other trails with similar altitudes and conservation statuses at the study site, this research does not include altitude replicates. Although the lack of spatial replication introduces potential geographic confounding, single-gradient sampling designs have been widely applied and accepted in tropical montane insect ecology where landscape-level replication is not feasible (e.g., Pyrcz & Wojtusiak 2002; Brehm et al. 2003; Zenker et al. 2015; Mertens et al. 2021). In many Neotropical regions, particularly within the highly fragmented Atlantic Forest, finding replicate sites can be difficult, as they may not exist in the area or in nearby locations, as is the case in this study.

Furthermore, our spatial autocorrelation analyses (Mantel test) indicated that species dissimilarity and richness patterns were independent of geographic distance alone. These analyses do not remove the potential for unmeasured site-specific differences to covary with elevation, but they provide additional context for interpreting the observed patterns. This design is appropriate for documenting fine-scale patterns within a continuous forest landscape, but broader inference about elevational effects would require replication of elevations across independent sites.

Data Analysis

Community Structure

All statistical analyses and graphical visualizations were performed in R version 4.3.3 (R Core Team, 2024).

To assess spatial autocorrelation, the geographic coordinates of each site were used to construct a Haversine distance matrix. The relationship between geographic distance and community dissimilarity was assessed using a Mantel test. Geographic distances were calculated from site coordinates, and community dissimilarities were estimated using the Jaccard index for presence-absence data and Bray-Curtis dissimilarity for abundance data.

To assess species diversity patterns, Hill numbers were calculated for orders q = 0, 1 and 2 (Hill 1973). At q = 0, abundances are ignored and diversity equals species richness; at q = 1 (exponential of Shannon entropy), species are weighted in proportion to their abundances; and at q = 2 (inverse Simpson concentration), abundant species receive disproportionately more weight, so that diversity reflects mainly the dominant species. Additionally, Rank-abundance plots were constructed for each site, allowing comparison of community richness and dominance across altitudes. A sample-based rarefaction curve was also generated using the R package iNEXT (Hsieh et al. 2016) to estimate species richness as a function of sampling effort, based on both individual counts and sample completeness.

To explore patterns of similarity among communities and assess whether they are structured by altitude, a Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis distances among sampling units (SUs) was performed, calculated from Hellinger-transformed abundances, using the function *metaMDS* from the vegan package (Oksanen et al. 2013). To account for unequal sampling, seven SUs (the number available at 1180 m) were randomly subsampled from each transect, so that each elevation is represented by seven points in the ordination. To test for significant differences among the clusters, a PERMANOVA was applied using the adonis2 function in vegan.

Beta-diversity was partitioned into turnover and nestedness components using presence-absence data. Total beta diversity and its components were calculated using the package betapart

(Baselga & Orme 2012). Sørensen dissimilarity (βSOR) was partitioned into turnover (βSIM) and nestedness (βSNE). Pairwise dissimilarities among communities were calculated and ordered according to the altitudinal distance between sampling sites.

Mimicry Ring Structure

Each Ithomiini species recorded in the study was assigned to a mimicry ring according to its wing coloration and pattern. The classification proposed by Doré et al. (2022) was used as a basis, with modifications to reflect finer phenotypic distinctions that are recognizable at the local scale. In addition, non-Ithomiini butterflies displaying color patterns similar to those of Ithomiini were also included in the corresponding mimicry rings and recorded during sampling.

For each species, two main descriptors were evaluated: (1) altitudinal distribution along the gradient and (2) relative abundance at each sampling location. Altitudinal distribution was characterized by the minimum and maximum recorded elevations, the abundance-weighted mean altitude, and the associated standard deviation. These values were graphically represented to illustrate both species occurrence and variation across the elevational gradient. Relative abundance was calculated as the proportion of individuals of a given species relative to the total number of individuals recorded at each location and was visualized using a heatmap along the elevational gradient.

To investigate whether mimicry composition varied along the altitudinal gradient, Bray-Curtis dissimilarities among communities were calculated based on mimicry-ring abundances. The single-species ring OLENA, which comprises only *Aeria olena*, the dominant species at most sites, was excluded from this analysis, so dissimilarities reflected changes in multi-species mimicry-ring composition rather than variation in the abundance of a single species. Partial Mantel tests were performed between mimicry dissimilarity and altitudinal distance, controlling for geographic distance among sampling sites. Geographic distances were calculated from sampling coordinates using Haversine distances. Because only four locations were sampled, significance was assessed by complete enumeration of all 24 possible permutations.

