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Climatic Niche Convergence in a Longhorned Beetle Genus: An Integrative Ecological–Evolutionary Analysis

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Understanding the factors that shape insect distributions is essential for interpreting biological systems and predicting their responses to environmental change. Species distribution models provide robust tools for examining these processes. This study highlights the complementary use of multivariate statistical approaches and phylogenetic reconstruction to integrate ecological and evolutionary perspectives. As a case study, we focus on the longhorned beetle genus *Exalphus*, a diverse group with well-established taxonomy but limited information regarding its environmental associations. The main objective was to detect climatic groupings within the genus and quantify the Neotropical biomes in which these assemblages are most strongly represented, as well as to evaluate whether these patterns exhibit any phylogenetic structure. To address these questions, we applied species distribution models, multivariate analyses, and phylogenetic inference. Two major

climatic assemblages emerged: one potentially associated with tropical rainforests and another potentially associated to savannas and seasonally dry forests. Ancestral state reconstruction suggested that the common ancestor of *Exalphus* likely inhabited humid forest environments, with subsequent transitions into drier conditions. However, species adapted to dry climates occurred across unrelated clades, indicating a lack of phylogenetic structure. This pattern supports repeated ecological convergence rather than shared ancestry, underscoring the evolutionary flexibility of Neotropical insects.

Keywords: Tropical rainforests, Seasonally dry forest, Species Distributions Models, Principal component analysis, Non-metric multidimensional scaling

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BACKGROUND

Climatic factors are among the primary determinants shaping the distribution of global biodiversity (Guisan and Thuiller 2005; Wieczynski et al. 2019; Coelho et al. 2023). Consequently, climate change acts as a disruptive force that threatens species unable to keep pace with global warming (Krebs 2020). This challenge is particularly pronounced for insects, due to their physiological limitations, since environmental temperatures directly influence their metabolic rates and development (González-Tokman et al. 2020; Liu et al. 2021; Halsch et al. 2021; Hayes et al. 2024). Many insect species exhibit limited plasticity in thermal tolerance, making rapid adaptation to rising temperatures difficult (González-Tokman et al. 2020). In addition to climate change, habitat loss and fragmentation resulting from deforestation, agricultural expansion, and urbanization represent significant threats to biodiversity and are major drivers of insect extinctions. These processes not only reduce the total habitat area but also degrade habitat quality and increase extinction risks by isolating populations (Cardoso et al. 2020). Therefore, understanding the factors that influence distribution patterns and the mechanisms sustaining insect species is crucial for their conservation (Diniz-Filho et al. 2010) and remains a central focus in insect ecology (Schowalter 2022).

The complex interactions among climatic factors present challenges in unraveling their collective impact on shaping insect distributions. Over the years, numerous studies have analyzed the environmental factors that influence the spatial distributions of insects, identifying a wide range

of variables such as temperature (Hayes et al. 2019 2024), precipitation (Eyre et al. 2010), habitat (Bell et al. 2019; Krauss et al. 2010), soil type (Liu et al. 2011), and vegetation (Tsafack et al. 2020). These variables interact in complex ways, underscoring the importance of multifaceted approaches in studying insect biogeography and informing conservation strategies.

Some of the most important questions in ecology and biogeography are to understand how organisms are distributed across space, what factors affect their occurrence, and why some areas host more species than others (Thuiller 2024). Ecological Niche Models (ENMs) and Species Distribution Models (SDMs) are useful tools to address those questions (Guisan and Thuiller 2005), while also helping to overcome limitations due to a lack of comprehensive knowledge about species' distributions referred to as the Wallacean shortfall (Peterson et al. 2011; Moctezuma et al. 2024). Species Distribution Models estimate the probability of a species inhabiting areas by correlating presence data with environmental parameters obtained by statistical methods (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Soberon and Peterson 2005; Peterson et al. 2011; Thuiller 2024). They have a wide range of applications, including species conservation (Franklin 2013).

Among insect groups of conservation concern, the family Cerambycidae Latreille, 1802, commonly known as longhorned beetles, is one of the most diverse and important families of Coleoptera. Globally, there are more than 35,000 cerambycid species (Svacha and Lawrence 2014; Taboada-Verona et al. 2016), and the subfamily Lamiinae is the most species-rich in most regions, particularly the tropics and subtropics (Monné et al. 2017; Marshall 2018; Rossa and Gocsal 2021). The genus *Exalphus* Restello, Iannuzzi and Marinoni 2001, belongs to the Acanthoderini, one of the most diverse tribes in Lamiinae (Monné 2024).

