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The evolution of ecological specialization underlies plant endemism in the Atlantic Forest

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• **Background and Aims** The evolution of ecological specialization is favoured under divergent selection imposed by increased environmental heterogeneity, although specialization can limit the geographical range of organisms, thus promoting endemism. The Atlantic Forest (AF) is an ancient montane domain with high plant endemism, containing different environments for plant specialization. *Miconia* is the most diverse genus of woody flowering plant within the AF domain, including AF-endemic and non-endemic lineages. We hypothesized that *Miconia* species have faced increased environmental heterogeneity and consequently have been selected towards increased specialization in the AF domain, and this increased specialization has greatly reduced species geographical ranges, ultimately promoting endemism. Hence, we made the following predictions: (1) AF-endemic species should face greater environmental heterogeneity than non-endemic species; (2) AF-endemic species should be more specialized than non-endemic species; (3) specialization should lead to smaller geographical ranges; (4) specialization and small geographical ranges among AF-endemic species should conform to a selection-driven evolutionary scenario rather than to a neutral evolutionary scenario; and (5) small geographical ranges among AF-endemic species should date back to the occupation of the AF domain rather than to more recent time periods.
• **Methods** We used geographical, environmental and phylogenetic data on a major *Miconia* clade including AF-endemic and non-endemic species. We calculated Rao's Q to estimate the environmental heterogeneity faced by species. We used georeferenced occurrences to estimate the geographical ranges of species. We applied environmental niche modelling to infer species niche breadth. We inferred the most likely evolutionary scenario for species geographical range and niche breadth via a model-fitting approach. We used ancestral reconstructions to evaluate species geographical range throughout time.
• **Key Results** Atlantic Forest-endemic species faced 33–60 % more environmental heterogeneity, with the increase being associated with montane landscapes in the AF. The AF-endemic species were 60 % more specialized overall, specifically over highly variable environmental gradients in AF montane landscapes. Specialization strongly predicted small geographical ranges among AF-endemic species and was a major range-limiting factor among endemic lineages. The AF-endemic species have evolved towards specialization and small geographical ranges under a selection-driven regime, probably imposed by the great environmental heterogeneity in AF montane landscapes. The AF-endemic species underwent a major reduction of geographical range immediately after their evolution, indicating a long-standing effect of selective pressures in the AF domain.
• **Conclusion** Environmental heterogeneity imposes selective pressures favouring ecological specialization and small geographical ranges among plant lineages in the AF domain. This selection-driven process has probably promoted plant endemism in the AF domain throughout its history.

Key words: Environmental heterogeneity, habitat specificity, hotspot, landscape complexity, Melastomataceae, *Miconia*, niche breadth evolution, range size, specialization.

INTRODUCTION

Ecological specialization can constrain the geographical range of organisms and, consequently, impact on spatial patterns of biodiversity. Specialization occurs when an organism can explore fewer types of conditions or resources than another organism (Devictor *et al.*, 2010), translating into an *n*-dimensional niche with narrower breadth (Hutchinson, 1957). Given their narrower niche requirements, specialists have fewer options of suitable areas than generalists (Brown, 1984). Consequently, specialists often have smaller geographical ranges than their generalist relatives (Slatyer *et al.*, 2013). The relationship between specialization and small geographical range becomes evident in plant species. For instance, when comparing monkeyflower species (*Mimulus* L.) in Western North America, species with narrower thermal tolerances are more geographically restricted than species with broader tolerances (Sheth and Angert, 2014). Nonetheless, small geographical ranges can

also result from geographical barriers, historical processes or biotic interactions acting upon plant species and plant dispersal traits (Sheth *et al.*, 2020). Additionally, specialization can still allow for large geographical ranges when suitable areas are widely available (Sheth *et al.*, 2020). Assessing the relative role of range-limiting factors is necessary to understand how species can become spatially concentrated, leading to the uneven distribution of biodiversity across the globe (Kier *et al.*, 2005; Jenkins *et al.*, 2013). Moreover, detecting major factors that constrain geographical range can aid conservation efforts to alleviate small geographical ranges, which forecast greater extinction risk (Staude *et al.*, 2020). Based on that, tracking plant specialization and where it can thrive could explain the origin of megadiverse regions and, ultimately, provide the means to manage them.

