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Journal

Biogeographia — The Journal of Integrative Biogeography, 41(2)

ISSN

1594-7629

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Publication Date

2026-06-10

DOI

10.21426/B6.61687

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Peer reviewed

Examining the ecological niche overlapping for six species of whip spider in the Andean Mountain system

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Keywords: Amblypygi, Microendemic, Niche overlaps, Species distribution.

SUMMARY

The relevant environmental variables for establishing Amblypygi populations and their ecological interactions are currently poorly studied. Delving deeper into this can help conserve this group of short-range-distribution species, which are useful as models in biogeographic research. In this study, we evaluated the distribution and overlapping patterns of ecological niche in six species of amblypygids (*Phrynus araya*, *P. panche*, *P. pulchripes*, *Heterophrynus batesii*, *H. boterorum*, *H. cervinus*) converging in the Andean ecosystems of Colombia, revealing a clear biogeographic segregation driven by environmental gradients: *Phrynus* species were associated with inter-Andean valleys with high thermal and water seasonality. While *Heterophrynus* occupied more stable and humid conditions of foothills and middle elevations. Overlap analyses showed significant divergence (e.g., $D=0.105$ between *P. panche* and *H. batesii*), with high unfilling values (up to 73.2%), indicating limited niche overlap and habitat specialization, although historical coexistence was detected in certain pairs of species (e.g., 99.1% stability between *H. cervinus* and *H. boterorum*). The ecological niche modeling (ENM), along with other approaches such as phylogeographic and behavioral ones, is crucial for identifying niche partitioning mechanisms and optimizing conservation strategies for endemic taxa in complex tropical landscapes.

INTRODUCTION

Ecological niche models (ENMs) are useful tools in ecology by linking environmental conditions with the potential distribution patterns of species (Guisan and Thuiller 2005), allowing us to anticipate their responses to future climate impacts (Thomas et al. 2004). The application of these models in environmental planning has proven to be effective in reducing extinction risks by identifying priority areas for conservation (Watson et al. 2011), and there is consensus in the scientific literature on their ability to significantly improve the effectiveness of conservation policies by providing quantitative bases for decision-making (Elith and Leathwick, 2009, Anderson et al. 2011).

Ecological niche models (ENMs) have been used in ecology studies during the last two decades, allowing the identification of optimal environmental conditions for the survival of species through the analysis of their occurrences and environmental variables (Anderson et al. 2011). These models have proven especially useful in biogeography, being used in 78% of recent studies on species distribution (Elith and Leathwick 2009), although they require careful selection of predictor variables and statistical validation to avoid misinterpretations (Araújo and Peterson 2012, Araújo et al. 2019, Sofaer et al. 2019). In the particular case of amblypygids, its application has made it possible to overcome sampling limitations and predict potential distributions even with scarce data (Chapin and Hebets 2016, Vásquez-Palacios and Chirivi Joya 2023), evidencing its versatility as a research and conservation tool.

Amblypygids (Amblypygi) are cryptic arachnids with low dispersal capacity and high dependence on stable microclimatic conditions, making them particularly sensitive to environmental disturbances (Chapin and Hebets 2016, Chapin 2019). This sensitivity, added to their habitat specificity, has motivated their use as bioindicators of ecosystem health (Chapin 2019, Vásquez-Palacios and Chirivi Joya 2023). Recently, ecological niche models (e.g. MaxEnt) have made it possible to predict their potential distribution under climate change scenarios, identifying critical areas for their conservation (Vásquez-Palacios and Chirivi Joya 2023). However, the accuracy of these models depends on the rigorous selection of environmental variables and algorithms (Vásquez-Palacios and Chirivi Joya 2023), highlighting the need to integrate empirical data to validate their projections.

Colombia has a high diversity of Amblypygi compared with other countries of America, especially, presenting different species of each genus of the family Phrynidae. This diversity is mostly concentrated on the Andean mountain system (Chiriví-Joya and de Armas 2012, Chirivi-Joya et al. 2020). Amazonian species have distribution ranges larger and spreader than those in the Colombian Andes (Weygoldt 2002), which could indicate that the geographic conditions allow niche differentiation, which is worth evaluating as a model in speciation processes. The delineation of ecological niches for the six species of whip spiders (Amblypygi) will follow protocols established by Anderson et al. (2011) and Kass et al. (2018), using algorithms such as MaxEnt to identify areas with optimal environmental conditions (Vásquez-Palacios and Chirivi Joya 2023). Niche overlap will be quantified using Schoener's D-index and null hypothesis testing (Anderson et al. 2011, Kass et al. 2018), considering macroclimatic variables (BioClim) relevant to this group (Chapin and Hebets 2016, Chapin 2019). Validation will incorporate independent data from biological collections to avoid overfitting (Anderson et al. 2011, Araújo et al. 2019). As top predators, their population fluctuations in response to environmental changes position them as effective bioindicators (Chapin 2019), capable of revealing alterations in the structure and function of Andean ecosystems.

MATERIALS AND METHODS

Study Area and taxon choosing

The study area includes areas of the North of South America, the species analyzed occupy habitats from 0 to 2000 meters above sea level, and, therefore, a wide climatic and/or environmental variability. We selected six species of Amblypygi that converge in the Colombian Andean Mountain system, and from which there are enough distribution records to assess their ecological niche. These are, *Phrynus araya* Colmenares and Villarreal, *Phrynus panche* Armas and Angarita, *Phrynus pulchripes* (Pocock), *Heterophrynus batesii* (Butler), *Heterophrynus boterorum* Giupponi and Kury, and *Heterophrynus cervinus* Pocock (Table 1). The species were selected for their value as ideal models for exploring patterns of diversification, biogeographic adaptation, and ecological niche dynamics in complex tropical environments. The species have either endemic or widespread distributions in the Andes, and in some

cases, distribution ranges reach the Amazonian and Orinoquian valleys. Also, in some cases, there are overlapping species distributions. These biogeographic characteristics allow us to investigate mechanisms of coexistence and competition in phylogenetically close, but ecologically divergent, taxa. The sensitivity of Amblypygi species to environmental variables (thermal seasonality, humidity) makes them indicators of eco-evolutionary processes in mountain gradients. From an applied perspective, understanding their ecological niches facilitates the design of precise conservation strategies for cryptic but functionally relevant groups in ecosystems threatened by climate change and fragmentation. All mapping and editing of the ecological niche models for the six species were carried out using QGIS 3.34 (QGIS.org 2025).