This genus currently comprises 18 described species, mainly distributed across the Amazon and Atlantic Forests of South America, renowned for their exceptional biodiversity but increasingly threatened by habitat loss and climate change (Ellwanger et al. 2020). A few records also exist from the Chaco and Caatinga ecosystems, that face similar threats from land-use and climate changes (Gasparri and Grau 2009; Silva et al. 2019; Costa et al. 2024). The Chaco is a complex of subtropical dry forest and savanna, characterized by pronounced seasonal droughts and high thermal variation (Myers et al. 2000), while the Caatinga, located in northeastern Brazil, is a semi-arid biome dominated by drought-adapted vegetation spiny woodlands (Queiroz et al. 2018; Bezerra-Gusmão et al. 2022). Although the taxonomy and phylogenetic relationships of *Exalphus* are well-established (Souza and Monné 2014; Souza et al. 2017; Tavakilian and Néouze 2013; Schmid 2014), the ecological factors determining the geographic distributions of its species remain poorly understood. Understanding ecology helps anticipate future impacts and safeguard species by

identifying their optimal areas (Thuiller 2024). For example, the protection of monophyletic groups is critical for conserving genetic diversity and preserving evolutionary lineages, ensuring the maintenance of the fundamental evolutionary processes that shape species and their adaptations (Mace 2004). In this sense, the genus *Exalphus* is a useful case study.

Multivariate statistical techniques enable us to identify associations between variables, reduce dimensionality, and structure information in a more comprehensible way, to facilitate interpretation (Chahouki 2011; Palacio et al. 2020). The primary objective of this study was to use multivariate statistical analyses and ecological niche modeling to assess the climatic affinities of the species belonging to the genus *Exalphus* (Cerambycidae: Lamiinae). We aimed to detect climatic groupings within the genus and quantify the Neotropical biomes in which these assemblages are most strongly represented, as well as to evaluate whether these patterns exhibit any phylogenetic structure. By combining multivariate environmental data, species distribution models, and phylogenetic reconstruction, we sought to elucidate how climatic factors have shaped the ecological diversification within the genus.

We hypothesized that *Exalphus* species will cluster into distinct climatic assemblages corresponding to major Neotropical biomes (*e.g.*, humid forests versus seasonally dry forests and savannas). The assemblages identified will be independent of phylogenetic relationships, reflecting convergent evolution in response to environmental pressures rather than common ancestry. This aligns with the theoretical framework proposed by Losos (2011), who explains that convergent evolution leads to similar ecological traits arising independently in unrelated lineages as adaptations to comparable environmental conditions. Furthermore, we expected that climatic conditions, rather than strict phylogenetic signal, will be the predominant force shaping the ecological affinities of *Exalphus* species. This expectation is consistent with macroevolutionary studies in Coleoptera (Hunt et al. 2007), which highlight niche shifts and convergence as recurrent drivers of diversification.

MATERIALS AND METHODS

Species records

A database was built using records extracted from the literature, which contain information on species distributions. Finally, the following collections were reviewed: AMNH - American Museum of Natural History. New York. United States of America. DZUP - Coleção de

Entomologia Pe. Jesus S. Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil. MZSP - Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil. USNM - National Museum of Natural History – Smithsonian Institution, Washington, D.C., United States of America.

All records were verified to determine their accuracy and validity using geographic information systems (QGIS 3.14). Localities that lacked geographic coordinates but included sufficient locality information were manually georeferenced based on the locality descriptions provided in the original records, and approximate geographic coordinates were assigned to the most likely locality. All records that were considered doubtful or unreliable, based on the literature, were removed. Additionally, species with a distribution only known from the type locality were not considered (*E. docquini* Tavakilian and Néouze 2013; *E. simplex* (Galileo and Martins 1998); *E. solangeae* Souza and Monné 2014, and *E. vicinus* Galileo and Martins 2003).

Variable selection

To characterize the ecological niches of the species, we extracted bioclimatic information from the WorldClim 2.0 database (http://worldclim.org/version2) at a spatial resolution of 30 arc-seconds (approximately 1 km²). The dataset comprises 19 bioclimatic variables derived from interpolated monthly temperature and precipitation records averaged over the period 1970–2000 (Fick and Hijmans 2017). The climate matrix was simplified by calculating the mean of each variable for each species. To determine whether the data followed a multivariate normal distribution, Mardia's test was performed using the MVN package (Korkmaz et al. 2014). Subsequently, Pearson correlation coefficients were calculated using the stats package in R (R Core Team 2025) to identify highly correlated variables and retain a final subset of non-collinear bioclimatic variables. The selected bioclimatic variables include Mean Diurnal Range (BIO2), Isothermality (BIO3), Maximum Temperature of the Warmest Month (BIO5), Precipitation of the Driest Month (BIO14), Precipitation of the Wettest Quarter (BIO16), and Precipitation of the Warmest Quarter (BIO18). These variables are not necessarily the most important for each species (since they interact differently across locations), but they were used because (1) they simplify comparisons between model results and (2) they resolve the issue of multicollinearity (Mercado et al. 2020).