Under the heterogeneity–specialization model, specialization is more likely to evolve and persist owing to divergent selective pressures imposed by different but spatially close environments (i.e. environmental heterogeneity) (Brown and Pavlovic, 1992). Each environment presumably imposes a challenge to organisms, thus requiring a specific trait set to maximize fitness (Levins, 1962). Hence, the more contrasting the environments, the more different their fitting trait sets become, such that mixed trait sets would provide reduced fitness in any environment (Levins, 1962). In an environmentally heterogeneous background, organisms are more likely to find contrasting environmental conditions when dispersing themselves or their propagules (Brown and Pavlovic, 1992). Under such a scenario, mixed-trait organisms will have reduced fitness regardless of the environment, whereas organisms with any fitting trait set will have enhanced fitness when dispersing to their respective suitable environment and reduced fitness otherwise (Brown and Pavlovic, 1992). According to these assumptions, fitting-trait organisms would become increasingly frequent in their respective suitable environment, and dispersals would be likely to lead to reduced fitness, thus favouring specialization (Brown and Pavlovic, 1992). This model has found support in different scales of plant biology. Plant ramets develop different carbon-allocation strategies in contrasting soil patches, revealing different suitable strategies across environments (Wijesinghe and Hutchings, 1999). Moreover, plant species have locally adapted populations in adjacent montane habitats, indicating that environmental differences promote selection-driven divergence despite geographical proximity (Hamann *et al.*, 2016). Finally, tree species in topographically complex forests display greater habitat specificity than those in more even forests (Potts *et al.*, 2004), suggesting specialization as the fittest response under greater environmental heterogeneity.

As consequence of specialization, environmental heterogeneity can also promote endemism via the spatial accumulation of species. Endemism occurs when organisms are found only in a given focal area (Anderson, 1994). This pattern has been assigned mainly to climatically stable areas (i.e. refugia) that have sheltered species during past climatic shifts (Haffer, 1969). Under the refugial model, climatic shifts drive populations to extinction outside refugia and, consequently, promote speciation by fragmenting large-ranged ancestral species into small-ranged descendant ones (Harrison and Noss, 2017). This model assumes that species cannot cope with novel climatic ranges (i.e. non-evolving niche breadths), thus undergoing an overall geographical range reduction (Harrison and Noss, 2017). Alternatively, the environmental heterogeneity model has long been hypothesized to underlie species diversity by promoting endemism (MacArthur, 1965; Ricklefs, 1976). Environmental heterogeneity favours specialization to different but spatially close niches (Brown and Pavlovic, 1992), and the resulting specialization impairs geographical expansion (Brown, 1984), ultimately promoting species accumulation in the focal area. Illustrating this process, tropical plant communities over increased topographic variation have greater spatial overlap among tree species than communities over more even terrains (Brown *et al.*, 2013) Likewise, phytogeographical domains with greater climatic heterogeneity harbour greater plant species diversity than their same-latitude but more homogeneous counterparts (Jiménez and Ricklefs, 2014). Following this, high plant endemism has been associated with specialization in environmentally complex regions (Asthon, 1969; Gentry, 1992). For instance, in the tropical Andes, many endemic plant species inhabit specific habitats along the steep montane gradients (Young *et al.*, 2002). Likewise, in South Africa's Cape Floristic Region, plant endemism is often associated with edaphic specialization across different soil types (Grobler and Cowling, 2021). Based on that, environmental heterogeneity has probably led to high plant endemism in various floras worldwide.

In the Neotropics, the Atlantic Forest (AF) domain is an acknowledged conservation hotspot (Myers *et al.*, 2000), harbouring ~14 900 plant species, of which 9800 (65 %) are endemic (Fig. 1A; The Brazil Flora Group, 2021). Endemism in the AF domain has often been related to forest refugia during the Pleistocene [2.58–0.01 million years ago (Mya); Carnaval and Moritz, 2008]. Proposed forest refugia currently contain greater genetic diversity of different plant species than non-refugial areas, supporting their past role as shelters (e.g. Turchetto-Zolet *et al.*, 2016; Leal *et al.*, 2018; Mäder *et al.*, 2021). However, as with most hypotheses of forest refugia, endemic plant lineages in the AF domains have been assigned to Pleistocene climatic shifts primarily based on ancestral reconstructions of geographical distribution, but without verifying the assumptions of geographical range reduction and speciation (Harrison and Noss, 2017). Although palaeo-projections based on niche modelling have indicated smaller geographical ranges during the Pleistocene (e.g. Bünger *et al.*, 2016), these projections assume species with non-evolving niches a priori (Soberón and Nakamura, 2009). At the same time, plant endemism has also been associated with environmental heterogeneity in the AF domain. Montane landscapes underlie steep environmental gradients and delimit different ecoregions in the AF domain (Neves *et al.*, 2017), thus providing a variable and spatially aggregated niche space. Accordingly, phylogenetic beta-diversity among plant communities is strongly correlated with mountain gradients in the AF domain (Mariano *et al.*, 2020), indicating specialization across montane habitats. Finally, montane regions have the greatest phylogenetic endemism in the AF domain (Brown *et al.*, 2020), suggesting specialization as a major promoter of plant endemism.