To test whether co-mimetic species co-occurred more often than expected at random, that is, whether mimicry-ring composition showed a non-random spatial association across the elevational gradient, species abundances were first pooled within mimicry rings for each sampling location, generating a ring-by-location abundance matrix. A chi-squared test of independence was then performed to assess whether the abundance distributions of mimicry rings differed among sampling locations. Because species within a mimicry ring may differ intrinsically in their spatial abundance distributions, the significance of the observed heterogeneity was assessed using a randomization procedure following the approach of DeVries et al. (1999) and Hill (2010). Mimicry-ring identities

were randomly reassigned among species while maintaining the observed number of species in each ring and preserving the abundance distribution of each species across sampling locations. For each of 9,999 randomizations, species abundances were pooled according to the randomized ring assignments and the chi-squared statistic was recalculated, generating an empirical null distribution. The one-tailed permutation P-value was calculated as ((b + 1) / (n + 1)), where (b) is the number of randomized chi-squared statistics equal to or greater than the observed statistic and (n) is the total number of permutations. The strength of deviation from the null expectation was quantified using the Standardized Effect Size (SES), calculated as the difference between the observed chi-squared statistic and the mean of the null distribution divided by its standard deviation (Gotelli & McCabe 2002). All mimicry rings were retained in this analysis, including rings represented by a single species, because singleton rings still provide information on the spatial distribution of individual mimicry patterns.

As a complementary test of whether co-mimetic species co-occur more often than expected at random, pairwise Bray-Curtis dissimilarities were calculated among species based on their abundance profiles across the four sampling locations. Dissimilarities were converted to similarities as 1 − Bray-Curtis dissimilarity. All pairwise comparisons among species were classified as either within-ring, when both species belonged to the same mimicry ring, or among-ring, when they belonged to different rings. For each mimicry ring containing at least two species, the mean pairwise similarity among its member species was calculated. The observed within-ring similarity was then calculated as the mean of these ring-specific values, giving each multi-species mimicry ring equal weight regardless of the number of species it contained. The same randomization procedure described above was used to generate the empirical null distribution, with the mean within-ring Bray-Curtis similarity recalculated after each randomization. The standardized effect size was calculated as the difference between the observed mean within-ring similarity and the mean of the null distribution divided by its standard deviation. Rings represented by a single species did not contribute within-ring species pairs, but their species remained in the dataset and participated in the randomization procedure.

Results

During the five months of sampling, 1295 individuals from 26 Ithomiini species were recorded, which represents 81% of the total species richness known from Serra do Japi (Brown & Freitas 2000; A.V.L.F. Freitas, unpublished data) (Fig. 2). An additional 83 individuals of 5 species of non-ithomiine butterflies belonging to the same mimicry rings as ithomiines were also reported: the Pieridae *Dismorphia astyocha* (Dismorphiinae), and the Nymphalidae *Heliconius ethilla* (Heliconiinae), *Consul fabius* (Charaxinae), *Lycorea halia*, and *Lycorea ilione* (Danainae) (Fig. 2). Five Ithomiini species present in the study site and not detected during the present sampling (*Callithomia lenea*,

Methona themisto, *Thyridia psidii, Melinaea ludovica* and *Tithorea harmonia*) belong to the transparent-yellowish (THEMISTO; first three species) and to the tiger (LYSIMNIA, last two species) mimicry rings.