Clustering of species by climatic assemblages

To determine the optimal number of climatic clusters, the average silhouette width criterion was applied to *k-means* clustering using the factoextra package (Kassambara and Mundt 2020). Species were subsequently classified using hierarchical clustering based on Euclidean distances and Ward's minimum variance method (Ward.D2), which minimizes within-cluster variance while maximizing between-cluster differences (Romesburg 2004; Murtagh and Legendre 2014). The robustness of the resulting dendrogram was assessed using the cophenetic correlation coefficient. Differences among the identified climatic groups were evaluated using a multivariate analysis of variance (MANOVA). Finally, once the climatic groups were defined, principal component analysis (PCA), implemented in the FactoMineR package (Lê et al. 2008), and non-metric multidimensional scaling (NMDS; $k = 2$), implemented in the vegan package (Oksanen et al. 2022), were performed because they provide complementary analytical perspectives. PCA identifies the primary axes of variation based on linear relationships among climatic variables, whereas NMDS is a non-parametric ordination method that better accommodates the complex structure of ecological datasets by preserving the rank order of pairwise dissimilarities among observations. All analyses were performed in R (R Core Team 2025), and figures were produced using the ggplot2 package (Wickham 2016).

Species Distribution Models (SDMs)

We used the accessible area approach to estimate the calibration area for each species (Rojas-Soto et al. 2024), using as biogeographic entities the biogeographic provinces of the Neotropical region (Morrone 2014) and their interaction with the species location data points. This final step was carried out with the assumption that the regions selected for each species could define the historically and ecologically accessible areas (Barve et al. 2011; Peterson et al. 2011; Mercado et al. 2020). The calibration, selection, and evaluation of the models were carried out using the kuenm package (Cobos et al. 2019) in R, which allows optimizing the complexity of models created with the Maximum Entropy algorithm (Maxent) (Phillips et al. 2023) and the dismo package (Hijmans et al. 2022). To obtain the candidate models, 10 regularization multipliers (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) and two “feature classes” were used: linear (l), quadratic (q), and their combinations. The number of "background" points was 10,000. A random partition of 70% of the data was used for model training, and the remaining 30% was used for evaluation. A total of 100 iterations was established for model construction. The evaluation of the models was based on the significance criteria of the partial ROC (values from 0 to 1), omission rate (< 5%), and complexity (delta AIC < 2). This enabled us to identify the combination of parameters that showed the best

performance, and select the best combination for each species. Ten replicas of each model were constructed, from which the average was obtained using the Cloglog output. The final models for each species were binarized (presence/absence) using the suitability values (probabilities) of each pixel, based on the "10 percentile training presence" threshold. This threshold corresponds to the probability value that includes 90% of the presence points, and helps minimize overdispersion caused by potential data errors (Peterson et al. 2011). Finally, the climatic groups formed overlapped with the shapefile of the biomes from Olson et al. (2001), and for the Neotropical seasonally dry forest (Banda-R 2016). Finally, the overlap percentage was calculated using QGIS 3.14 geoprocessing tools.

Phylogenetic analysis and ancestral character reconstruction

The phylogenetic hypothesis of the genus *Exalphus* was replicated using the morphological dataset published by Souza et al. (2017), which comprises 33 species (*Alphus* White 1855; *Ateralphus* Restello, Iannuzzi and Marinoni 2001 and *Exalphus*) and 44 characters (27 binary and 17 multistate). The complete character list, coding scheme, and data matrix are available in Souza et al. (2017: Table 1), and were used here without modification. The matrix was analyzed using TNT v1.6 (Goloboff and Morales 2023), with all characters treated as unordered and equally weighted. A traditional search was performed with 1000 random addition replicates, employing tree bisection reconnection as the branch-swapping algorithm, and 50 trees retained per replicate. Support values for clades were estimated by bootstrap resampling with 1000 pseudoreplicates, each including random addition sequences and TBR branch swapping (100 replicates per pseudoreplicate, up to 50 trees retained). Support is expressed as GC values (Group present/Contradicted frequency; Goloboff et al. 2003), which provide a more reliable measure than absolute bootstrap frequencies. This analysis yielded four most parsimonious trees, one more than the three originally reported by the authors. Subsequently, one of the resulting trees—whose topology was identical to that illustrated in Souza et al. (2017)—was pruned to retain only 14 *Exalphus* species included in the multivariate analyses, along with a single outgroup, *Cotyzineus bruchi* (Melzer 1931), identified in the original analysis as the closest relative to the genus.