Occurrence data

The occurrence records of the six species were obtained through data collected by us and compared with information from the GBIF online records using the R *spocc* packages and the *occ_search* function of the *rgbif* package (R Core Team 2025), which perform a simplified search in the GBIF database using Wallace (Kass et al. 2018a, 2021, Owens et al. 2023). The GBIF database was selected, as it has sufficient and up-to-date information for Amblypygi (GBIF Secretariat 2023). Records were filtered by removing those with no coordinates or with exact duplicate coordinates (Table 1). The data downloaded in .csv format contains information such as scientific name, coordinates, geographic location, and elevation. Only records without estimation of uncertainty in georeferencing were preserved (Kass et al. 2018a, 2021, Anderson et al. 2020).

Table 1. List of species and number of occurrences used by ecological niche modeling.

Species	Original and use records models	Records GBIF
<i>Phrynus araya</i>	4	2
<i>Heterophrynus cervinus</i>	8	76
<i>Phrynus pulchripes</i>	8	36
<i>Phrynus panche</i>	15	4
<i>Heterophrynus boterorum</i>	27	39
<i>Heterophrynus batesii</i>	37	400
Total	64	557

Environmental data

Environmental data were obtained by downloading the 19 bioclimatic variables from WorldClim (Fick and Hijmans 2017) at a resolution of 0.5 arcmin (~1 km²), using the *envs_worldclim* function with a geographic reference point (mapCntr) to ensure correct regional extraction. The environmental values were extracted for each presence record using *raster::extract*, following a debugging process that included: (1) elimination of duplicate records in the same raster cell, (2) exclusion of records with NA values in the environmental variables, and (3) integration of the filtered environmental values in the table of occurrences. This process ensured that only spatially and environmentally unique records were retained for modeling, meeting data quality requirements (Hijmans et al. 2005, Fick and Hijmans 2017, Kass et al. 2018a, 2021), using the raster package in the R program.

Ecological Niche Modeling

The occurrence data processing included a thinning procedure to reduce sampling bias and spatial autocorrelation (Sillero and Barbosa 2021). Using the *poccs_thinOccs* function of the *wallace* package (Kass et al. 2021), a minimum distance filter of 1 km between records was applied, preserving only one occurrence per cell of 1 km², since this type of arachnid has low mobility. This approach ensures that the retained points represent spatially independent units, meeting the independence assumptions required for species distribution modeling and preventing artificial inflation of model performance due to sampling clusters (Hijmans et al. 2005, Boria et al. 2014, Varela et al. 2014, Aiello-Lammens et al. 2015, Kass et al. 2018a, 2021, Sillero and Barbosa 2021).

The spatial extent for the models was defined, incorporating environmental characteristics

to compare with the presence records of the six species (Peterson et al. 2011, Kass et al. 2018a, 2021). Background point sampling was carried out by defining a study area based on the minimum convex polygon around the species presence records, applying a buffer of 0.2 degrees using the *penvs_bgExtent* function. Subsequently, environmental variables were masked to restrict them to this geographical extension using *penvs_bgMask* (Williams and Jackson 2007, Kass et al. 2018a, 2021). 10,000 random background points were sampled within this area using *penvs_bgSample*, representing the environmental conditions available for the species (Hijmans et al. 2005, Guevara et al. 2018, Kass et al. 2018a, 2021). Finally, the values of the environmental variables for each background point were extracted using *raster::extract*, and integrated into a structured table that includes spatial and environmental metadata, allowing the presence conditions to be contrasted with those available in the study area (Kass et al. 2021).

The partitioning of spatial data for training and validation of the model was performed using the "hierarchical checkerboard" (cb2) method implemented in the *part_partitionOccs* function, using an aggregation factor of 4 (Feng et al. 2019, Sillero and Barbosa 2021). This technique divides both presence records and background points into spatially independent groups, ensuring that training and validation data do not share geographic proximity and thus reducing the risk of spatial overfit and autocorrelation (Araújo et al. 2019, Sofaer et al. 2019). The environmental mask delimited the study area to ensure the ecological representativeness of the partitions (Muscarella et al. 2014, Kass et al. 2018a, 2021).

Ecological niche modeling was implemented using the maxnet algorithm (implemented in ENMeval V2.0) using the *model_maxent* function (Phillips et al. 2006, Elith et al. 2011, Kass et al. 2018a, 2021). Multiple combinations of parameters were evaluated: regularization multipliers (rm: 1-5, increasing by 1) and feature classes (linear (L), product (P), hinge (H), quadratic (Q)), with clamping disabled to avoid artificial extrapolations (Warren and Seifert 2011, Radosavljevic and Anderson 2013, Muscarella et al. 2014, Hijmans et al. 2017, Kass et al. 2018a, 2021, Regos et al. 2019, Sofaer et al. 2019). The model was adjusted using presence data, background points, and spatial partition groups for validation, running in sequential model (Muscarella

et al. 2014, Kass et al. 2018a, 2021). This approach made it possible to identify the optimal configuration that balances complexity and predictive capacity, minimizing overfitting according to the ENMeval evaluation criteria (Kass et al. 2018a, 2021).

The visualization methodology consisted of generating an environmental suitability map from the Maxent model using the *predictMaxnet* function (Peterson et al. 2011, Kass et al. 2018a, 2021), using the "cloglog" output type and without clamping restrictions. A quantile threshold ("qtp" = 0.05) was applied to convert continuous predictions into a binary presence/absence map, defined by the 5th percentile of suitability values at points of occurrence (Merow et al. 2013, Yackulic et al. 2013, Hijmans et al. 2017, Phillips et al. 2017, Kass et al. 2018a, 2021). The visualization was implemented with the leaflet package, overlaying layers of: (1) umbralized prediction (blue/gray for presence/absence), (2) occurrence records (red dots), and (3) study background polygon (blue outline) (Kass et al. 2018a, 2021). This approach allowed to spatially represent the potential distribution of the species and contrast it with the field data.

The evaluation of the model was performed using the *evalplot.stats* function of the ENMeval package (Muscarella et al. 2014, Kass et al. 2021), using the metric "auc.diff" (difference between training and validation AUC) as an evaluation statistic to compare the performance of different parameter configurations (Merow et al. 2013, Radosavljevic and Anderson 2013, Sofaer et al. 2019, Kass et al. 2021, Sillero and Barbosa 2021). This metric allowed the optimal model to be identified by contrasting regularization multipliers ("rm") and feature classes ("fc"), where low auc.diff values indicate greater generalizability and less overfitting. The resulting graphical visualization facilitated the selection of the ideal balance between model complexity and predictive capacity.