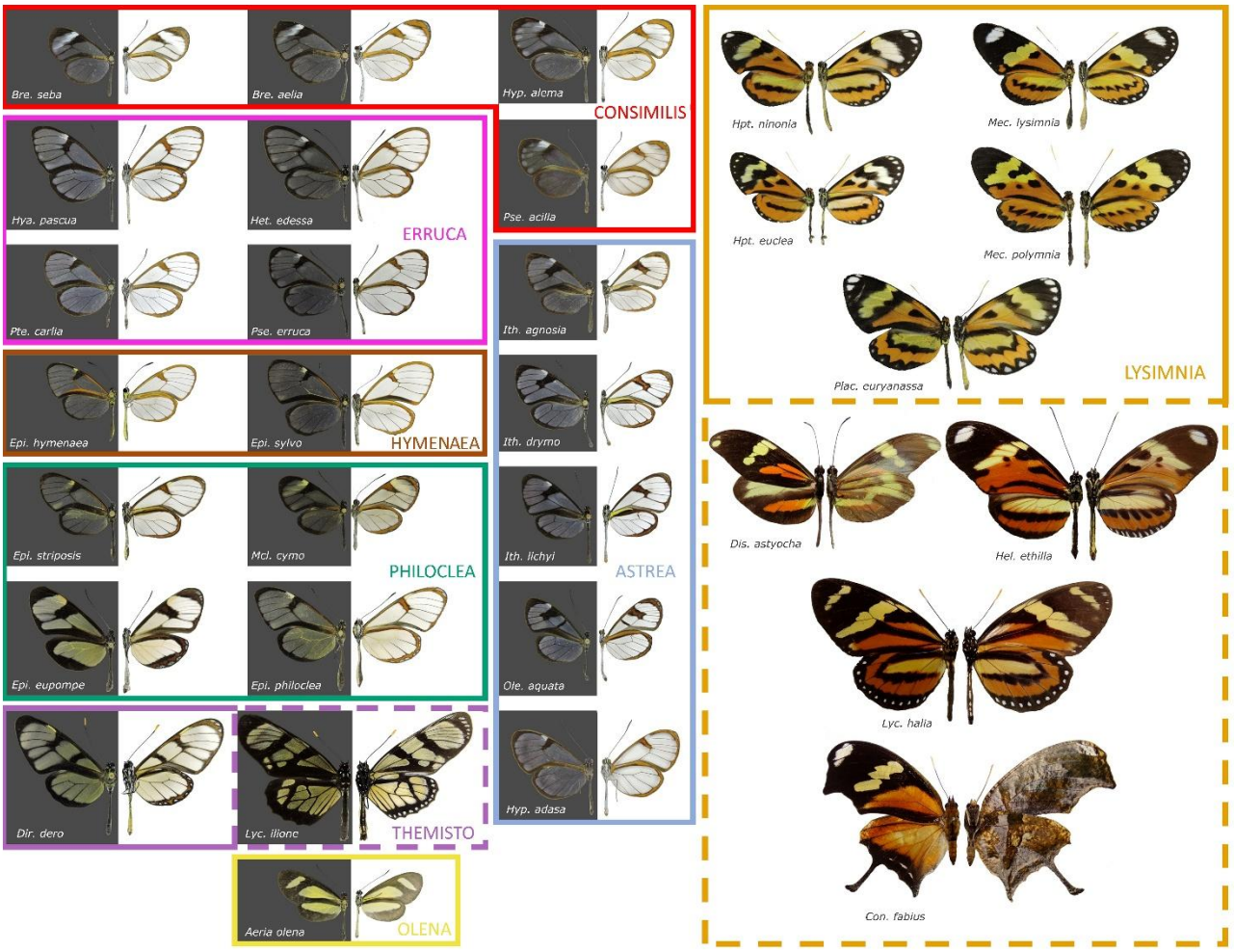

Fig. 2 Ithomiini species recorded in this study, classified into eight mimicry rings (ring names indicated at the bottom right). Solid boxes delimit Ithomiini mimicry rings, while dashed boxes indicate mimetic species outside the tribe that converge on similar warning patterns. For each species, dorsal (left; dark background to emphasize transparent wing areas) and ventral (right; light background) wing surfaces are presented.

Community Structure

No significant relationship was found between geographic distance and community dissimilarity. Mantel tests revealed non-significant correlations for both presence-absence data (Jaccard: $r = 0.30$, $p = 0.29$) and abundance data (Bray-Curtis: $r = 0.38$, $p = 0.25$), indicating no detectable spatial structuring of communities among the sampled sites.

Species richness at each site ranged from 12 to 21, with the highest richness observed at 1000 m, the lowest at 1180 m, and intermediate values at 850 m (18 species) and 1300 m (17 species) (Fig. 3A, order $q = 0$). As the diversity order increases ($q = 1$, when relative abundances are taken into

account), the effective number of species, decreases across all sites, leading to more similar values among them. When greater weight is given to common species (q = 2), the diversity pattern changes, with the 1300 m community exhibiting the greatest diversity (Fig. 3A).

