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https://doi.org/10.1590/SciELOPreprints.11070

Submitted on: 2025-01-14
Posted on: 2025-01-29 (version 1)
(YYYY-MM-DD)

Fantastic plants and where to find them: niche occupancy analysis in neotropical epiphytic species

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ABSTRACT

Aim: Niche occupation and organism diversification are interrelated processes that shape biodiversity. This study investigates the relationship between niche occupation, phylogenetic relationships, and species distribution within the genus *Microgramma* (Polypodiaceae), a group of neotropical epiphytic ferns.

Location: Neotropic.

Taxon: Genus *Microgramma* (Polypodiaceae, ferns).

Methods: We analyzed eight species from the Scaly clade, exploring patterns of co-occurrence and allopatry in relation to their environmental characteristics through species distribution modeling and predicted niche occupation profiles. Niche overlap was assessed based on the degree of environmental similarity and spatial co-occurrence.

Results: Niche occupation varied significantly among phylogenetically close species, while niche overlap was greater among phylogenetically distant species. Broadly distributed species tended to co-occur, suggesting niche divergence that facilitates coexistence by occupying distinct niches within the same region. In contrast, allopatric species exhibited differentiation in their environmental niche occupation for specific variables. Despite being geographically separated, allopatric species demonstrated greater environmental similarity with each other than with broadly distributed species, indicating niche convergence.

Main Conclusions: Environmental factors play a key role in shaping niche occupation strategies in *Microgramma*. Broadly distributed species show patterns of niche divergence to enable coexistence, while allopatric species exhibit niche convergence despite their geographical separation. These findings provide insights into co-occurrence dynamics and diversification in neotropical epiphytic ferns.

Keywords: allopatry, divergence, ferns, niche overlap, predicted niche occupancy.

Introduction

Biodiversity arises from a complex mosaic of relationships and interactions, with two key processes standing out: organism diversification and the ecological niche occupation (Bolnick et al. 2003; Fine 2015; Futuyma and Moreno 1988). Diversification has been extensively studied, revealing patterns often influenced by ecological and evolutionary constraints (Niklas 1997; Schneider et al. 2004; Yoder et al. 2010). Concurrently, niche occupation reflects how species interact with their environment and with one another, playing a pivotal role in shaping community structure (Holt 2009; Hutchinson 1991; MacArthur and Levins 1967; Rappoldt and Hogeweg 1979).

The spatial, geographic, and ecological range of a species is primarily determined by its ecological niche, which represents the intersection of multiple environmental, biotic, and abiotic factors, including geographic characteristics, interaction dynamics, and organism dispersal (Hutchinson 1991). The fundamental niche represents the full range of environmental conditions that support a species' persistence, while the realized niche represents a narrower subset constrained by the effects of dispersal, biotic interactions, and, for animals, behavioral factors (Peterson et al. 2011).

As predicted by the theory of niche conservatism (Wiens and Graham 2005), phylogenetically closely related species are expected to exhibit similar niches due to their shared ancestry (Cooper et al. 2011; Peterson 2011). This pattern is often maintained through evolutionary mechanisms such as stabilizing selection and gene flow (Cooper et al. 2010; Pyron et al. 2015). However, niche divergence can arise in response to new environmental pressures, driven by factors such as genetic drift, competition, and dispersal (Gordon 2000; Wiens et al. 2010; Wu et al. 2023).

The maintenance of communities is closely linked to species co-occurrence (Keddy 1992), which is influenced by stabilizing mechanisms such as resource partitioning, population density variations, and the effects of environmental factors operating in the same space and time (Chesson 2000). Additionally, some species possess specific traits that allow them to exploit different resources, reducing competition and promoting niche partitioning (Schoener 1974). The interaction between species and their environment results in diverse patterns of distribution and niche occupation (Carscadden et al. 2020; Sheth et al. 2020; Soupe et al. 2015). Dispersal is one of the most critical processes influencing species distribution, as it enables the exploration of areas with potential occurrence (Wu et al. 2023). Long-distance dispersal (LDD) events promote the colonization of new locations (Wu et al. 2023). Although these events are rare and challenging to quantify and predict (Nathan 2006), they are key processes in shaping the current distribution of plants (Jordano 2017). Fern spores, due to their small size and lightweight nature, can travel long distances through the atmosphere, facilitating their dispersal (Kessler 2010). Additionally, species in the order Polypodiales possess spores that are catapulted by sporangia over greater distances, increasing their likelihood of entering wind currents (Llorens et al. 2016; Schneider 2001). Notably, dispersal may be more efficient for epiphytic ferns compared to terrestrial species within a forest (Raynor et al. 1976).

Microgramma (Polypodiaceae) comprises approximately 30 predominantly epiphytic fern species that inhabit tropical forests (Almeida et al. 2021). These species are distributed throughout the Neotropics, from Florida to Argentina, with a single species occurring in Africa, Madagascar, and the Indian Ocean islands (Almeida et al. 2021). The Scaly clade, which includes eight neotropical species, encompasses both widely distributed species occupying extensive areas of the Neotropics and endemic species from the Atlantic Forest (Brazil), the Andes, and the Caribbean. With this combination of sympatric and allopatric species distributions and complete sampling in the most recent phylogenetic inference for the group (Almeida et al. 2021), the Scaly clade provides a robust model for investigating niche occupation dynamics in neotropical ferns.

Within this context, our study aims to investigate: (1) how niche occupation varies in terms of environmental characteristics among species that co-occur and those distributed in allopatry, and (2) whether niche overlap is greater between phylogenetically close or distant species. We hypothesize that phylogenetically close species will share similar environmental preferences only in cases of low geographic overlap. Conversely, when species co-occur, we expect their environmental preferences to exhibit lower overlap. Given the clade's extensive distribution across the Neotropics, we anticipate finding low niche conservatism, reflecting an exploration of ecological space to minimize competition.

Material and Methods

Data Gathering and Cleaning

This study focused on eight species of *Microgramma* from the Scaly: *Microgramma dictyophylla* (Kunze ex Mett.) de la Sota, *M. latevagans* (Maxon & C.Chr.) Lellinger, *M. nana* (Liebm.) T.E.Almeida, *M. percussa* (Cav.) de la Sota, *M. piloselloides* (L.) Copel., *M. reptans* (Cav.) A.R.Sm., *M. tecta* (Kaulf.) Alston, and *M. tobagensis* (C.Chr.) C.D.Adams & Baksh.-Com. (Table 1). Species occurrence data were obtained from online repositories, including the Global Biodiversity Information Facility (GBIF - https://www.gbif.org/; DOIs listed in Table S1), SpeciesLink (https://specieslink.net/), and the Virtual Herbarium Reflora (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/ConsultaPublicoHVUC/ConsultaPublicoHVUC.do).