Niche Overlay

The analysis of ecological niche overlap between the six species was carried out using the *ecospat* package in R (Barve et al. 2011, Anderson 2013, Di Cola et al. 2017), following three methodological stages: (1) the reduction of environmental dimensionality through a principal component analysis (PCA) using the *espace_pca* function (Broennimann et al. 2012, Guisan et al. 2014, Kass et al. 2018a, 2021), which projected the bioclimatic variables (*bio01-bio19*)

in a two-dimensional space for all species and their environmental backgrounds; (2) the estimation of the occupancy density in the environmental space was estimated with the *espace_occDens* function, which calculated the potential distribution areas in the PCA axes; and (3) the quantification of niche overlap using the *espace_nicheOv* function (derived from *ecospat.niche.overlap*), which computed the D and I indices of overlap (Schoener 1968, Warren and Seifert 2011, Araújo et al. 2019) and ran similarity tests (100 iterations). Finally, niche dynamics (expansion (magenta), stability (blue), unfilling (yellow), abandonment (green) were visualized with *ecospat.plot.niche.dyn* and statistical significance with *ecospat.plot.overlap.test*, revealing patterns of ecological divergence between species. All possible connections between the six species have been analyzed (13), however, for practical visualization purposes, only the connections that showed significant niche overlap between the species are presented.

RESULTS

Ecological niche modeling

Models of potential distribution of habitat suitability were obtained for six species of Amblypygi with confirmed presence for Colombia. Figure 1A shows the potential distribution model for *P. araya*, in the Northeast region of Colombia, on the eastern flank of the Eastern Andes and reaching the western coast of Lake Maracaibo in Venezuela, most of the model is located over mountainous areas and in areas adjacent to these elevations. Areas shaded in red indicate the potential distribution, suggesting suitable habitats for this species. The model predicts two distinct areas of potential distribution, one to the north near the Perijá mountain range and another to the south over the Eastern Mountain range.

On the other hand, for the species *P. panche*, the potential distribution model predicts the species in the inter-Andean zones between the central and eastern mountain ranges in Colombia. The model shows that the ideal habitat conditions for this species are located where large valleys are formed near the Magdalena River and bordering the foothills of the mountain range (Fig. 1B). For the species *P. pulchipers*, the potential distribution model identifies two areas with habitat suitability, in the inter-Andean valley between the central and eastern mountain

range, and another further north, only on the eastern mountain range, in a mountainous area. Both areas are very small in size (Fig. 1C).

With respect to the genus *Heterophrynus*, the potential distribution model for *H. cervinus* shows areas with suitable habitat conditions in central and southern Colombia, in part of the inter-Andean valley, and in the foothills of the central and eastern mountain range of Colombia (Fig. 1D). Likewise, for the species *H. boterorum*, the potential distribution model is showing that the species is restricted to the mountain area in the central mountain range in central Colombia, where two areas with potential habitat suitability are identified, one located on the western flank and the other on the eastern flank, delimited by the highest areas of the mountains (Fig. 1E). Finally, it was found that for the species *H. batesii*, two large areas with potential habitat suitability distribution are identified, the largest over part of the eastern plains and the Colombian Amazon, and the other of a smaller area is located between the inter-Andean valley of the central and eastern mountain ranges bordering the foothills in each mountain range (Fig. 1F).

Different species of Amblypygi have distinct geographic and altitudinal distributions, suggesting specific adaptations to different ecological habitats (Fig. 2). The distribution of *P. araya* is concentrated in northeastern Colombia, in both low and medium-elevation areas. *P. pulchripes* has a limited distribution, mainly in a small mountainous region of central Colombia. *P. panche* is found in the central mountainous region of Colombia. *H. cervinus* has a wide distribution spanning several elevations in western Colombia. *H. batesii* and *H. boterorum* also show specific distributions, but with *H. batesii* occupying areas in the east and *H. boterorum* areas in south-central Colombia (Fig. 2).

The spatial segregation of *P. araya* and *P. panche* could indicate an evolutionary divergence driven by adaptation to different ecological niches and geographic barriers. The coexistence of *H. cervinus* with other species in the same region suggests niche differentiations. Differences in ranges suggest that each species has specific adaptations to environmental conditions, such as temperature, humidity, and availability of shelters. Altitude seems to play an important role, as some species are restricted to certain elevations while others have a wider distribution (Fig. 2).