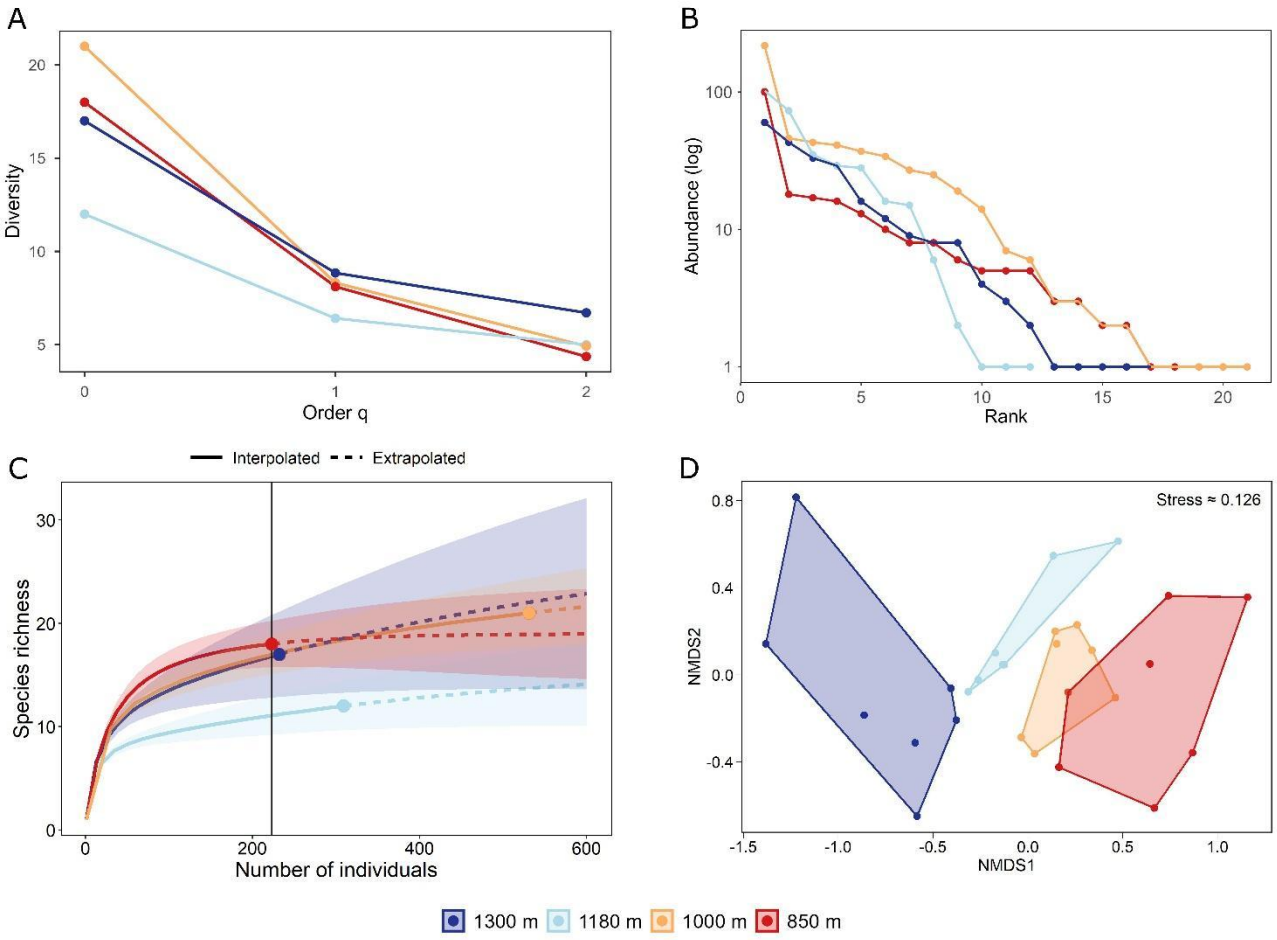

Fig. 3 Diversity and community structure of Ithomiini butterflies along an elevational gradient in Serra do Japi, southeastern Brazil. **(A)** Hill numbers for diversity orders q = 0, 1, and 2 across the four sampled elevations, showing changes in effective species richness when increasing weight is given to common species. **(B)** Rank-abundance curves illustrating differences in species dominance and evenness among elevations; abundance is shown on a logarithmic scale. **(C)** Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) curves of species richness with 95% confidence intervals (shaded areas). The vertical black line indicates the standardized sampling size used to compare communities. **(D)** Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities in species composition, showing the separation of butterfly communities along the elevational gradient. Convex hulls represent communities at each elevation. Points represent sampling units.