Duplicate records were manually removed, and all entries were verified for taxonomic accuracy, excluding those identified only to the genus level. Geographic coordinates were reviewed and corrected, with coordinates assigned to records with clear occurrence descriptions using tools such as Google Earth and Google Maps. Records lacking geographic descriptions were excluded, and those with potentially ambiguous data were reviewed to ensure verification by specialists; unverified records were discarded. Initially, 12,998 records were retrieved. After filtering, 4,596 records were retained for analysis. All species were confirmed to have sufficient records for model construction, with each species represented by more than ten data points.

Climatic data

Current climatic data were obtained from CHELSA (Karger et al. 2017). Additional variables included cloud cover (seasonality and annual mean) (Wilson and Jetz 2016), Enhanced Vegetation Index (EVI) (Jiang et al. 2008), Global Elevation (Fick and Hijmans 2017), and

SRTM (Van Zyl 2001). All layers were resampled to a resolution of 30 arc seconds (~1 km) using a Neotropics mask, clipped through Quantum GIS 3.16 (2022).

To address collinearity among environmental variables (correlated variables), the Variance Inflation Factor (VIF) was calculated using the R package *usdm* (Naimi 2016), with a cutoff value of 0.7 (Pradhan and Setyawan, 2021). Out of 25 environmental layers obtained, 11 were selected for analysis: Mean Diurnal Temperature Range (Bio02), Isothermality (Bio03), Mean Temperature of Wettest Quarter (Bio08), Precipitation of Driest Month (Bio14), Precipitation Seasonality (Bio15), Precipitation of Warmest Quarter (Bio18), Precipitation of Coldest Quarter (Bio19), Cloud Seasonality, Terrain Rugosity, EVI Dissimilarity, and Global Elevation.

Species distribution modeling

The SDM function in the BioDinamica software (Oliveira et al. 2019) was used to generate species distribution models. Five algorithms with different logic based on presence-only data were applied: Multivariate Adaptive Regression Splines (MARS) (Friedman 1991), Support Vector Machines (SVM) (Vapnik 1998), Generalized Boosted Models (GBM) (Friedman et al. 2000), Random Forests (RF) (Breiman 2001), and Maximum Entropy (MaxEnt) (Phillips et al. 2006). A split of 75% of the records was used for training and 25% for testing, to construct and validate the models. Binary models were generated using a threshold configuration of maximum sensitivity plus specificity. Model evaluation was based on the receiver operating characteristic (ROC) area under the curve (AUC) values and the true skill statistic (TSS). Model performance was classified as follows: AUC below 0.7 indicates poor performance, 0.7–0.8 good performance, 0.8–0.9 very good performance, and above 0.9 excellent performance (Manel et al. 2001). For TSS, values above 0.6 were considered good (Allouche et al. 2006). All subsequent analyses were performed using R v. 4.2.1 (R Core Team 2022) and RStudio v. 4.2.764 (Rstudio Team 2024).

To quantify minimum and maximum tolerance ranges and the environmental occupation of each species for each sampled environmental variable, predicted niche occupation (PNO) profiles were generated (Evans et al. 2009). Additionally, the areas under the density curves were quantified and analyzed to interpret the degree of overlap for each pair of species in their respective environmental variables using the *raster* package.

Pairwise niche overlap was calculated using the same set of binary species distribution models, based on equivalence (Schoener's D) and similarity (Hellinger's I) indices, as proposed by Warren et al. (2008, 2010) and implemented in the *dismo* package. These indices range from 0, indicating no overlap, to 1, indicating complete niche overlap between the compared models (Warren et al. 2010).

The Bayesian Inference tree presented by Almeida et al. (2021) was used to assess the correlation between niche distance and patristic phylogenetic distance, calculated using the *ape* package v. 5.7 (Paradis and Schliep 2019). For *M. tobagensis*, which appears non-monophyletic in Almeida et al.'s (2021) tree, we removed the terminal positioned as sister to *M. reptans* and retained the terminal grouped with *M. piloselloides*, as it represents a larger distribution area. A pairwise phylogenetic distance matrix was constructed from the results. The correlation between niche distances (equivalence index D and similarity index I) and phylogenetic distance was tested using the Mantel test, implemented in the *vegan* package (Oksanen et al. 2013).

Results

The consensus models generated by all algorithms demonstrated good performance, with high AUC values (>0.9) and TSS values (>0.7) (Table 1). The species distribution model (SDM) for *Microgramma dictyophylla*, found in northern South America, primarily in lowland Amazonian forests (Figure 1), recovered suitability areas that matched its known distribution, along with additional suitable areas in Central America, the Caribbean, and a small coastal region in northeastern Brazil (Figure 2A). The model for *M. latevagans* recovered suitability restricted to the species' known range, primarily in high-altitude areas of the Andes in Bolivia, Ecuador, and Peru (Figure 2B). *Microgramma nana*, which occurs in the Amazon region, also showed small additional areas of suitability in eastern South America, where the species has no known occurrences (Figure 2C). The model for *Microgramma percussa*, a species widely distributed throughout the Neotropics and with the largest range in the clade, did not show significant expansions beyond its known range (Figure 2D).

The model for *M. piloselloides*, which occurs in the Antilles, Mexico, Guatemala, and Costa Rica, also identified small areas of suitability in the Andes of Colombia and Bolivia, as well as in eastern Brazil (Figure 2E). *Microgramma reptans*, a species with a broad distribution across Central America, Mexico, and Bolivia, as well as disjunct populations in northern Amazonia and the Atlantic Forest of Bahia, Brazil, showed no significant expansions in its model relative to its known range (Figure 2F). For *M. tecta*, the only species in the clade endemic to the Atlantic Forest, the resulting model showed suitable environmental areas also in the Andean regions of Peru and Bolivia (Figure 2G). Lastly, the model for *M. tobagensis*, which occurs in Central America, Peru, Bolivia, Guyana, Venezuela, and disjunctly in the Brazilian Atlantic Forest, indicated slightly more extensive areas of suitability in the western Brazilian Amazon (Figure 2H).