Miconia Ruiz & Pav. (Melastomataceae) *sensu* Michelangeli *et al.* (2019) is the most diverse genus of woody flowering plants in the AF domain, containing different endemic lineages in this domain (Flora do Brasil, 2020). *Miconia* species have berry fruits dispersed by various vertebrates and some insects,
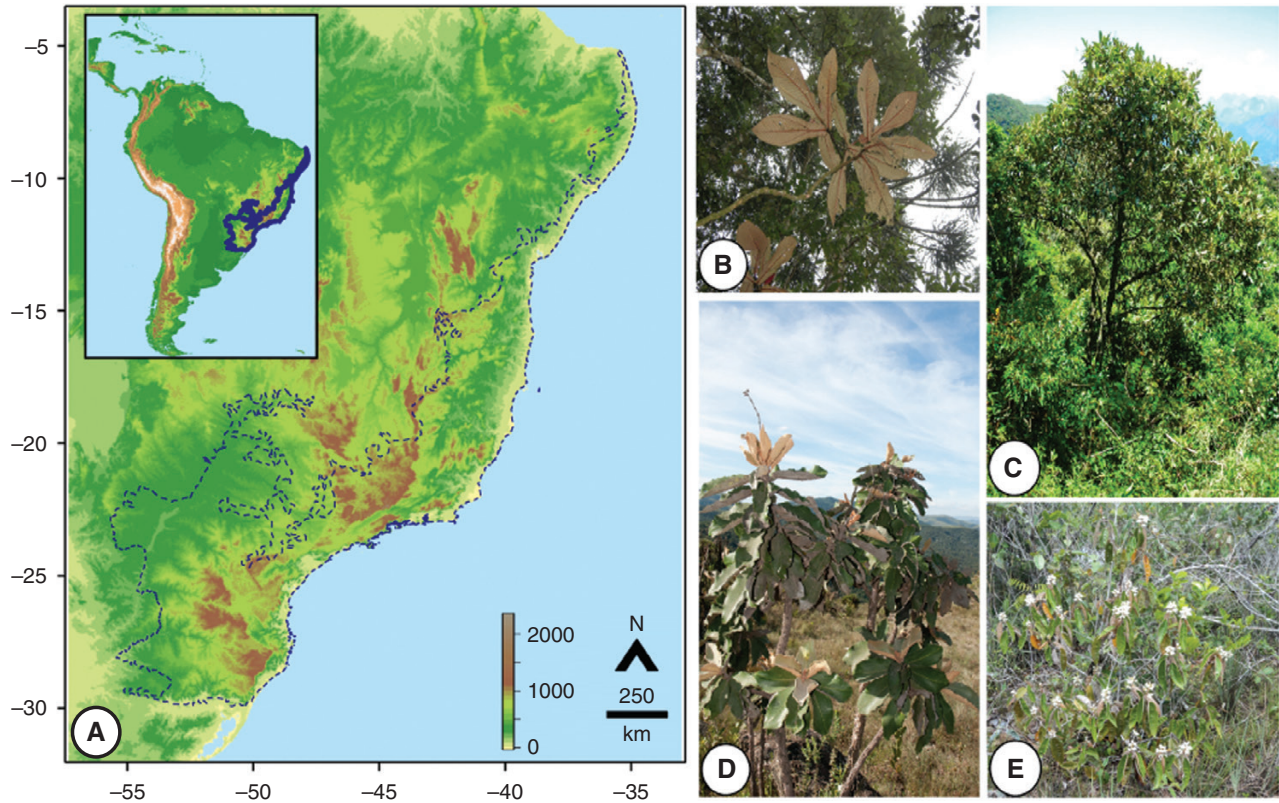
FIG. 1. The Atlantic Forest (AF) domain in the Neotropics and some representative *Miconia* species from this study. (A) The elevational variation in the Neotropics, and more specifically, in the AF domain. Colour scale at the bottom right indicates elevation (in metres). The AF boundaries are represented by blue lines. (B) *Miconia robusta* Cogn. under a forest canopy in the AF. (C) *Miconia formosa* Cogn. on a forest border in the AF. (D) *Miconia ferruginata* DC. in a *campos rupestres*. (E) *Miconia macuxi* Meirelles, Caddah & R. Goldenb. in an Amazonian *campinarana*.