To evaluate whether the climatic groupings identified through multivariate statistical analyses (see above) reflect phylogenetic structure, each *Exalphus* species was assigned to one of two previously defined Climatic Assemblages: Assemblage A (affinity mainly for humid forests) or Assemblage B (seasonally dry forest and savanna affinity). These affiliations were encoded as a

binary character (state 0 = Assemblage A; state 1 = Assemblage B) and optimized onto one of the most parsimonious trees using the Fitch algorithm (Fitch 1971).

RESULTS

Species clustering based on climatic affinities

The average silhouette method indicated that the optimal number of clusters was two, as this value maximizes the mean silhouette coefficient across all observations (Fig. 1A). Additionally, based on the hierarchical clustering analysis, two groups were observed: climatic assemblage "A" consisted of the species: *E. cavifrons* (Bates 1872); *E. aurivillii* (Lane 1970); *E. lichenophorus* (Lane 1965); *E. colasi* (Lane 1965); *E. foveatus* (Marinoni and Martins 1978); *E. spilonotus* Restello, Iannuzzi and Marinoni 2001; *E. biannulatus* (Aurivillius 1921); *E. cicatricornis* Schmid 2014 and *E. malleri* (Lane 1955). Meanwhile, climatic assemblage "B" was represented by the species: *E. zellibori* (Lane 1955); *E. confusus* Restello, Iannuzzi and Marinoni 2001; *E. leuconotus* (Thomson 1860)*; E. gounillei* (Lane 1973) and *E. guaraniticus* (Lane 1955) (Fig. 1B). The MANOVA indicated significant differences between climatic assemblages A and B ($F = 17.51$, $p = 0.0007$), showing that the groups differed in at least one of the dependent variables. This finding suggests that the independent variable (climatic assemblages) has a statistically significant effect on the bioclimatic variables.

Regarding the principal component analysis (PCA), the first two dimensions explained 67.8% of the cumulative variance, with 47.7% attributed to the first dimension and 20.1% to the second (Fig. 1C). Isothermality (BIO3) had the highest contribution (27.81%) in the first dimension, followed by precipitation of the wettest quarter (BIO16) at 22.61%, and precipitation of the driest month (BIO14) at 17.94%. In dimension 2, max temperature of the warmest month (BIO5) accounted for 44.81%, followed by precipitation of the warmest quarter (BIO18) with 25.96%, and mean diurnal range (BIO2) with 16.80% (Fig. 1D–E). The stress value of 0.08 in the NMDS analysis indicates that the representation of the data in the reduced space is reasonably good. This value suggests that the original distances between the samples are well preserved in the projected space, with minimal distortion (Fig. 1F).