The predicted niche occupation profiles (PNOs) showed high overlap in environmental variable ranges among species, particularly for those with broader distributions, such as *M. dictyophylla*, *M. nana*, *M. reptans*, and *M. percussa*. Exceptions were observed in more restricted species, especially *M. latevagans* (Figure 3). The tolerance range for mean diurnal temperature (Bio02) varied from 1–13°C, with density peaks at 7°C for *M. latevagans* and 4°C for *M. tobagensis* (Figure 3). For isothermality (Bio03), the range varied from 15–80%, with peaks at 25% for *M. tecta* and 60% for *M. latevagans*. The mean temperature of the wettest quarter (Bio08) ranged from 0–28°C, with a significant density peak difference in *M. latevagans*, which showed a narrower range at lower temperatures compared to other species. Precipitation of the driest month (Bio14) varied from 0–25 mm, with a density peak for *M. latevagans* at 1 mm. Precipitation seasonality (Bio15) varied from 0–13 mm, with slight differences, such as peaks at 6 mm for *M. latevagans* and 2.5 mm for *M. tobagensis*. Precipitation of the warmest quarter (Bio18) ranged from 0–130 mm, with little variation. Precipitation of the coldest quarter (Bio19) varied from 0–75 mm for *M. latevagans*, *M. piloselloides*, and *M. tecta*, and from 0–150 mm for the other species. Cloud seasonality varied from 0–26 mm across all species, with similar peaks between *M. piloselloides* and *M. tobagensis*. Terrain roughness showed similar variation across all species except for *M. latevagans*, which exhibited higher terrain roughness values. The tolerance range for Enhanced Vegetation Index (EVI) dissimilarity showed a homogeneous occupation pattern among all lineages. Elevation varied from 0–2000 m for all species models, except for *M. latevagans*, which ranged from 0–5100 m (Figure 3).

Niche overlap analysis based on Schoener's D metric revealed the highest overlaps between the models for *M. percussa* and *M. reptans* (78%), *M. dictyophylla* and *M. reptans* (67%), and *M. dictyophylla* and *M. percussa* (65%). The model for *M. nana* showed 49% overlap with *M. tobagensis* and 48% with *M. dictyophylla*, while *M. piloselloides* exhibited 48% overlap with *M. tecta*. Other notable combinations included *M. percussa* and *M. tobagensis* (36% overlap) and *M. nana* and *M. piloselloides* (33% overlap). Among the lowest overlaps, *M. latevagans* showed only 7% overlap with *M. tecta* and *M. piloselloides*, and 1% with *M. dictyophylla*, *M. percussa*, and *M. reptans*. Similarly, the model for *M. reptans* showed low overlap with *M. tecta* (5%), while *M. tecta* showed a 15% overlap with *M. tobagensis* (Figure 4).

Niche overlap analysis based on Hellinger's I metric yielded higher values than Schoener's D in all species comparisons. The highest similarities were observed between *M. percussa* and *M. reptans* (92%), followed by *M. dictyophylla* and *M. reptans* (86%), and *M. dictyophylla* and *M. percussa* (84%). The model for *M. nana* showed 63% overlap with *M. tobagensis* and 60% with *M. percussa*. The model for *M. piloselloides* showed a high overlap with *M. tecta* (63%). Among the lowest similarities, the model for *M. latevagans* showed only 4% overlap with *M. reptans* and 10% with *M. dictyophylla*, while *M. tecta* showed 15% overlap with *M. reptans* and 26% with *M. tobagensis*. The model for *M. reptans* showed 60% overlap with *M. tobagensis* and 15% with *M. tecta* (Figure 4).

The Mantel test revealed a moderate positive correlation between patristic phylogenetic distance and niche overlap, with statistical significance observed only for the niche similarity metric I ($r^2 = 0.383$, $P = 0.045$). For the niche equivalence metric D, the correlation was not statistically significant ($r^2 = 0.356$, $P = 0.069$; Figure 5).

Discussion

Contrary to the expectations of the niche conservatism hypothesis (Wiens et al. 2010), our results show that phylogenetically close species within the Scaly clade share fewer environmental preferences than phylogenetically distant species, even in the absence of co-occurrence. On the other hand, species with restricted distributions, such as *M. latevagans*, *M. tecta*, and *M. piloselloides*, despite being phylogenetically distant and not co-occurring, exhibit greater niche and PNO overlap among themselves than with broadly distributed species. This pattern partially suggests potential niche convergence.

A relationship was observed between co-occurrence and environmental suitability areas in broadly distributed species, regardless of phylogenetic distance (Figure 1). The species *M. percussa*, *M. reptans*, and *M. dictyophylla* showed high overlap across all environmental variables analyzed in the PNOs (Figure 3 – Supplementary Material S1

) and high niche overlap in both equivalence and similarity metrics (D and I; Figure 4). Studies have demonstrated the relationship between distribution range, niche breadth, and phylogenetic proximity (Chen et al. 2024). Unlike species with more restricted niches, generalist species are believed to be less vulnerable to climate change (Devictor et al. 2010; Saupe et al. 2015), as they exhibit greater tolerance to alterations in environmental conditions (Chen et al. 2024; Colles et al. 2009). In this regard, our results support this idea, indicating that species with larger environmental suitability areas can exploit a broader range of environmental conditions (Figure 3).

Two main factors may be associated with this observed pattern. First, the high dispersal capacity of spores, a hallmark of ferns, is directly related to their distribution (Kessler 2010). This characteristic allows them to reach diverse environments with heterogeneous microclimates, enabling co-occurrence and promoting widespread distribution (Haufler 2000; Kessler 2010). Secondly, the epiphytic habit may play an important role in niche occupation dynamics, as evidence suggests significant differences in the influence of environmental factors on terrestrial and epiphytic ferns (Adriana et al. 2023). While terrestrial ferns are more influenced by local characteristics, such as soil type and vegetation structure, epiphytes depend more directly on climatic conditions, such as temperature and humidity (Adriana et al. 2023). Furthermore, competition is presumed not to be the primary force shaping the assemblage of vascular epiphytes (Benzing 2008; Burns and Zotz 2010; Zotz and Hietz 2001). By exploiting different microhabitats within trees, these plants may reduce competition for environmental resources (Burns and Zotz 2010). However, it is worth noting that studies on the structure and dynamics of vascular epiphytes are often biased taxonomically, with a greater focus on orchids and bromeliads, while other groups receive less attention (Zotz and Hietz 2001). These results provide robust insights into niche occupation dynamics on a broad scale; however, future studies are needed to investigate the ecological mechanisms enabling the co-occurrence of epiphytes with broad geographic distributions, employing population-level approaches to capture local structures.