which act as keystone species in different Neotropical ecosystems (Messeder *et al.*, 2021). *Miconia* species mainly rely on bees for pollination, although fruit and seed production also happen via apomixis, reducing pollination dependence (Renner, 1989). Hence, *Miconia* species have great dispersal potential, which becomes evident in their invasiveness over island systems (Meyer and Florence, 1996). However, different *Miconia* lineages display high levels of endemism in the AF domain (Reginato and Michelangeli, 2016; Goldenberg *et al.*, 2018), indicating range-limiting factors associated with this domain. One such lineage is the *Miconia* supersect. *Discolores* Caddah & Goldenberg (Fig. 1B–E), a major clade (~77 spp.) whose species occur in the AF and other Neotropical domains (Caddah *et al.*, 2022). In this group, most endemic species (~25 spp.) are restricted to the AF domain, while a few are restricted to other Neotropical domains (Caddah *et al.*, 2022). In turn, non-endemic species (~50 spp.) are spread over the Neotropics, mostly in the AF, Amazonia, Caatinga, Cerrado and Mesoamerican domains in different combinations (Caddah *et al.*, 2022). This pronounced endemism in the AF domain has previously been related to Pleistocene refugia (Caddah *et al.*, 2022), but without an evaluation of species geographical range during this period. Nonetheless, species with different geographical distributions also occupy a different range of habitats, indicating the evolution of different niche breadths. The AF-endemic species inhabit evergreen or semi-deciduous forests at montane elevations (>500 m). In contrast, non-endemic

species can occupy riverine forests, white-sand woodlands (*campinaranas*), Neotropical savannas or rocky grasslands (*campos rupestres*) (Caddah *et al.*, 2022). Based on that, the *Miconia* supersect. *Discolores* allows evaluation of the relative impact of historical processes and ecological specialization on plant endemism in the AF domain.

In the present study, we investigated whether plant endemism in the AF would result from the evolution of specialization owing to greater environmental heterogeneity in this domain, using *Miconia* supersect. *Discolores* as a study system. We hypothesized that *Miconia* species have faced increased environmental heterogeneity and, consequently, have been selected towards increased specialization in the AF domain, and this increased specialization has greatly reduced the geographical range of species, ultimately promoting endemism. Hence, we made the following predictions: (1) AF-endemic species should face greater environmental heterogeneity than non-endemic species; (2) AF-endemic species should be more specialized than non-endemic species; (3) specialization should lead to smaller geographical ranges; (4) specialization and small geographical ranges among AF-endemic species should conform to a selection-driven evolutionary scenario rather than to a neutral evolutionary scenario; and (5) small geographical ranges among AF-endemic species should date back to the occupation of the AF domain rather than to more recent time periods. For the first prediction, we applied a spatial metric to estimate environmental heterogeneity around species distributions. For the

second prediction, we inferred environmental specialization of species via niche modelling. For the third prediction, we measured species geographical range and inferred its association with environmental specialization. For the fourth prediction, we applied a model-fitting approach to infer the most likely evolutionary scenario of environmental specialization and geographical range. For the fifth prediction, we applied ancestral reconstructions to assess species geographical ranges over time.

MATERIALS AND METHODS

Unless otherwise stated, we performed data analyses in the R environment v.4.1.0 (R Development Core Team, 2021). The R code and all datasets are available at https://github.com/eknery/specialization_endemism_AF. Throughout, we have cited only the main functions and their respective R packages. We considered a significance level of 0.05 for frequentist statistical tests.

Study area

Our study area was the AF domain in the Neotropics (Fig. 1A). This phytogeographical domain is located within coordinates 02°50′–33°45′S and 34°45′–55°15′W, encompassing an area of 1 110 182 km² (IBGE, 2012).The AF largely overlaps the eastern Brazilian highlands, ranging from sea level to 2892 m above (IBGE, 2012). From south to north, three major mountain ranges divide the domain: the Serra Geral, the Serra do Mar and the Serra da Mantiqueira. These mountain ranges have probably resulted from different geological processes from the Early Cretaceous to the Palaeogene (145–23 Mya; e.g. Hiruma *et al.*, 2010). Despite its mainly tropical latitude, the AF domain hosts different climatic zones, from wet tropical to subtropical with dry seasons or frosts (Alvares *et al.*, 2013). Soil types vary the most from east to west, following the elevational gradient, including variation regarding granulation, drainage and organic matter content (Cunha *et al.*, 2019).