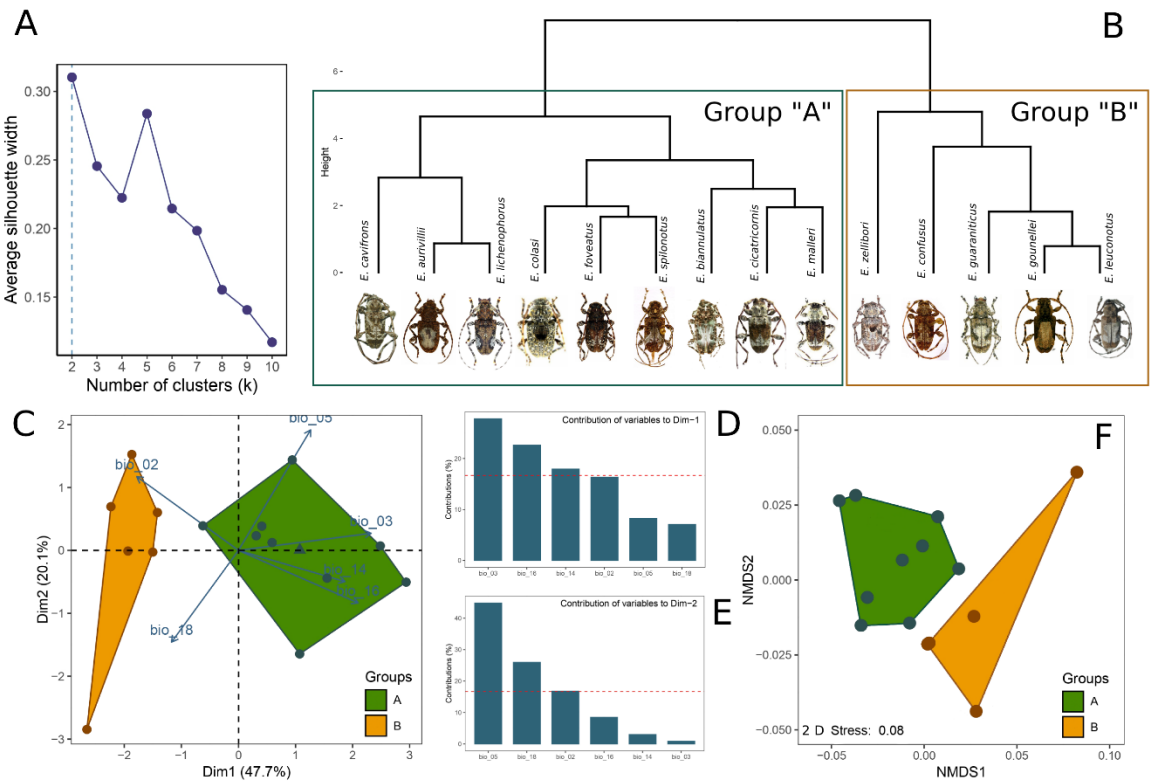

Fig. 1. Main ecological assemblages for the species of *Exalphus*, defined by (A) optimal number of climatic clusters (silhouette method) (B) hierarchical classification (C) principal component analysis (D–E) bioclimatic variable contributions in the PCA and (F) non-metric multidimensional scaling analysis.

Three species, with fewer than five available records, were excluded from the geographical reconstructions of ecological assemblages (*E. zellibori*; *E. confusus* and *E. cicatricornis*). The eleven selected models were statistically significant, with an average omission rate of 2% and average AUC values of 1.50. Due to *E. foveatus* exhibiting an excessively broad distribution (Monné 2024), it was not assigned to the climatic assemblage "A".

Two climatic assemblages were identified based on species similarities. Climatic assemblage “A” showed a strong association with tropical rainforests (67.3%) (Fig. 2A–D) and savannas (38.54%) (Fig. 2C–F), while its connection to seasonally dry neotropical forests was relatively low, reaching only 12.43% (Fig. 2B–E). In contrast, climatic assemblage "B" exhibited a higher affinity for savannas (64.8%) (Fig. 2F–I) and seasonally dry neotropical forests (60.4%) (Fig. 2E–H), while its relationship with tropical rainforests was lower, accounting for only 29.3% (Fig. 2D–G).