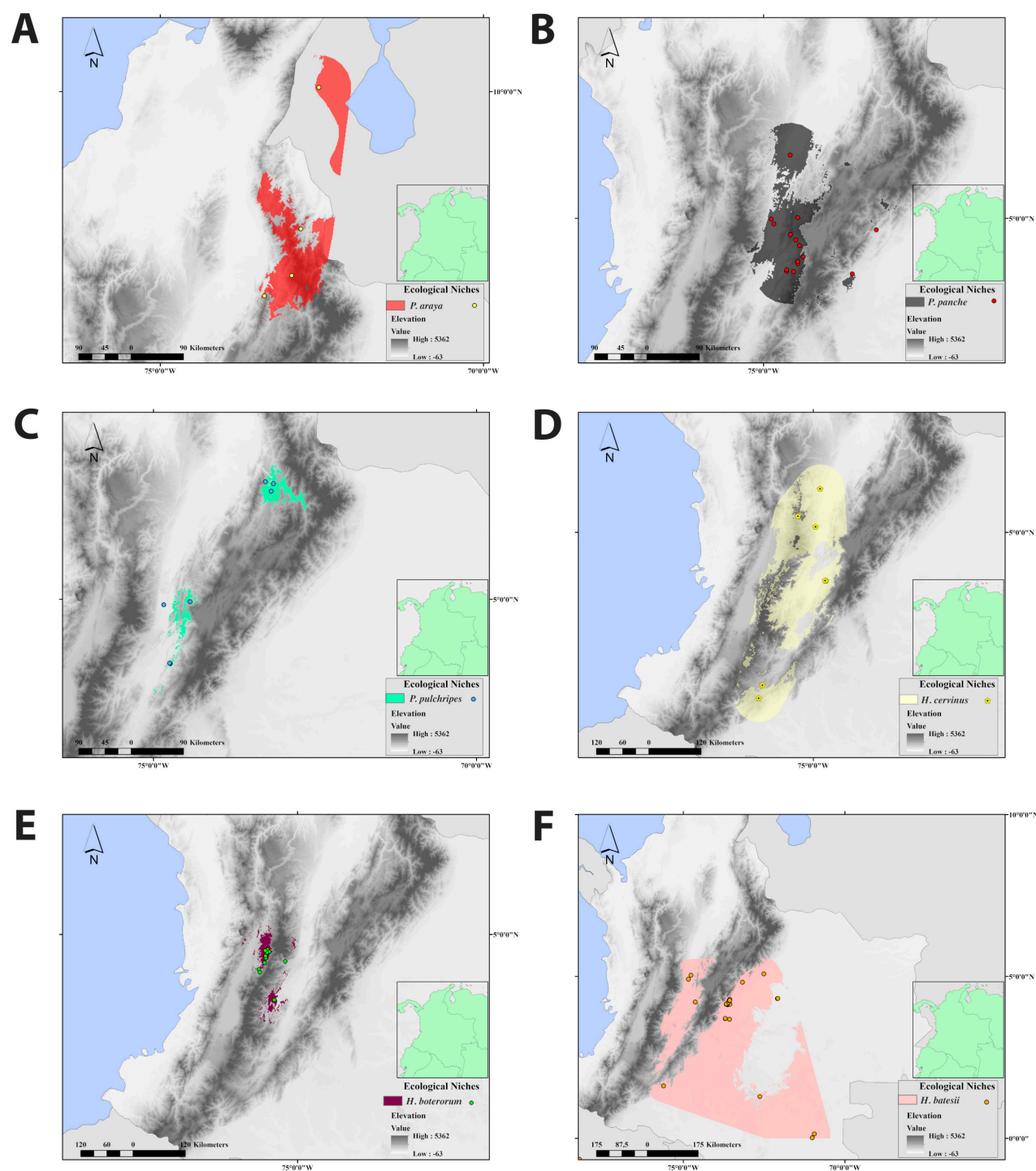


Figure 1. Ecological niche models (ENMs) for the six Amblypygi species analyzed in Colombia. A: *P. araya*; B: *P. panche*; C: *P. pulchripes*; D: *H. cervinus*; E: *H. boterorum*; F: *H. batesii*.

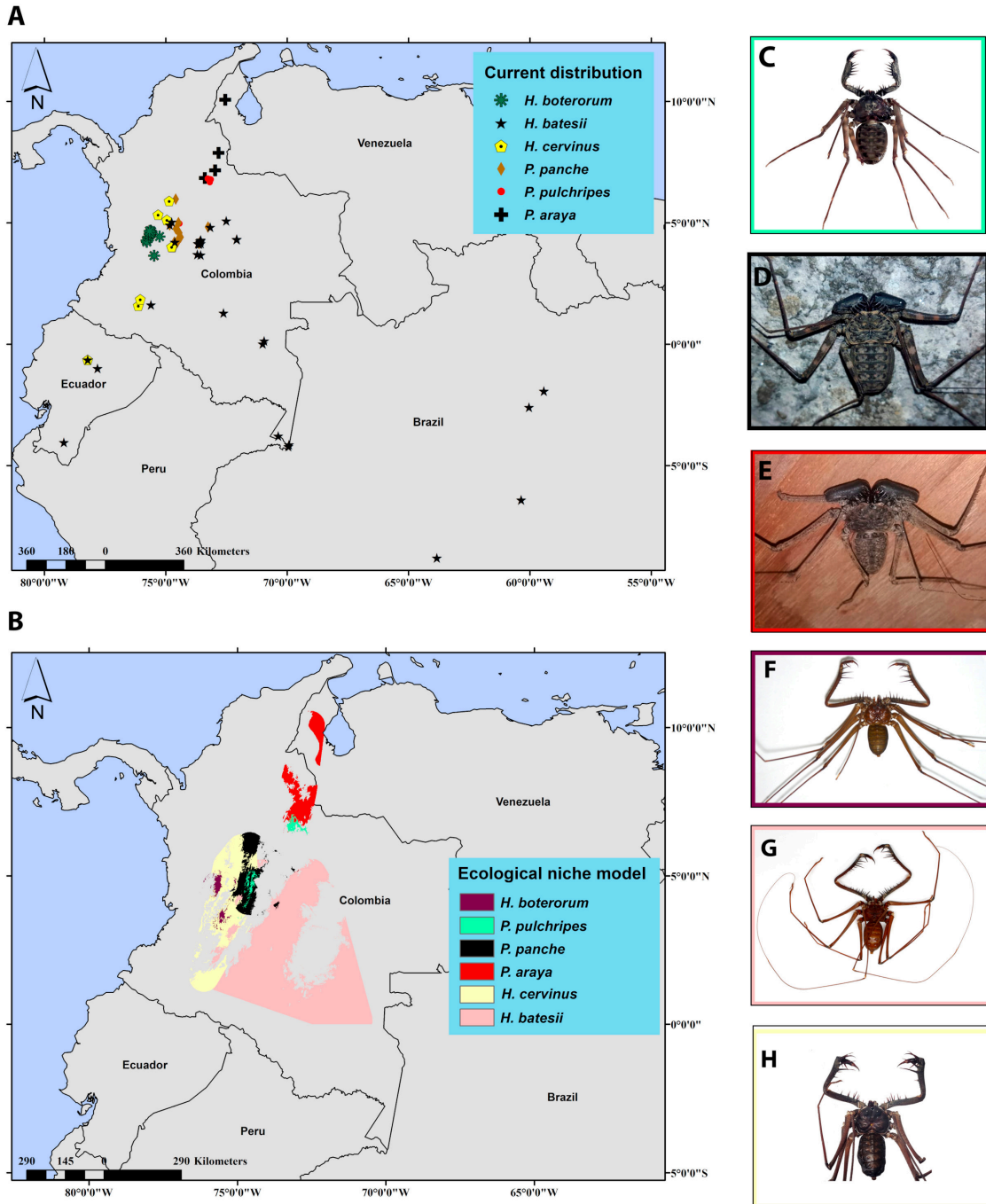


Figure 2. A: Species distribution. B: Integration of the ecological niche model (EMM) distribution for six Amblypygi species in Colombia. The colored areas represent the potential distribution of each species, based on its ecological niche model. C: *P. pulchripes* (green). D: *P. panche* (black). E: *P. araya* (red). F: *H. boterorum* (purple). G: *H. batesii* (pink). H: *H. cervinus* (yellow).