Contrarily, our results indicate that *M. latevagans*, endemic to the Andes, occupies a highly specialized niche restricted to high-altitude areas, where temperature and precipitation conditions differ significantly from those of the other species (Figure 3). This pattern is evidenced by the low niche equivalence (I) and similarity (D) overlaps with other species (Figure 4). Studies on species from mountainous regions in distinct groups, such as neotropical frogs and treefrogs, reveal similar patterns, with differentiated niches when compared to lowland species (Bandeira et al. 2020; Coelho et al. 2023). The specialization of *M. latevagans* in high-altitude areas (Figure 3 – Global Elevation) may reflect its diversification during the Miocene, coinciding with the uplift of the Andes, particularly in the central region (Garzione et al. 2008). Among the clades recovered in *Microgramma*, the Scaly clade is the oldest, dating back approximately 23 million years (Almeida et al. 2021). Most divergences within this clade appear to have occurred during the Miocene or early Pliocene (Almeida et al. 2021). It is well-documented that much of the current geography of South America was shaped during the Miocene (Steinthorsdottir et al. 2020). In this context, the geographic isolation caused by the Andean uplift, combined with processes of ecological specialization, may have facilitated the establishment of *M. latevagans* as a distinct lineage, both evolutionarily and ecologically.

Microgramma tecta, endemic to the Atlantic Forest (Brazil), exhibited distinct density differentiation in the climatic variable of isothermality, which may play a central role in thermal stability (Figure 3). The analysis of PNOs reveals that isothermality overlap is relatively consistent among most species; however, *M. tecta* stands out by presenting a distinct range with higher density (Figure 3). Additionally, the species shows relatively low niche overlap with other species in terms of both equivalence (D) and similarity (I), except with *M. piloselloides* (Figure 4). These findings align with previous studies linking thermal variables to patterns of distribution and diversification in neotropical plants (Barros et al. 2020; Culumber and Tobler 2018; Padilha et al. 2024). The differentiation in this environmental variable may highlight the importance of temperature for the endemism of this species. Evidence suggests that the Atlantic Forest and the Amazon Rainforest were connected in the past (Sobral-Souza et al. 2015). The Andean uplift and climatic changes during the Eocene/Miocene likely resulted in the formation of a drier area, geographically separating them (Sobral-Souza et al. 2015). It can be proposed that the divergence of *M. tecta* is related to geographic isolation, combined with specialization processes in specific temperature zones.

The low niche overlap rates between phylogenetically close species, such as *M. tobagensis* and *M. piloselloides* (D: 24%; I: 38%; Figure 4), suggests adaptations to specific microclimates and geographic isolation, potentially driven by selective pressures (Czortek et al. 2021). These results challenge the expectation that closely related species share similar niches, indicating that environmental divergences may play a key role in driving different niche occupations (Peterson 2011; Wiens and Graham 2008; Wiens et al. 2010). Previous studies on various organisms, including animals and plants, have demonstrated niche differences between sister species, whether driven by geographic isolation, environmental differences, or climatic variables (e.g., Almendra et al. 2021; Cuervo et al. 2021; Mejia et al. 2022; Prochazka et al. 2024).

Niche divergence among closely related species may reflect environmental specialization relative to the ancestral niche (Pyron et al. 2015). The rare areas of co-occurrence (e.g., Guatemala and Costa Rica) can be explained by the fact that *M. tobagensis* and *M. piloselloides* represent the most recent divergence within the genus *Microgramma*, with an estimated age of less than 1 million years (Almeida et al. 2021). It is well-established that, over time, species may develop specific traits that allow them to exploit different resources, reducing competition intensity and potentially leading to niche partitioning (Schoener 1974). This suggests that current patterns of co-occurrence in present-day environments may influence how niches are shaped over time (Wiens and Graham 2005). Selection may act differently on populations inhabiting different optima (areas of high suitability) if phenotypes adapted to these optima were already present in the ancestral population (Pyron et al. 2015). In this context, the recent speciation of these two lineages could be related to their restricted niche requirements. We suggest that further studies, using population-level data, be conducted to better clarify the divergence of these two species and the processes at play.

The endemic species *M. latevagans* from the Andes, *M. tecta* from eastern Brazil, and *M. piloselloides* from the Caribbean (Figure 1), despite being phylogenetically distant and not co-occurring, exhibited greater niche and PNO overlap with each other than with other species in the clade (Figure 4; Supplementary Material S1). While *M. latevagans* showed low overlap with all species, the overlap percentage increased when compared to *M. tecta* and *M. piloselloides* (Figure 4; Supplementary Material S1). *Microgramma tecta* and *M. piloselloides* exhibited the highest niche and PNO overlap when compared to each other (Figure 4; Supplementary Material S1). The highest overlaps among these three species in environmental variables were observed for isothermality, precipitation of the coldest quarter, and global elevation (Supplementary Material S1). These patterns provide evidence of potential niche convergence among these endemic species.

Evolutionary signatures of niche convergence have been identified in diverse organisms across different environmental contexts (Ahmadi et al. 2021; Nyari and Reedy 2013; Nzei et al. 2024; Popescu et al. 2024). However, in the case of *M. latevagans*, *M. tecta*, and *M. piloselloides*, these species appear to share an environmental relationship in their areas of suitability, particularly in regions with lower temperatures. This suggests a historical restriction over time among species within this clade.

Microgramma nana exhibited niche overlap higher than 50% for the similarity metric (*I*) with most species in the clade, except with *M. latevagans*, *M. tecta*, and *M. piloselloides*–species with restricted distributions. For the equivalence metric (*D*), *M. nana* showed niche overlap below 50% with all species (Figure 4). Although all models had good validation values (Table 1), the distribution models for *M. nana* presented the lowest metric values among the species in the clade (Table 1). Although *M. nana* is considered to have a wide distribution in the Amazon, we believe it is undersampled, which may have affected both its distribution model and subsequent analyses. Sampling bias in ferns and lycophytes within the Brazilian Amazon has been previously documented (Almeida and Salino 2016), underscoring the urgent need for increased botanical collection efforts in this region.

The relationship between phylogenetic distance and niche overlap revealed a moderate and significant correlation within this clade, with species that are more phylogenetically distant tending to have greater niche overlap (Figure 5). This trend is more pronounced for niche similarity (*I*) than for niche equivalence (*D*). Our results indicate that the tendency for phylogenetic niche conservatism does not appear to be present in the studied group.