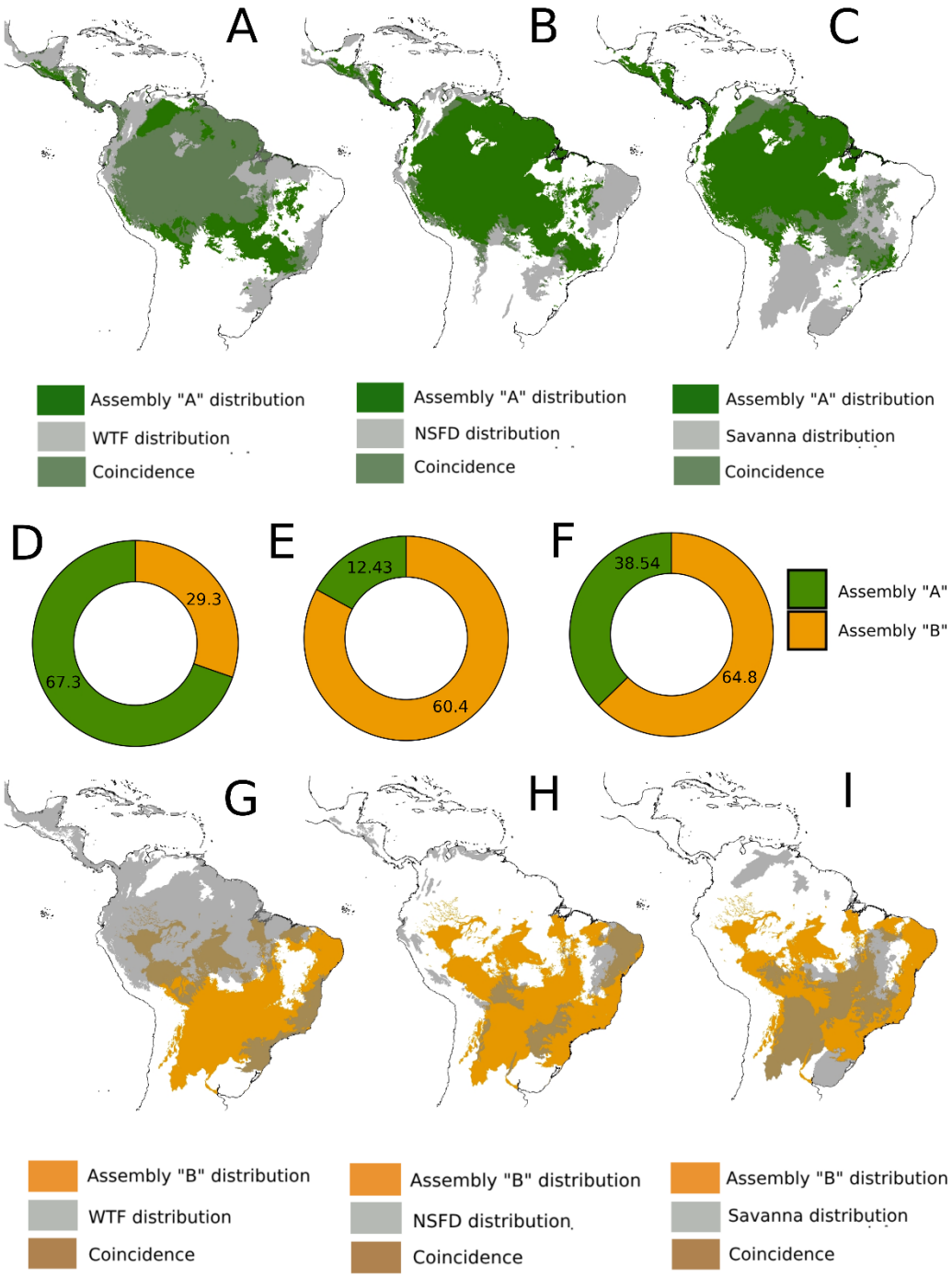

Fig. 2. Geographical reconstruction of ecological assemblages. climatic assemblage "A" (A–C), Percentage of overlap with each biome (D–F), climatic assemblage "B" (G–I). WTF: Wet tropical forest and NSDF: Neotropical seasonally dry forest.

Phylogenetic analysis

The parsimony analysis yielded four most parsimonious trees, each with a tree length of 111 steps, a consistency index (CI) of 0.56, and a retention index (RI) of 0.87. The pruned topology used for further analyses is shown in Figure 3A. In this tree, the genus *Exalphus* forms a monophyletic group with highest support (GC=92), consistent with the phylogenetic hypothesis of

Souza et al. (2017). Several internal clades are recovered with moderate to high GC node support. *E. spilonotus*, *E. foveatus*, and *E. confusus* appear as basal lineages relative to the rest of the genus. A well-supported clade (GC=90) is composed of *E. zellibori* and *E. colasi*. Further along the tree, *E. aurivillii, E. biannulatus*, and *E. gounellei* are placed in an intermediate position as sister to two derived clades: one formed by *E. guaraniticus* and E. *leuconotus* with low support (GC=58), and another composed of *E. lichenophorus*, *E. malleri*, *E. calvifrons*, and *E. cicatricornis* with low support (GC = 63) (Fig. 3A).