The analysis of the models for the six species reveals varying levels of adjustment and generalization. For *P. araya* (Fig. 3A), good results are obtained with $rm = 4$ and $fc = LQ$ or H (values ~ 0.36 – 0.38), effectively controlling overfitting. *P. panche* (Fig. 3B) shows the best performance, with

very low values (0.09–0.16) indicating excellent generalization, especially with high regularization ($rm = 4$) and simple features (H , L). In contrast, *P. pulchripes* (Fig. 3C) requires strong regularization ($rm = 4$) to reduce overfitting, achieving values of 0.09–0.12 with $fc = H$ or L . *H. cervinus* (Fig. 3D)

presents the greatest fitting difficulties, with extremely low values (0.02–0.07) suggesting possible underestimation or critical instability, confirming the challenge of modeling this species. *H. boterorum* (Fig. 3E) exhibits satisfactory and stable performance (values 0.07–0.125), with $rm = 4$ and $fc = H$ or L as optimal. Finally, *H. batesii* (Fig. 3F) shows robust behavior (0.075–0.10) without abrupt

changes, being suitable with $rm = 3–4$ and $fc = LQ$. Overall, the graphs validate the text recommendations: use medium-high regularization ($rm = 3–4$) and linear or quadratic features (L, LQ) for most species, except for *H. cervinus*, where no configuration achieves a completely satisfactory fit.

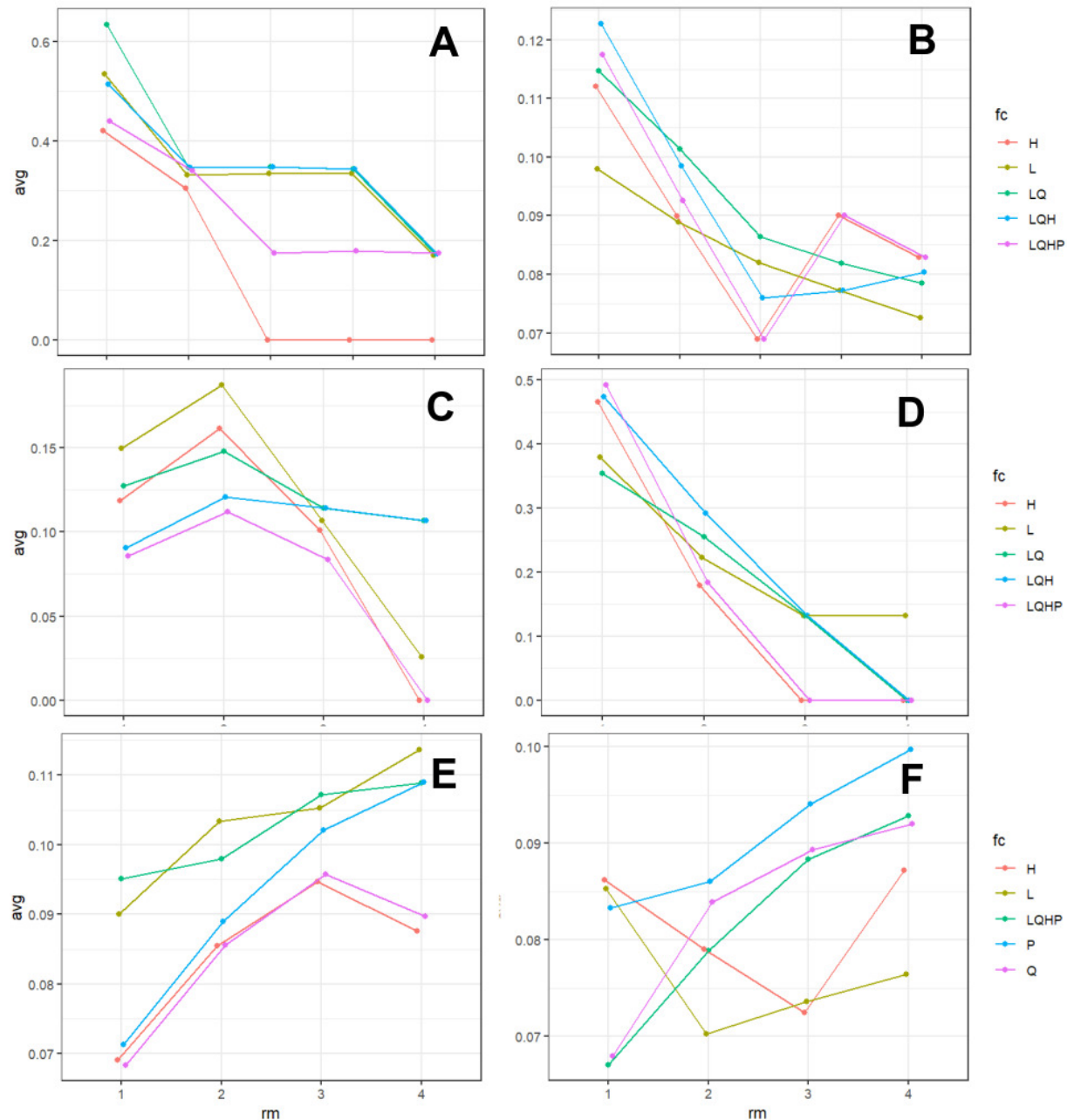


Figure 3. Adjustment and generalizability of ecological niche models for six amblypygid species as a function of the regularization multiplier (rm) and feature classes (fc). A: *P. araya*, B: *P. panche*, C: *P. pulchripes*, D: *H. cervinus*, E: *H. boterorum*, F: *H. batesii*. rm : value regularization multiplier, fc : model features, avg: average values. L: line, Q: quadratic, H: hinge, P: product. Axes x value of regularization multipliers, tested between 1 and 4 in increments of 1 to optimize accuracy and axis Y represent the average of value regularization multipliers.