Rank-abundance curves revealed differences in species dominance and evenness among elevations (Fig. 3B). Communities at 850 m and 1000 m showed higher abundances distributed across several species. By contrast, the 1180 m community exhibited lower richness and a faster decline in

309 species abundances across ranks, indicating greater dominance by a few species. The 1300 m
310 community maintained relatively high evenness with the lower abundance of the dominant species.
311 Species accumulation curves indicate that additional sampling effort would likely reveal the
312 presence of additional species, particularly at elevations where extrapolated richness curves did not
313 approach an asymptote (i. e., 1000 m and 1300 m, Fig. 3C). Although estimated richness differed
314 slightly among elevations, overlapping confidence intervals suggest no differences in sampling
315 completeness or expected richness among communities.
316 The NMDS ordination revealed clear differences in species composition among elevations,
317 forming four distinct clusters (Stress = 0.126; Fig. 3D). Despite some overlap, species composition
318 differed significantly among communities (PERMANOVA: $F = 11.92$, $R^2 = 0.31$, $p = 0.001$).
319 Taxonomic beta-diversity among communities was moderate (βSOR = 0.40) and was driven
320 primarily by species turnover (βSIM = 0.25), whereas nestedness contributed less to total dissimilarity
321 (βSNE = 0.15). Pairwise comparisons based on presence-absence data revealed substantial variation
322 in the relative contribution of these components along the altitudinal gradient (Online Resource 2).
323 The highest turnover values were observed between 1300 m and 850 m (βSIM = 0.35), indicating
324 strong species replacement between the lowest and highest elevations. By contrast, comparisons
325 involving 1180 m and 850 m showed no turnover (βSIM = 0), with differences being entirely explained
326 by nestedness (βSNE = 0.20), suggesting that the 1180 m community represented a subset of the 850
327 m community.
328 The altitudinal distribution of butterfly species showed a pattern of stratification, with some
329 species prevalent in lower elevations while others were more common or exclusive to higher altitudes
330 (Fig. 4A). Relative abundance patterns further supported the altitudinal stratification observed among
331 species (Fig. 4B). *Aeria olena* was the dominant species at all elevations except the highest site (1300
332 m), where its abundance was markedly reduced.

333 Mimicry Ring Structure

334 All recorded species were categorized into one of eight distinct mimicry rings (Fig. 2). One of
335 these rings (OLENA) consists of a single species, *Aeria olena*, whose wing pattern did not resemble
336 that of any other butterfly recorded in the study area.
337 Some transparent mimicry rings became increasingly abundant at higher elevations (Fig. 4C).
338 Most species with mean elevational distributions above 1100 m belonged to transparent mimicry rings,
339 and all species restricted to 1300 m exhibited transparent wing patterns. By contrast, tiger-patterned
340 species were generally more frequent and abundant at lower elevations. Nevertheless, some of these,
341 particularly *Hypothyris ninonia* and *Mechanitis lysimnia*, also reached high abundances at higher

elevations. Intermediate elevations showed greater overlap among mimicry rings, with representatives of multiple mimetic phenotypes co-occurring within the same communities (Fig. 4C).