Conclusion

We observed that co-occurrence among phylogenetically distant species, particularly those with broad distributions, is linked to the sharing of similar environmental characteristics. This suggests that species with wider geographic distributions can exploit a broader range of environmental conditions within their niche occupation profiles. This trend is supported by the ease of fern spore dispersal and the epiphytic habit of the group, which likely facilitates co-occurrence in diverse environmental contexts by allowing greater exploration of their niche areas. Furthermore, endemic species exhibited distinct patterns of differentiation in specific environmental variables, suggesting that specialization to particular environmental conditions may play a central role in defining their geographic distributions. Our results revealed niche divergence among closely related species and niche convergence among distantly related species, with the latter sharing environmental similarities in their areas of suitability despite their phylogenetic distance. These findings underscore the importance of understanding the environmental factors that shape niche occupation strategies, contributing to a more comprehensive understanding of co-occurrence and diversification in neotropical epiphytic fern species.

Author Contributions

T.E.A. and K.S.L. conceived the idea. K.S.L., L.V.L., and T.E.A. designed the methodology. K.S.L. and T.E.A. collected the data. K.S.L., L.V.L., and T.E.A. conducted the analyses. All authors critically contributed to the drafts and the final version.

Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 (88887.910465/2023-00) awarded to K.S. Lima and (88887.937988/2024-00) awarded to L.V. Lima We thank CNPq for the research grant (317091/2021-2) awarded to T.E. Almeida. The authors thank Annelize Frazão, André Gasper, Marcelo Bueno, and Samuel Gomides for their valuable contributions to earlier versions of this manuscript.

Conflict of interest

The authors declare no conflict of interest.

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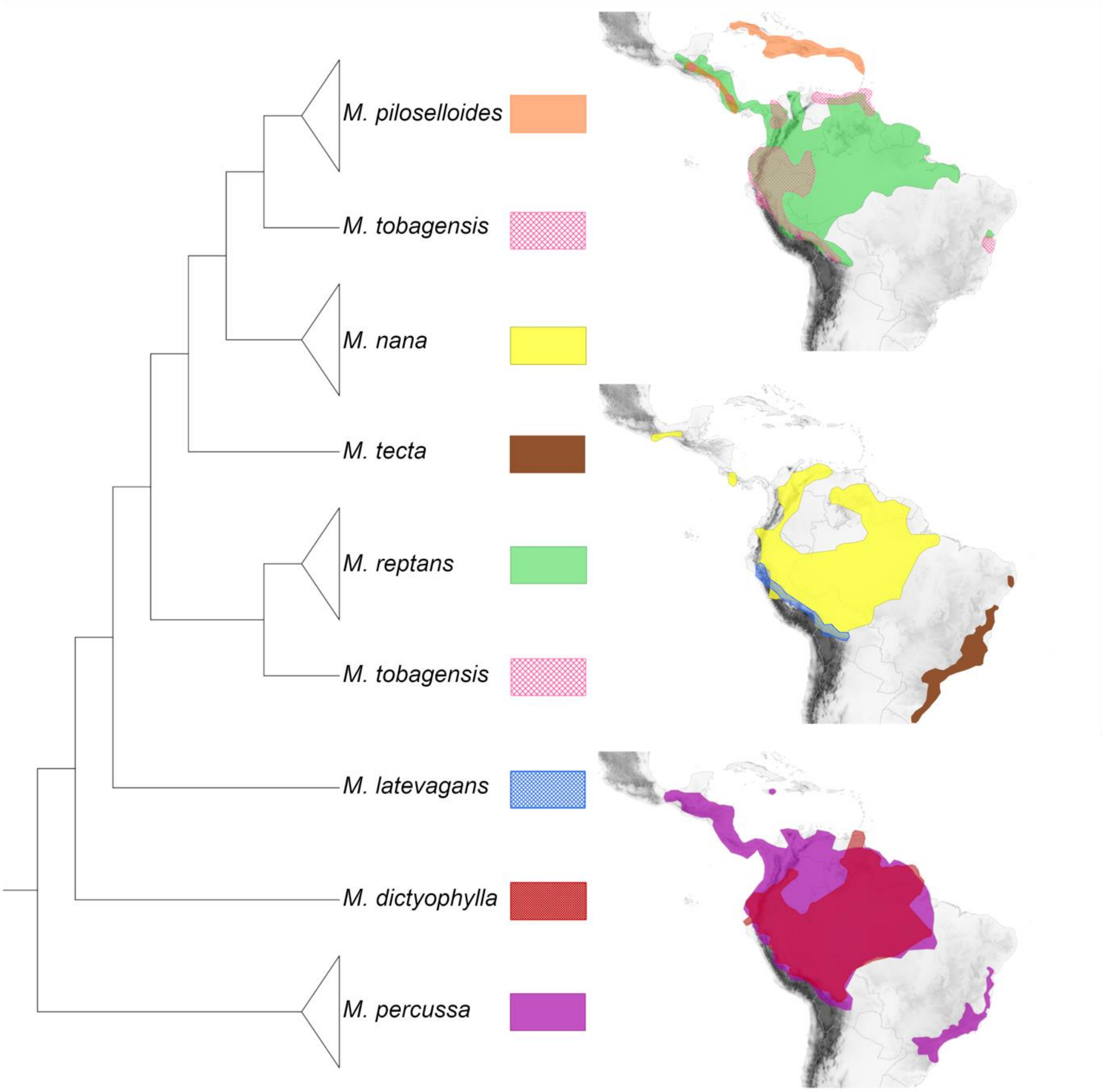


Figure 1 - Occurrence areas of Scaly clade species used in this study and phylogenetic relationships within the clade, based on the majority consensus tree resulting from Bayesian inference presented by Almeida et al. (2021).