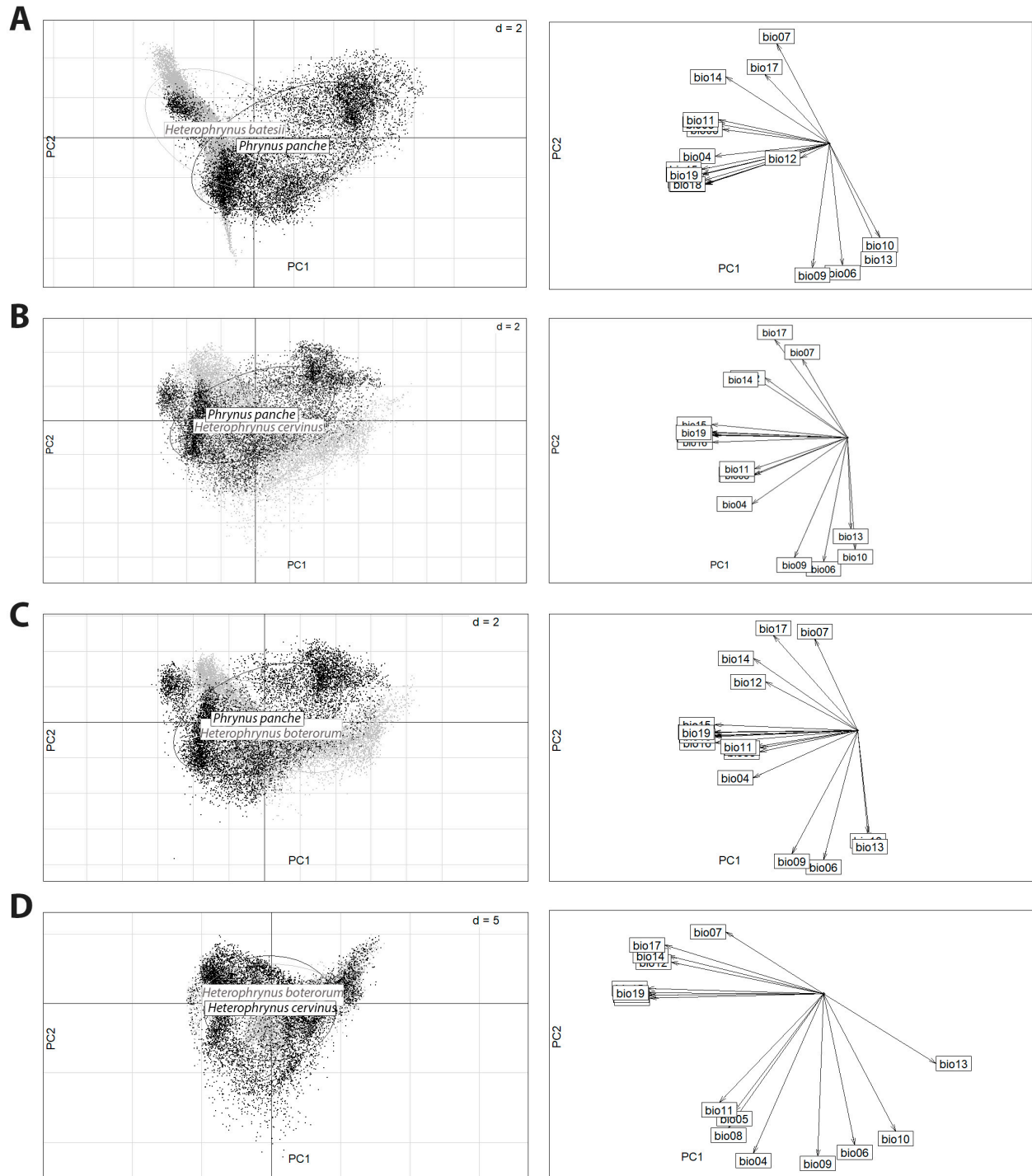


Figure 4. Principal components and vectors for the environment space of species in the overlap analysis. A: Overlap analysis of *H. batesii* vs *P. panche*; B: Overlap Analysis for *H. cervinus* vs *P. panche*; C: Overlap Analysis for *H. boterorum* vs *P. panche*; D: Overlap Analysis for *H. cervinus* vs *H. boterorum*.

Overlap ecological niche

The PCA analysis reveals different degrees of ecological niche differentiation between the species studied: while *H. batesii* and *P. panche* (Fig. 4A), *H.*

cervinus and *P. panche* (Fig. 4B), as well as *H. boterorum* and *P. panche* (Fig. 4C), present a moderate differentiation (distance $d=2$). *P. panche* is consistently associated with environments of greater

thermal and hydrological seasonality, reflected in extreme BIO5 (maximum temperature of the warmest month) and BIO6 (minimum temperature of the coldest month) values, along with high variability in seasonal temperatures (BIO10 and BIO11), typical of dry inter-Andean valleys. In contrast, the other species (*H. batesii*, *H. cervinus* and *H. boterorum*) prefer more stable and humid conditions, characteristic of the Amazonian foothills and mid-elevations, where the mean annual temperature (BIO1) is more constant, and rainfall is less seasonal.

The most evident niche divergence is observed between *H. cervinus* and *H. boterorum* ($d=5$) (Fig. 4D), distributed in contrasting environmental zones in terms of rainfall seasonality and temperature. This separation is influenced by variables such as BIO8 (mean temperature of the wettest quarter) and BIO9 (mean temperature of the driest quarter), which define the thermal extremes associated with rainfall regimes, as well as by the temperatures of the warmest (BIO10) and coldest (BIO11) quarters.

The analysis of niche overlap shows contrasting patterns between species: *H. batesii* and *P. panche*, present low overlap ($D=0.105$, $I=0.204$) without statistical significance ($p>0.05$), with high expansion (0.588) and unfilling (0.532), indicating a strong niche partition where each species occupies different environments (*P. panche* in seasonal valleys, *H. batesii* in moist foothills) (Fig. 5A). On the contrary, *H. cervinus* and *P. panche* present a statistically significant ($D=0.256$, $I=0.404$) moderate-high overlap ($p<0.01$), with high stability (0.806) and unfilling (0.721) (Fig. 5B), suggesting equivalent niches and prolonged coexistence in similar microhabitats of transition zones, which reflects evolutionary conservation of niches in these species.