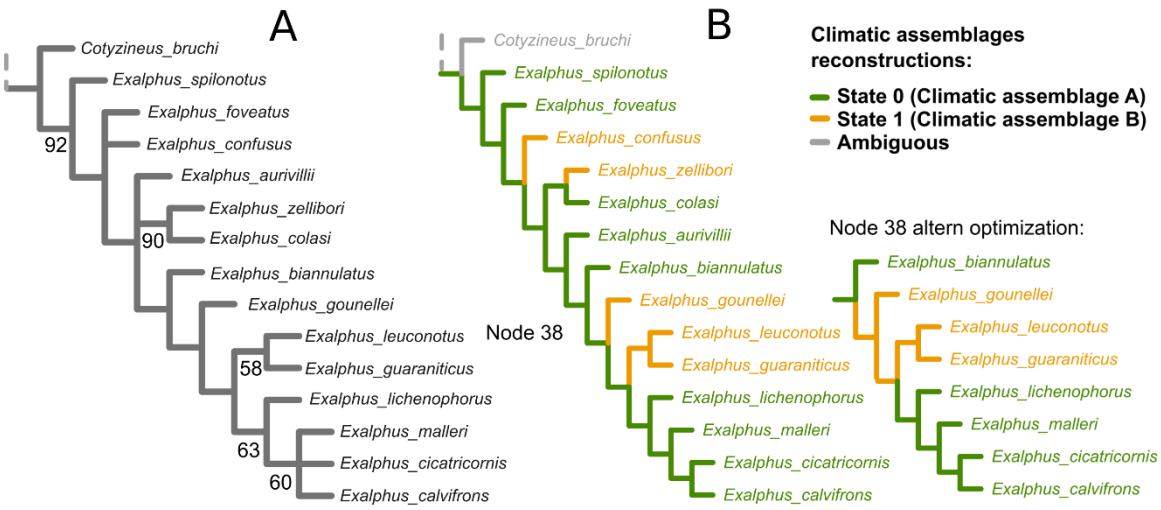

Fig. 3. Phylogeny and ancestral state reconstruction of climatic assemblages in *Exalphus*. (A) Strict consensus tree pruned to include only *Exalphus* species and the outgroup *Cotyzineus bruchi*. Support values are expressed as GC frequencies. (B) Ancestral state reconstruction of climatic assemblages in *Exalphus*. Ancestral climatic affinities (state 0 = Climatic Assemblage "A", green; state 1 = Climatic Assemblage "B", orange; ambiguous = gray) were mapped onto one of the most parsimonious trees obtained from morphological data. The left panel shows the primary reconstruction, while the right panel presents an alternative optimization of node 38, illustrating the ambiguity in ancestral state assignment for that clade.

Ancestral character reconstruction

The ancestral character-state reconstruction of climatic affinity, mapped onto this tree (Fig. 3B), revealed a convergent pattern across the phylogeny. Species belonging to Climatic Assemblage A (affinity mainly for humid forests, state 0) and Climatic Assemblage B (seasonally dry forest and savanna affinity, state 1) occur in unrelated clades, indicating multiple independent origins of both conditions within *Exalphus*. Node 38 was reconstructed ambiguously, with two alternative scenarios: (i) a humid forest ancestor followed by a shift to seasonally dry habitats in *E. gounellei*, *E. leuconotus*, and *E. guaraniticus*; or (ii) a seasonally dry ancestor with subsequent reversals to humid forest in other lineages.

DISCUSSION

Main findings

The formulation of integrative hypotheses about biodiversity distribution is key to understanding the factors shaping biological diversity across the planet (Searcy and Shaffer 2016). Here, we use the genus *Exalphus* as a case study to examine the drivers of its Neotropical distribution and their relationship to species clustering based on climatic affinities. Our analyses revealed: (i) two distinct climatic assemblages—group A, primarily species from tropical rainforests, and group B, strongly associated with savannas and seasonally dry forests—strongly supported by cluster analysis, MANOVA, and ordination, with isothermality, precipitation seasonality, and maximum temperature as the main predictors; (ii) ecological niche models indicating clear spatial segregation between rainforest and dry forest/savanna assemblages; and (iii) phylogenetic reconstruction confirming the monophyly of *Exalphus* but revealing non-conserved climatic affinities, with multiple independent transitions between humid and seasonally dry environments, suggesting convergent evolution driven by climate rather than inheritance from a common ancestor.

Climatic assemblages: species potentially associated with humid biomes

The high affinity of climatic assemblage "A" for the humid forest biome could primarily be associated with biological factors such as their natural history, feeding strategies, and behavior (Linsley 1959; Linsley 1961; Noguera 2014); ecological factors like their association with host plants (Tavakilian et al. 1997), canopy cover, decomposing organic matter, or even physical factors related to the host potential, such as wood density (Lanuza-Garay and Barrios 2018; Torres et al. 2024; Sullivan et al. 2025), which are essential for understanding these affinities and their diversity. Following this premise, our study shows that climatic assemblage "A" primarily occupies the Amazonian forests, which constitute the most biodiverse area on the planet (Myers et al. 2000). Compared to other tropical forests in Africa and Asia, the Amazon hosts more plant species than any other place on Earth, with an estimated 50,000 species found within the Amazon Basin alone (Hubbell et al. 2008). This region corresponds to an area of high diversity and endemism across various taxonomic groups (Rahbek and Graves 2001; ter Steege et al. 2003; Tognelli and Kelt

2004). The diverse vegetation types, such as forests, dwarf forests, and shrubs, have allowed cerambycid beetles to exhibit preferences for certain hosts and different forest strata, as demonstrated by several studies conducted over many years of monitoring from the Guiana Shield to the southwestern Amazon (Berkov and Tavakilian 1999; Fassbender et al. 2014; Albert et al. 2012; Lee et al. 2014; Li et al. 2017).