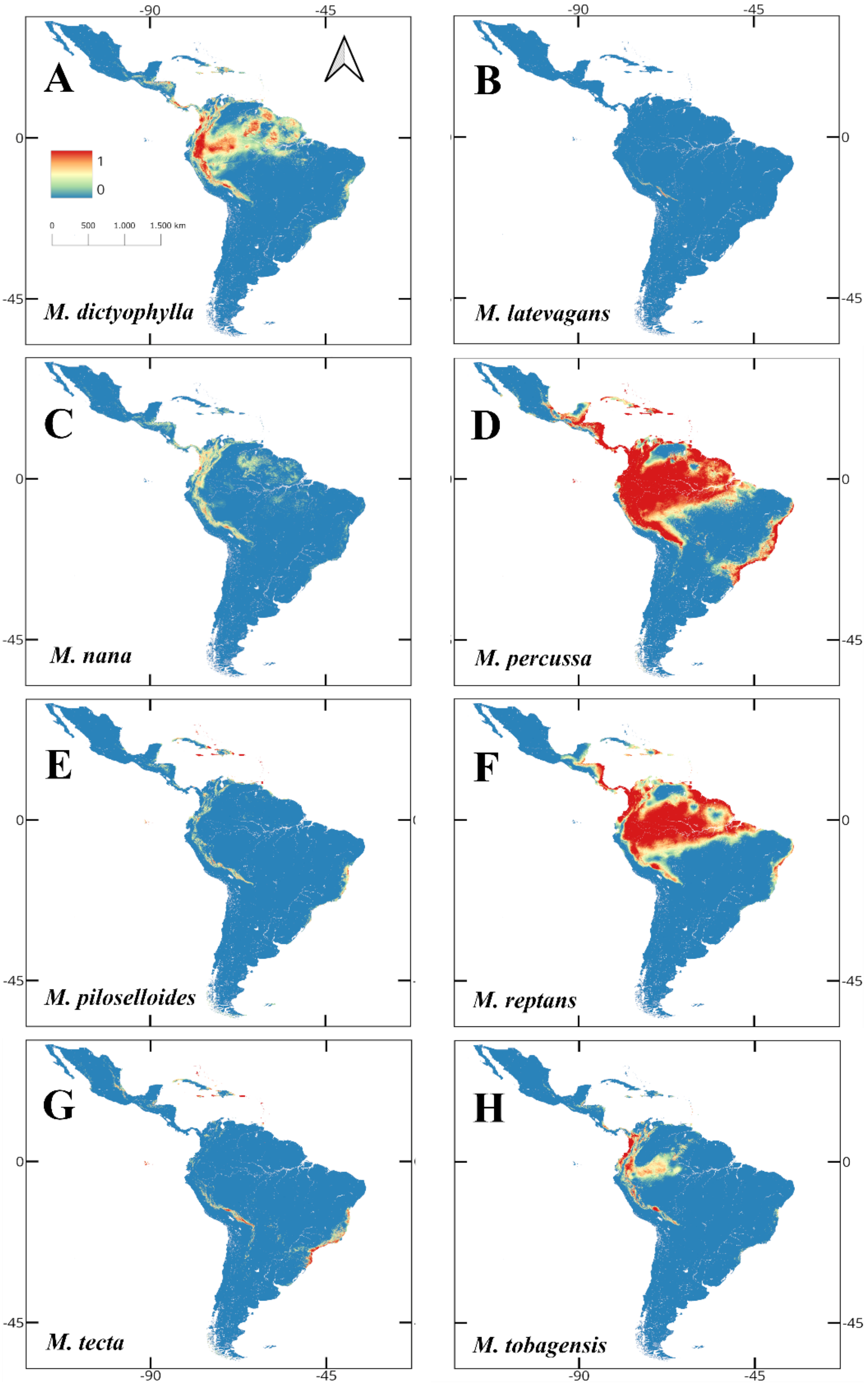


Figure 2 - Consensus species distribution models of the Scaly clade, Microgramma, derived from five ecological niche modeling algorithms (MARS, SVM, GBM, RF, and MaxEnt). Red areas represent regions of high suitability, while blue areas indicate low suitability. A. M. dictyophylla, B. M. latevagans, C. M. nana, D. M. percussa, E. M. piloselloides, F. M. reptans, G. M. tecta, H. M. tobagensis.

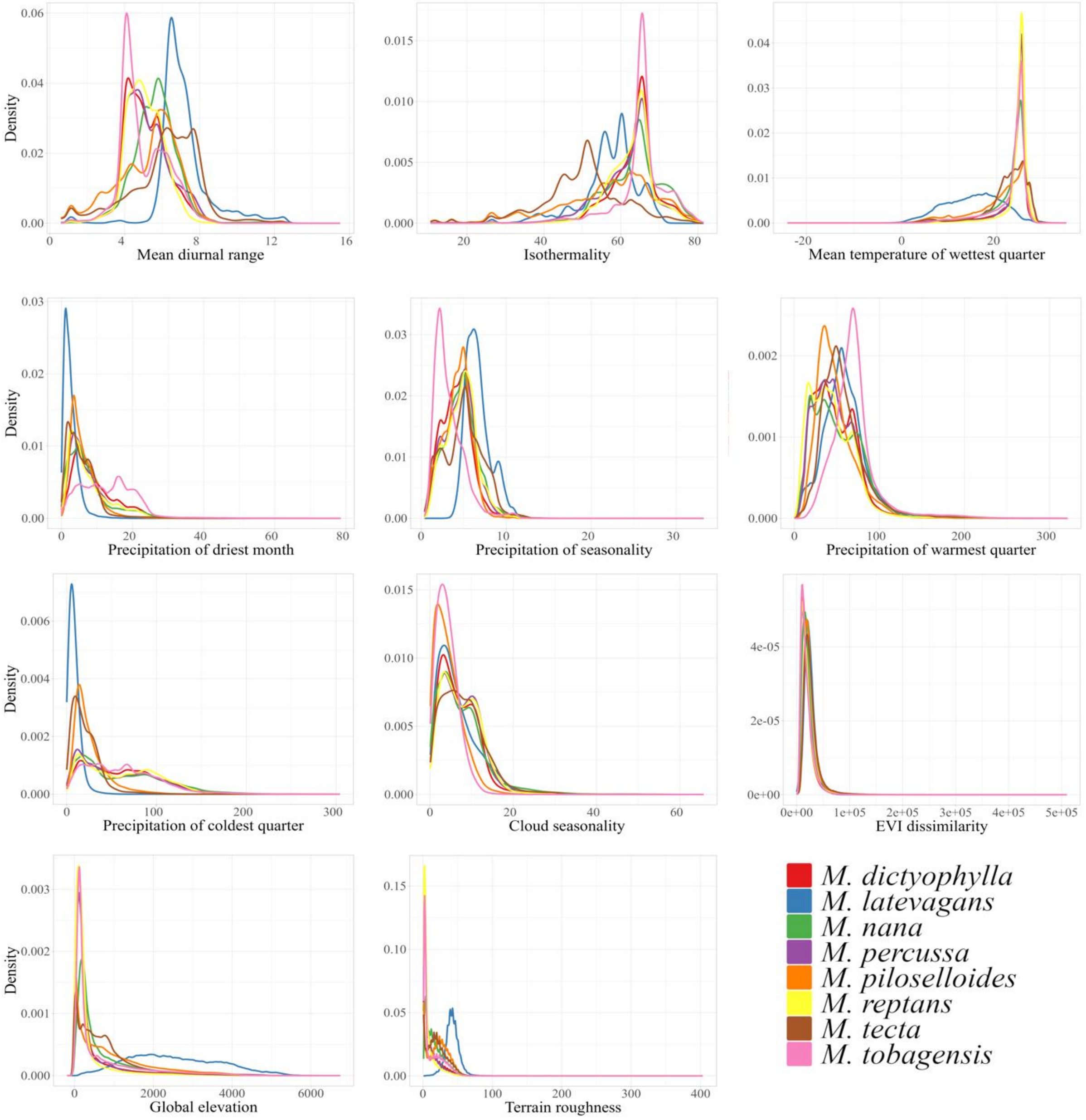
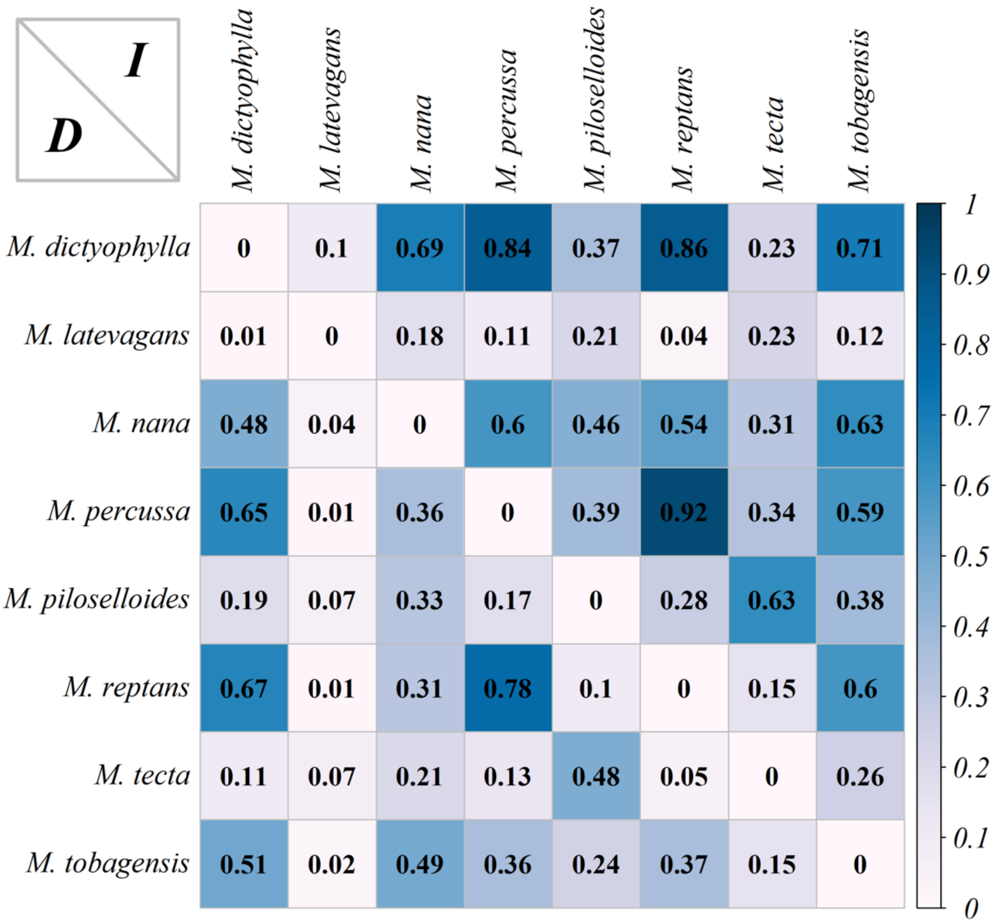