P. panche and *H. boterorum* have low but significant overlap ($D=0.223$, $p=0.03$), with a high proportion of unshared niche (unfilling=73.2%), indicating a marked ecological divergence where each species occupies different environments, possibly due to habitat specialization or competitive exclusion (Fig. 6A). In contrast, *H. cervinus* and *H. boterorum* have a moderate and significant overlap ($D=0.230$, $p=0.03$) with extremely high stability (99.1%), suggesting that they share a common environmental core and have historically coexisted in similar mountain microhabitats, although with an important portion of non-overlapping niche

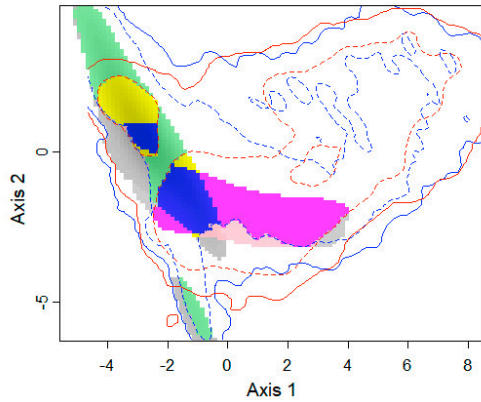
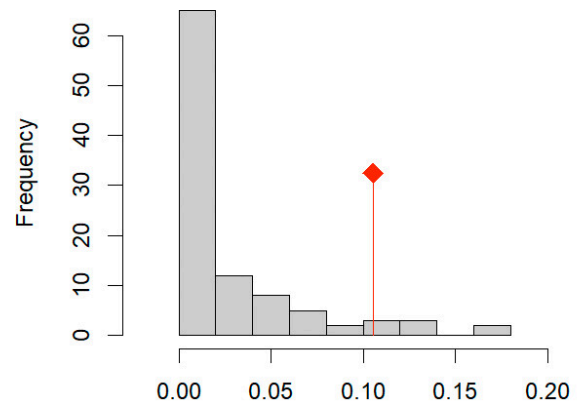
(unfilling=73.8%) reflecting their partial geographic segregation (Fig. 6B).

DISCUSSION

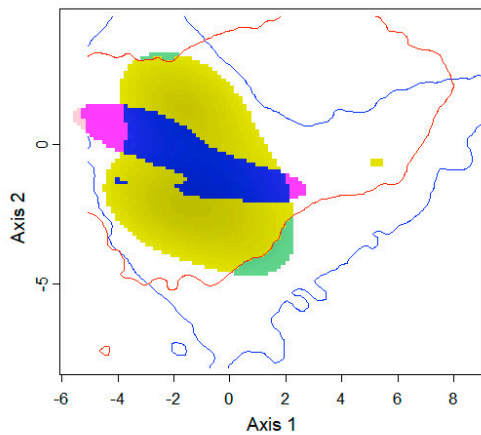
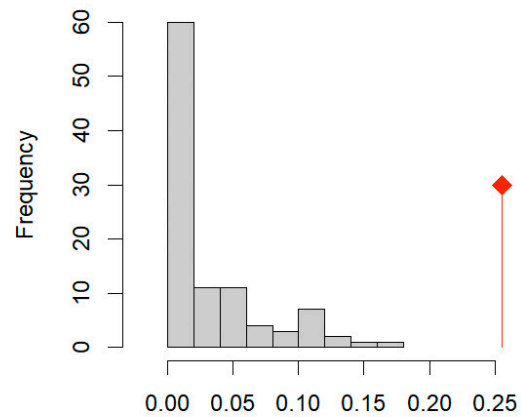
The results of this study reveal consistent patterns of ecological niche divergence between species of amblypygids of the genera *Phrynus* and *Heterophrynus* in the Colombian Andes. The limited overlap observed between *P. panche* - *H. batesii* ($D = 0.105$), and *P. panche* - *H. boterorum* ($D = 0.223$), together with the high unfilling values (up to 73.2%), indicates a strong resource partition driven by adaptations to contrasting environmental conditions. These findings are consistent with the principle of competitive exclusion (Warren et al., 2008), where coexistence is facilitated by specialization in distinct microhabitats, particularly along thermal and water seasonality gradients. The statistical significance of these differences ($p < 0.05$ in most cases) supports that they are not random variations, but structured ecological patterns.

The marked environmental segregation between congeneric species (*H. cervinus* vs *H. boterorum*; $D = 0.230$ but with 99.1% stability) suggests that, despite being morphologically and ecologically similar, these taxa have experienced adaptive divergence in response to local environmental pressures. High stability reflects niche conservation in historically shared conditions, while unfilling (73.8%) indicates expansion into new environments not occupied by the congener. This pattern coincides with the speciation mechanisms described by Broennimann et al. (2012) in mountain systems, where isolation by adaptation to different altitudinal levels promotes diversification.

Phylogenetically, the evaluated species belong to the same family, Phrynidae, traditionally considered monophyletic, as well as the two subfamilies included in this research, Heterophryninae (*Heterophrynus*) and Phryninae (*Phrynus*) (Weygoldt 2000). The divergence of the species of the family could start in the Miocene, together with the Andes rising as molecular analyses have previously shown (Chirivi-Joya et al. 2025). This is coherent with our results, suggesting that the altitudinal gradient promotes different environmental conditions that generate niche divergences. The species that present a high niche overlap are not necessarily from the same genus, but those that are distributed in close areas. These results can be

A***H. batesii* vs *P. panche*****Similarity test**

D
p.value = 0.06931

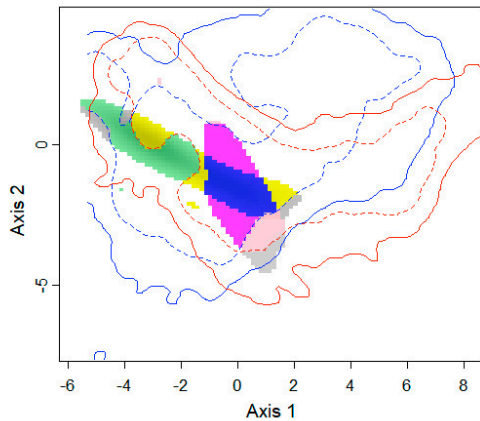
B***H. cervinus* vs *P. panche*****Similarity test**

D
p.value = 0.0099

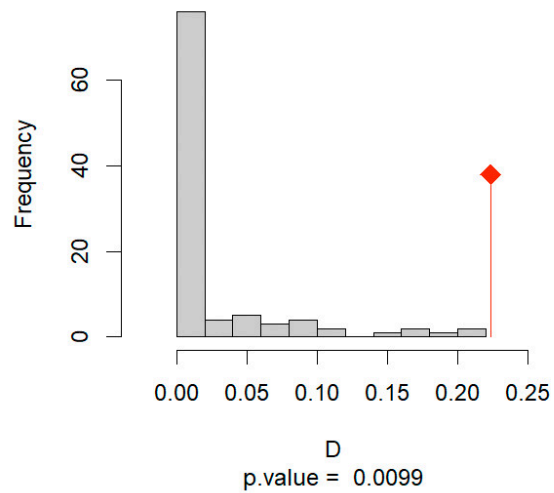
Figure 5. Overlap analysis and ecological niche similarity test for two species evaluated in this study. The left panel shows the environmental sample spaces for the pairs of species analyzed niche dynamics (expansion (color magenta), stability (color blue), unfilling (color yellow), abandonment (green) and in the right panel the frequency histogram for the similarity test in the ecological niches of the species is presented, the red line represents the value of the similarity index (D) in each comparison. A: *H. batesii* vs *P. panche*; B: *H. cervinus* vs *P. panche*.