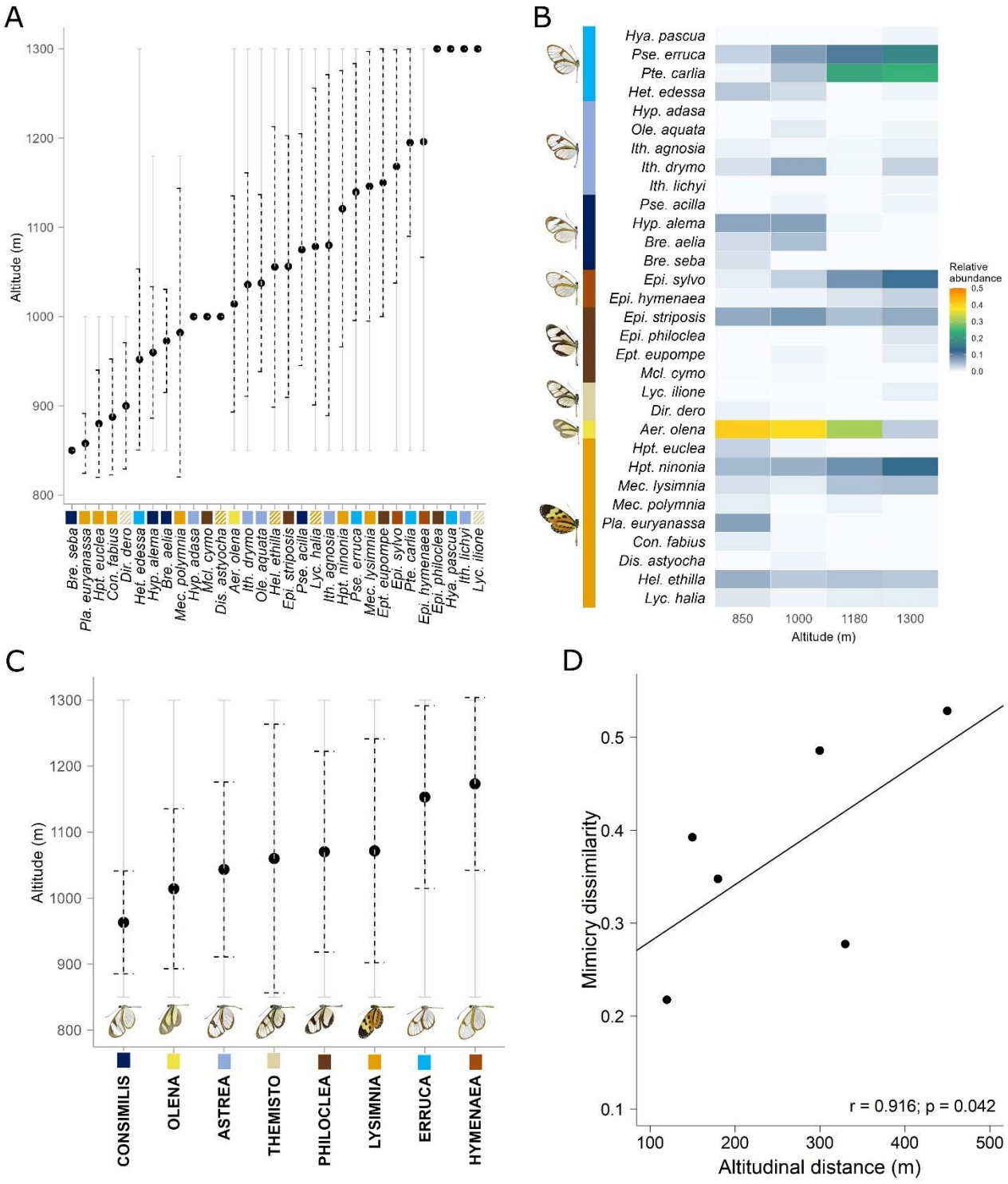

Fig. 4 Patterns of mimicry-ring composition along the altitudinal gradient in Ithomiini butterfly communities from Serra do Japi, southeastern Brazil. **(A)** Mean altitude of occurrence for each species (black circles), with vertical lines representing the standard deviation around the abundance-weighted mean elevation (black dashed) and the minimum and maximum recorded elevations (gray). Species

are ordered by their mean elevational occurrence. Colored squares below the x-axis indicate the mimicry ring to which each species belongs, as shown in Figure 2. Dashed-patterned squares correspond to non-Ithomiini mimetic species. **(B)** Relative abundance of each species across the four sampled elevations (850, 1000, 1180, and 1300 m). **(C)** Mean elevational distribution of the eight mimicry rings recorded along the Serra do Japi gradient. Black circles indicate the abundance-weighted mean altitude of occurrence for each mimicry ring, with vertical lines representing the standard deviation around the abundance-weighted mean elevation (black dashed). **(D)** Relationship between altitudinal distance and mimicry dissimilarity (Bray-Curtis) among communities, based on the abundances of multi-species mimicry rings (excluding the single-species ring OLENA). The graph shows the Mantel test results.

Mimicry composition varied along the altitudinal gradient. Bray-Curtis dissimilarities based on the abundances of multi-species mimicry rings increased with altitudinal distance (Fig. 4D), and the partial Mantel test revealed a positive relationship between mimicry dissimilarity and altitudinal distance while controlling for geographic distance (Mantel $r = 0.916$, $p = 0.042$, the lowest p-value attainable with four sites). Communities located at closer elevations therefore tended to have more similar mimicry composition, whereas communities separated by greater altitudinal distances showed greater differences in the relative abundance of mimicry rings. Including the ring OLENA weakened this relationship ($r = 0.563$, $p = 0.25$), indicating that multi-species rings rather than the dominant *Aeria olena* carried the elevational signal in mimicry composition.

Mimicry-ring abundances varied substantially among sampling locations. The observed chi-squared statistic was 351.47, which was higher than the mean expected under the species-randomization null model (mean = 244.62; SD = 68.35), corresponding to a positive standardized effect size (SES = 1.56). However, the observed value was only marginally non-significant (one-tailed $p = 0.0502$; Online Resource 3), lying at the edge of the null distribution. Thus, although mimicry-ring abundances differed among sampling locations, these differences were no greater than expected given the species-specific abundance distributions, indicating no clear tendency for co-mimetic species to co-occur along the gradient.