Figure 3 - Predicted niche occupancy profiles of the eight Microgramma species, represented by density plots based on presence pixels from the binary species distribution models as a function of environmental variables. Density peaks correspond to environmental areas where the species models indicated the highest suitability. Each line in the graph represents a species, highlighting the variation in density under different environmental conditions.



	M. dictyophylla	*M. latevagans*	*M. nana*	*M. percussa*	*M. piloselloides*	*M. reptans*	*M. tecta*	*M. tobagensis*
M. dictyophylla	**0**	**0.1**	**0.69**	**0.84**	**0.37**	**0.86**	**0.23**	**0.71**
M. latevagans	**0.01**	**0**	**0.18**	**0.11**	**0.21**	**0.04**	**0.23**	**0.12**
M. nana	**0.48**	**0.04**	**0**	**0.6**	**0.46**	**0.54**	**0.31**	**0.63**
M. percussa	**0.65**	**0.01**	**0.36**	**0**	**0.39**	**0.92**	**0.34**	**0.59**
M. piloselloides	**0.19**	**0.07**	**0.33**	**0.17**	**0**	**0.28**	**0.63**	**0.38**
M. reptans	**0.67**	**0.01**	**0.31**	**0.78**	**0.1**	**0**	**0.15**	**0.6**
M. tecta	**0.11**	**0.07**	**0.21**	**0.13**	**0.48**	**0.05**	**0**	**0.26**
M. tobagensis	**0.51**	**0.02**	**0.49**	**0.36**	**0.24**	**0.37**	**0.15**	**0**

Figure 4 - Niche overlap values using the generated models (Figure 2), analyzed with the equivalence metric, Schoener's D distance (Warren et al. 2008), shown on the lower left diagonal, and the similarity metric, Hellinger’s I distance (Warren et al. 2008), shown on the upper right diagonal.