A

P. panche* vs *H. boterorum

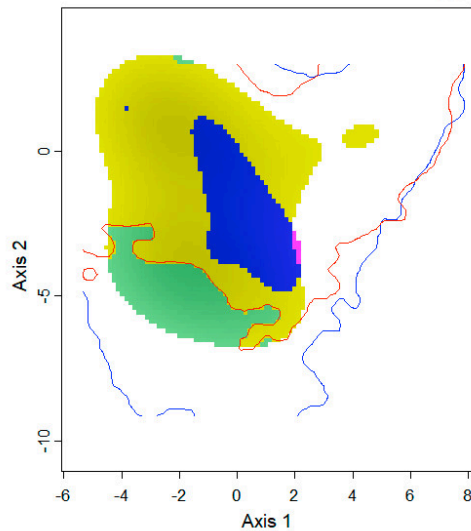


Similarity test



B

H. cervinus* vs *H. boterorum



Similarity test

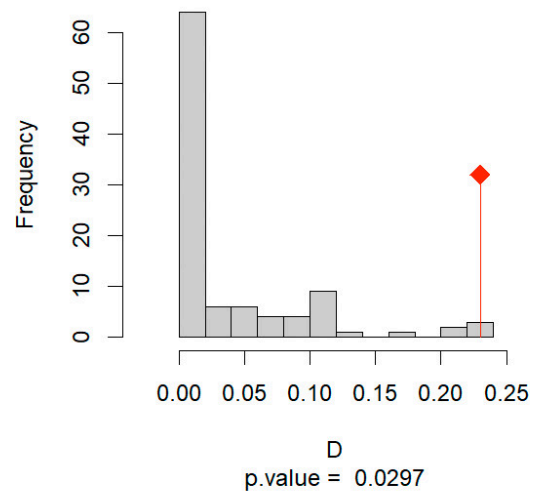


Figure 6. Overlap analysis and ecological niche similarity test for two species evaluated in this study. The left panel shows the environmental sample spaces for the pairs of species analyzed niche dynamics (expansion (magenta), stability (blue), unfilling (yellow), abandonment (green)) and in the right panel the frequency histogram for the similarity test in the ecological niches of the species is presented, the red line represents the value of the similarity index (D) in each comparison. A: *P. panche* vs *H. boterorum*; B: *H. cervinus* vs *H. boterorum*.

conditioned by the variables included in our analysis; however, species such as *P. panche* showed more overlap with closely distributed *Heterophrynus* than with the other *Phrynos*. On the other hand, the species *H. boterorum* and *H. cervinus* have a very similar niche, but this is probably more related to their close distribution than to phylogenetic proximity.

From a methodological perspective, the integration of ecological niche models (ENMs) with niche overlap analysis has proved to be useful in identifying priority areas for conservation (Chapin 2019), which can be observed in this case in the inter-Andean valleys between the central and eastern mountain ranges, where several species coexist, such as *H. boterorum*, *H. batesii*, *H. cervinus*, *P. panche*,

P. pulchripes; and in the northern foothills of the eastern mountain range, where *P. pulchripes* and *P. araya* inhabit. In addition, we also identified some areas in the foothills of the central mountain range and the Amazon region where *H. batesii* and *P. panche* potentially could interact. Parameter optimization in Maxent models (regularization multipliers 1-5 and LQHP features) allowed minimizing overfitting (auc.diff < 0.15 at optimal settings), as recommended for taxa with constrained distributions (Araújo et al. 2019, Kass et al. 2021, Sillero and Barbosa 2021). The application of spatial partitioning techniques ("hierarchical checkerboard") ensured robust evaluations of the predictive capacity of the models, avoiding spatial autocorrelation (Muscarella et al., 2014).

These results have direct implications for the conservation of endemic taxa in Andean landscapes. The identification of areas with high niche stability (e.g. *H. cervinus* and *H. boterorum*) suggests priority areas for protection, where multiple species coexist in a sustainable manner. Conversely, areas with high unfilling represent opportunities for conservationist expansionism through ecological corridors (Chapin 2019). Combining ecological niche models (ENMs) with niche dynamics analysis provides evidence for prioritizing conservation efforts in regions with high diversity and increasing anthropogenic threats. This is particularly relevant for cryptic arthropods such as amblypygids, which are often underestimated in management plans.

Species like *P. pulchripes* and *P. araya* have restricted potential distributions, concentrated in small mountainous areas or along the eastern Andean flank, making them especially vulnerable to habitat loss. In contrast, species like *H. cervinus* show wider distributions in central and southern Colombia, but still depend on specific ecological conditions associated with the Andean foothills and inter-Andean valleys. Niche overlap analyses further highlight distinct patterns of ecological specialization: while *P. panche* is consistently associated with seasonally dry inter-Andean valleys characterized by extreme temperature variability. Species such as *H. batesii* and *H. boterorum* occupy more stable, humid environments in the foothills and mid-elevations of the Amazon.

The niche divergence observed between *H. cervinus* and *H. boterorum*, along with their high niche stability, suggests that these congeners maintain distinct climatic niches while potentially

coexisting through microhabitat differentiation along humidity and temperature gradients. Taken together, these findings underscore the importance of incorporating small-scale environmental heterogeneity and species-specific niche requirements into conservation planning, particularly for understudied groups such as amblypygids, whose distribution patterns and ecological tolerances are often overlooked in traditional assessments.

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Submitted: 17 December 2025

First decision: 14 March 2026

Accepted: 14 May 2026

Published online: 10 June 2026

Edited by Giuseppe Nicolosi