Pairwise Bray-Curtis similarity in abundance distributions among species across elevation was also slightly higher within mimicry rings than among rings when all species pairs were considered (mean within-ring similarity = 0.263; mean among-ring similarity = 0.225). However, compared with the species-randomization null model, the observed mean within-ring similarity (0.213) was slightly lower than the null expectation (mean = 0.230; SD = 0.049), resulting in a negative standardized effect size (SES = -0.36) and a non-significant one-tailed probability ($p = 0.593$). Therefore, co-mimetic species did not co-occur more often than expected from their species-specific abundance patterns alone.

Discussion

Taxonomic turnover along the elevational gradient

Although the sampled elevational range was relatively small, Ithomiini communities differed in species composition among the sampled locations. Taxonomic beta-diversity was primarily driven by species turnover rather than nestedness, indicating that communities at different elevations were characterized mainly by species replacement rather than progressive species gains or losses. Because each elevation was represented by a single sampling location, elevational effects cannot be statistically separated from site-specific effects. Therefore, the observed differences are interpreted as variation among locations situated along an elevational gradient rather than as replicated effects of elevation.

Similar patterns have been reported in other tropical montane systems, where changes in temperature, humidity, vegetation structure, and resource availability shape butterfly distributions along elevational gradients (Molina-Martínez et al. 2013; Carneiro et al. 2014; Fougeray et al. 2026). In Ithomiini, differences among locations may reflect variation in several environmental and biological factors that covary with elevation, including temperature, humidity, vegetation structure, and resource availability. Ithomiini species are also known to respond to microclimatic conditions, which may influence their activity, development, host-plant use, and survival (Willmott & Mallet 2004; Elias & Joron 2015). However, the relative contribution of these factors cannot be disentangled with the present observational design.

Species richness was highest at the intermediate elevation (1000 m), possibly reflecting the overlap of assemblages associated with lower and upper portions of the gradient. Other Neotropical montane butterfly communities show similar transition zones, where species from distinct elevational assemblages co-occur at intermediate altitudes (Pyrcz & Wojtusiak 2002; Pyrcz et al. 2009). An alternative, non-exclusive explanation is provided by the Mid-Domain Effect (MDE), a null model in which the elevational domain is treated as a bounded space, and species elevational ranges are constrained within its lower and upper limits (MDE; Colwell and Hurtt 1994; Colwell and Lees 2000; Jetz and Rahbek 2001). Under this framework, random placement of species ranges within the bounded domain can generate greater range overlap toward its center, producing a mid-domain peak in species richness through geometric constraints alone, even in the absence of environmental gradients or other ecological mechanisms (Colwell et al. 2004). Although we did not explicitly test the MDE, the occurrence of a richness peak at intermediate elevation may be consistent with both the overlap of elevational assemblages and geometric constraints imposed by the limits of the sampled gradient.

Elevational variation in mimicry-ring composition

In addition to taxonomic turnover, mimicry-ring composition varied with elevation. Communities at similar elevations had more similar mimicry compositions, whereas those separated

by greater elevational differences showed increased mimetic dissimilarity. Some transparent mimicry rings became proportionally more abundant at higher elevations, whereas most tiger-pattern ring species were generally more associated with lower elevations, although exceptions were observed. A similar pattern has been reported in the Andes, where transparent ithomiines become more frequent at higher elevations (Ossola et al. 2025) and tiger-patterned species are associated with lower elevations (Chazot et al. 2014). Finding the same trend along a short gradient in a remote Atlantic Forest mountain suggests that common drivers may shape the elevational distribution of transparency in Ithomiini. These differences may reflect variation in light environment and habitat structure along the gradient (Elias & Joron 2015).

Transparent patterns are thought to be less detectable in shaded or visually complex environments, where transparency may enhance background matching while maintaining participation in Müllerian mimicry systems (Papageorgis 1975; Brown 1988; Arias et al. 2019). This interpretation, however, does not apply consistently across all transparent rings. Some transparent rings, particularly CONSIMILIS and ASTREA, were proportionally more abundant at lower elevations. In Serra do Japi, *Brevioleria plisthenes*, from the CONSIMILIS ring, was the only species historically recorded until the 1990s (Brown 1992), whereas three additional co-mimetic species, *Hypoleria alema*, *Brevioleria seba*, and *Heterosais edessa*, all common at the nearby semideciduous forests (e.g. Carreira et al. 2025), became established in the area only after the 2000s (A.V.L.F., unpublished data). These species are typically associated with warmer forests at lower altitudes, suggesting that recent changes in habitat and local climate may have contributed to their establishment in the study area. Increasing regional temperatures associated with urban expansion, forest disturbance, and broader climatic warming may therefore contribute to recent shifts in the composition and distribution of Ithomiini assemblages in the Atlantic Forest (see also Uehara-Prado & Freitas 2009).