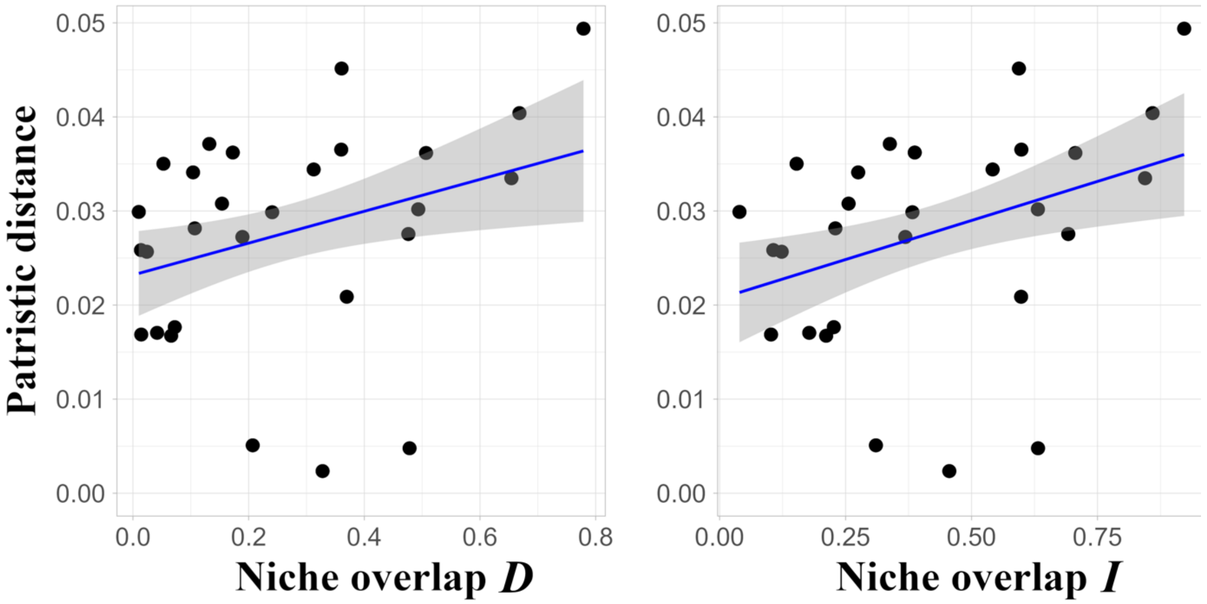


Figure 5 - Correlation between patristic phylogenetic distance and niche overlap, based on niche equivalence (*D*) and niche similarity (*I*) metrics, evaluated using the Mantel test. Trend lines in the graph illustrate the relationship between phylogenetic distance and niche overlap, suggesting that phylogenetically more distant species tend to share niche characteristics to a greater extent.

Tabela 1 - *Microgramma* species of the Scaly clade, number of records used per species, and validation metrics values for the models: area under the curve (AUC) and true skill statistic (TSS).

Espécies	**N° de registros**	**AUC**	**TSS**
M. dictyophylla	507	0.96	0.80
M. latevagans	21	0.98	0.86
M. nana	124	0.90	0.74
M. percussa	2392	0.96	0.88

M. piloselloides	254	0.97	0.91
M. reptans	950	0.96	0.86
M. tecta	142	0.99	0.91
M. tobagensis	207	0.98	0.90

SUSUPPLEMENTARY MATERIAL

Figure S1 - Density overlap of the area under the curve of predicted niche occupancy (PNO) profiles for the eleven environmental variables analyzed in this study.

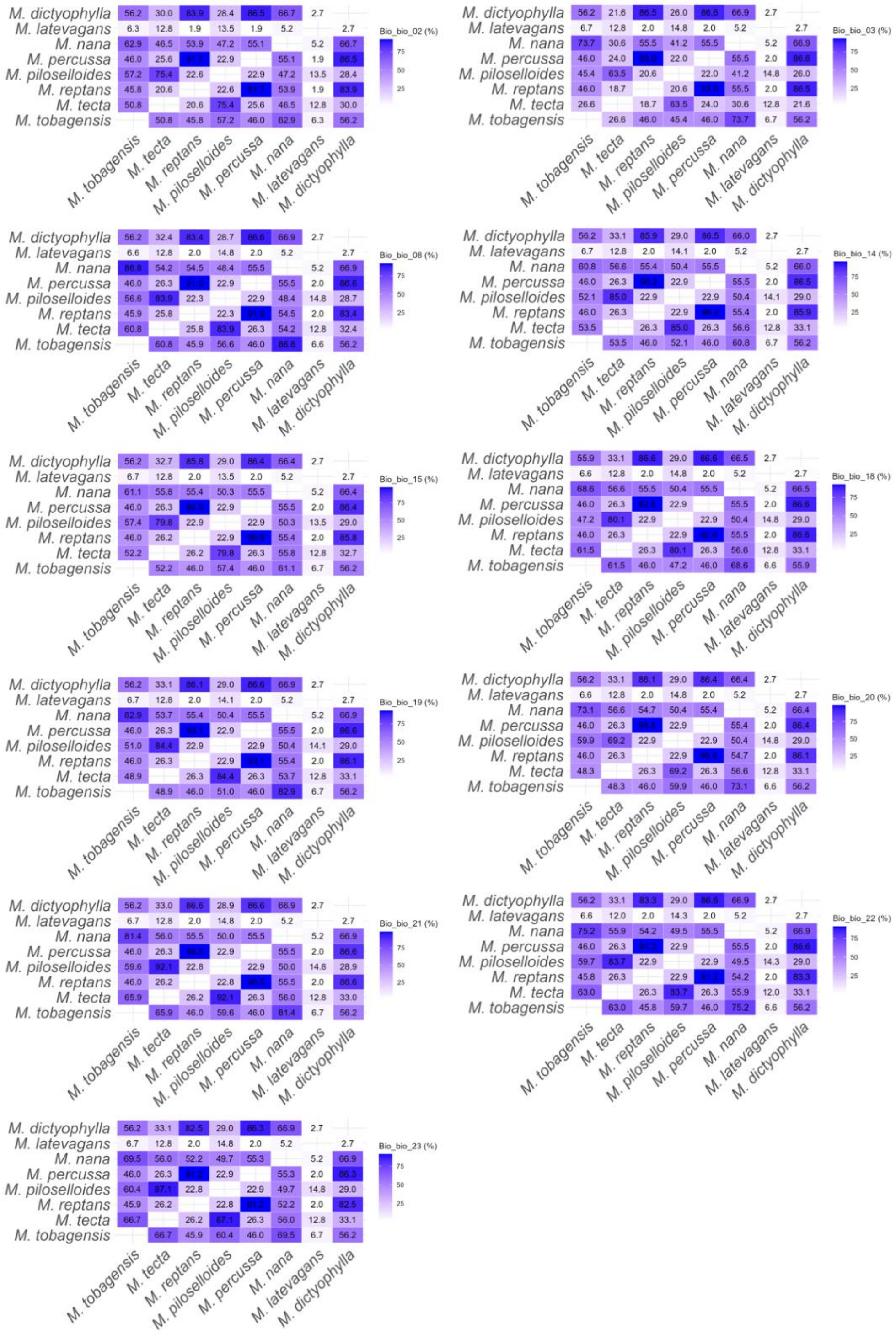


Tabela S1 – DOI referentes aos arquivos baixados no GBIF

Clado Scaly	**Doi - GBIF**

Microgramma dictyophylla	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.xdgaxa
Microgramma latevagans	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.dpr6u7
Microgramma nana	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.tuprbv
Microgramma percussa	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.2cvq9m
Microgramma piloselloides	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.bzjh38
Microgramma reptans	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.dgb69w
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Microgramma tecta var. nana	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.a5n9s9
Microgramma tobagensis	GBIF.org (11 December 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.v73t99

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