Climatic assemblages: species potentially associated to savannas and seasonally dry forests

In contrast, climatic assemblage "B" exhibited a strong association with savannas, seasonally dry neotropical forests, and the Atlantic Forest. The savannas extend over vast areas of southern Brazil, particularly within the Cerrado ecoregion (Oslon et al. 2001). This region is characterized by a variety of phytophysiognomies, including a vegetation gradient dominated by herbaceous formations, grasses, shrubs, and forests, creating a distinct microclimate and diverse food resource availability (Evangelista et al. 2021). Additionally, the forests that comprise the Atlantic Forest are among the 25 most biodiverse areas in the world, with estimates suggesting they harbor more than 70% of terrestrial species (Myers et al. 2000; Habel et al. 2019). This region encompasses a wide range of vegetation types, including dense ombrophilous forests, seasonal deciduous forests, and mangroves, among others (Almeida 2016). This climatic group was also strongly associated with the Chaco and Caatinga ecoregions, which are part of the seasonally dry neotropical forests. These are characterized by vegetation ranging from thorny shrublands to deciduous and semi-deciduous forests (Murphy and Lugo 1995). These ecoregions are also distinguished by trees with smaller basal areas and fewer epiphytes per hectare (Murphy and Lugo 1986; Gentry 1995; Pennington et al. 2000). One of the most diverse plant families in this ecosystem is Fabaceae (Pérez-García et al. 2010; Linares-Palomino et al. 2010; Arruda et al. 2011). Species such as *Eperua falcata* Aublet 1775; *E. rubiginosa* Miquel 1851; *Heterostemon* sp Desf 1818 and *Macrolobium bifolium* (Aublet 1805) have been reported as host plants for *Exalphus* species (Monné 2024). This pattern of separation between the Amazon and the Atlantic Forest was also documented by Silva de Miranda et al. (2018) and Mercado et al. (2020), who provided evidence that these forests, previously considered a single biome of humid tropical forest, are floristically distinct, and their climatic niches generally do not overlap. This has a significant effect on the distribution of *Exalphus* species.

Ancestral character reconstruction

Although the ecological clustering of *Exalphus* species into distinct climatic assemblages was supported by multivariate and distributional analyses, the ancestral character reconstruction revealed no clear phylogenetic structure underlying these patterns. The species assigned to climatic assemblage B (associated with seasonally dry forests and savannas) were recovered in multiple unrelated clades, suggesting that adaptation to these environments may have occurred independently. These results point to a homoplastic distribution of climatic affinity within *Exalphus*, consistent with convergent ecological evolution. Similar patterns have been reported in other Cerambycidae, where ecologically similar species may not be closely related, and host use or habitat preference varies independently of phylogenetic relationships (Berkov and Tavakilian 1999). This apparent lack of association between phylogeny and climate niche may be indicative of ecological plasticity within the genus or changes in environmental conditions throughout the evolutionary history of lineages. This possibility is further substantiated by the extensive ecological associations that Neotropical Cerambycidae have documented (Machado et al. 2012). Conversely, the observed pattern may be the consequence of incomplete resolution in the phylogenetic topology or from constraints in the morphological dataset; the Souza et al. (2017) analysis was originally proposed to resolve phylogenetic relationships within *Ateralphus*. However, the integration of numerical ecology, distribution modeling, and phylogenetic reconstruction offers a more nuanced perspective on diversification in *Exalphus*, underscoring the significance of incorporating both ecological and evolutionary signals when interpreting the biogeographic patterns of species. According to Hunt et al. (2007), this interpretation is consistent with broader macroevolutionary studies in Coleoptera that emphasize convergence and niche shifts as recurring drivers of diversification.

CONCLUSIONS

Finally, the climatic and distributional relationships between *Exalphus* and the studied ecosystems suggest a strong shared biogeographic history, providing an opportunity to elucidate how climatic constraints have influenced the evolutionary processes and diversification of the genus within these ecosystems. However, the loss of biodiversity in the studied ecosystems, largely driven by the rapid destruction of habitats, limits our understanding of these relationships. Critical areas, such as the Atlantic Forest, require urgent conservation measures, as they are expected to continue to face high pressure in the future. The combined approach of numerical ecology and distribution

modeling presented in this paper has enabled us to identify the climatic space for *Exalphus* species, the shared ecological requirements, and, consequently, similar distributions, which can be used to understand better the dynamics of interactions between species and neotropical ecosystems.

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