By contrast, tiger-patterned species tend to be more conspicuous and may be favored in brighter habitats, such as edges and open forests (Brown 1992), where predators can more efficiently detect warning signals. Tiger-patterned ithomiines might also benefit from crypsis inside the pockets during the dry season, as their coloration can blend with fallen dry leaves (Brown 1988). These contrasting possibilities highlight that the relationship between mimicry phenotype and elevation may depend on multiple environmental factors rather than on a single selective mechanism.

Species-specific responses within mimicry rings

The two randomization analyses provided no clear evidence that mimicry-ring identity was associated with species' spatial distributions. Although mimicry-ring abundances differed substantially among sampling locations, the observed heterogeneity was only marginally greater than expected

under the species-randomization null model. Similarly, species sharing a mimicry ring did not show greater similarity in their abundance distributions across elevations than expected by chance. Thus, the turnover in mimicry composition appears to result primarily from the distributions of individual species within multi-species rings rather than from coordinated responses of co-mimetic species. Species sharing warning patterns may therefore differ substantially in their ecological requirements and environmental tolerances.

These results suggest that variation in mimicry-ring composition primarily reflects the cumulative distributional responses of individual species rather than coordinated responses of co-mimetic species, at least in the spatial scale of this study. Species sharing warning patterns may therefore differ considerably in their ecological requirements, environmental tolerances, and responses to local conditions. This distinction is important because mimicry rings represent evolutionary and ecological associations based on shared warning signals, but they do not necessarily constitute ecological units with similar habitat distributions.

Müllerian mimicry can promote convergence in warning signals through predator-mediated and frequency-dependent selection (Müller 1879; Sherratt 2008), but phenotypic convergence does not necessarily imply convergence in habitat use or environmental tolerance. By contrast, previous studies have shown that co-mimetic species tend to share multiple dimensions of their ecological niche, including elevation, microhabitat and climatic niche, more often than expected from their phylogenetic relationships (Elias et al. 2008; Chazot et al. 2014; Doré et al. 2023; Pérochon et al. 2025). The absence of such a pattern in Serra do Japi may reflect limited statistical power, given the smaller number of species and the shorter elevational gradient compared with Andean studies. Alternatively, the Atlantic Forest was colonized more recently by Ithomiini lineages (Chazot et al. 2019), which may have allowed less time for convergence in elevational niche among co-mimics.

Broader implications and perspectives

The results highlight that Ithomiini community composition and mimicry-ring representation can change over relatively short elevational distances. Importantly, the two patterns were not necessarily generated at the same organizational level: taxonomic turnover reflected species replacement among locations, whereas changes in mimicry-ring composition emerged from the different distributions of individual species. This distinction suggests that mimicry-ring composition should not necessarily be interpreted as a direct proxy for species' environmental responses.

Because tropical montane systems are particularly vulnerable to climate change (Böhmer 2011; Mata-Guel et al. 2023), understanding how butterfly communities and mimicry rings are distributed along elevational gradients also has conservation implications. Butterflies may alter their elevational

distributions in response to seasonal climatic variation (Brown & Mielke 1972; Illán et al. 2012), suggesting that ongoing environmental changes could redistribute montane assemblages according to species-specific physiological tolerances (Menéndez 2007; Sheldon 2019; Gueratto 2023). Mountains can function both as refuges for lowland species tracking suitable climatic conditions (Chen et al. 2009) and as centers of endemism for high-elevation taxa with narrow physiological tolerances (Khaliq et al. 2014).

For Ithomiini butterflies, climate-driven shifts may alter not only species composition but also the structure of local mimicry systems. Because Müllerian mimicry depends on the local coexistence of multiple defended species sharing similar warning signals, differential responses among co-mimetic species could, in principle, weaken local mimicry rings (Urban et al. 2012; Doré et al. 2023; Pérochon et al. 2025). At the scale of this study, however, species distributions appeared largely independent of mimicry-ring membership, suggesting that the local assembly of co-mimics may be governed mainly by species-specific responses rather than by mutualistic association. Such effects may be particularly relevant in tropical montane systems, where species with narrow environmental tolerances may be unable to track rapidly shifting climatic conditions (Colwell et al. 2008; Sheldon et al. 2011). Preserving environmental heterogeneity across elevational gradients may therefore be important not only for maintaining taxonomic diversity but also for conserving the ecological and evolutionary interactions underlying tropical butterfly communities and mimicry assemblages.

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