Study system

Our study system was the *Miconia* supersect. *Discolores*, a plant lineage including shrubs, treelets and trees (Fig. 1B–E). Given that lineage-wise ecological data are not available, we surveyed studies recording variation in *Miconia* species fitness associated with environmental conditions. We considered studies including any species in the *Miconia* supersect. *Discolores*, and we assumed that other species in the group would probably be affected by the same environmental conditions. Those environmental variables affecting fitness components were considered relevant for ecological niche modelling. Species in the *Miconia* supersect. *Discolores* are mostly dominant locally in forest habitats (Arellano and Macía, 2014), and their fruit dispersal relies mainly on birds (Allenspach and Dias, 2012; Maruyama *et al.*, 2013; Santos *et al.*, 2017). Their seeds are dormant-like and can withstand mild dry seasons in soil (Silveira *et al.*, 2013; Escobar and Cardoso, 2015*a*), and they require high light availability for germination (Escobar and Cardoso, 2015*b*). Moreover, seed germination is reduced

under increased temperature variation (Oliveira *et al.*, 2014; Escobar and Cardoso, 2015*b*). After recruitment, seedling growth is not limited by soil nutrient availability (Denslow *et al.*, 1998), but it decreases sharply in alkaline soils (Haridasan, 1988). Once established, mature plants reach lower photosynthetic rates during dry seasons (Monteiro and Prado, 2006), and they also display reduced flowering in shady conditions (Silva *et al.*, 2016).

Environmental variables

To estimate environmental heterogeneity and model species environmental niches, we selected four variables that reflect environmental conditions that affect the fitness of the study *Miconia* species, as previously highlighted above. We also favoured a minor set of variables to avoid niche model overfitting (Mod *et al.*, 2016). We downloaded raster layers of the diurnal temperature range (diurnal range/annual range, in degrees Celsius), precipitation seasonality (coefficient of variation, in millimetres), solar radiation (in kilojoules per square metre per day) and soil pH from the WorldClim and WoSIS repositories (Fick and Hijmans, 2017; Batjes *et al.*, 2020). We set the coordinate reference system to WGS84 and raster resolution to 2.5′ (~5 km × 5 km grid cells). At this resolution, grid cells can encompass different communities where a species inhabits, hence they represent well the environmental conditions experienced by the whole species across its geographical distribution [i.e. beta niche *sensu* Ackerly *et al.* (2006); see *Environmental niche modelling* section for further explanation]. Hereafter, we term the grid cells 'sites'.

Phylogenetic reconstruction

To enable comparative phylogenetic analyses, we conducted a molecular-based phylogenetic reconstruction of the *Miconia* supersect. *Discolores*. To date, the most comprehensive phylogenetic study on the *Miconia* supersect. *Discolores* has included 57 species, but sampling has focused mostly on the AF domain (Caddah *et al.*, 2022). Hence, we sought to improve species sampling from other geographical domains by including unpublished but already-curated molecular data from GenBank (Benson *et al.*, 2005). Our phylogenetic sample covered most species (66 spp., 85 %) from the *Miconia* supersect. *Discolores* (92 % cover the AF domain, and 82 % cover other domains altogether) (Caddah *et al.*, 2022). To improve inferences on the last common ancestor, we included 16 allied species of the *Miconia* supersect. *Discolores* (Goldenberg *et al.*, 2008). To allow divergence time estimates, we also included 30 species representing the major clades of *Miconia* (Goldenberg *et al.*, 2008). We set *Eriocnema fulva*, *Physterostemon fiaschii* and *Physterostemon thomasii* as the outgroup. Based on preliminary analyses, we excluded two species (*Miconia amoena* and *Miconia eriodonta*) that reduced the overall support of phylogenetic hypotheses. Our phylogenetic sampling included 115 species.

The molecular dataset included all loci sequenced for more than half of the species in the *Miconia* supersect. *Discolores*: the nuclear ribosomal ETS and ITS, and the plastidial intergenic spacers *accD-psaI*, *atpF-atpH*, *psbK-psbL*, *trnS-trnG*. We

retrieved sequences from GenBank (Supplementary data Table S1), and we aligned same-locus sequences with MAFFT, under the GINSi strategy (Katoh and Standley, 2013). The aligned sequences provided 3894 characters. We assessed congruence and substitution patterns of sampled loci by functions of the 'phangorn' package (Schliep *et al.*, 2017). To assess congruence among loci, we first generated neighbour-joining bootstrap trees ($n = 100$) for each locus using the *NJ* function. Then, we compared trees by a principal coordinate analysis on the Robison and Foulds' distance (1981) using the *RF.dist* function. To assess substitution patterns in each locus, we evaluated 18 substitution models by the corrected Akaike information criterion (AICc) using the *modelTest* function. Loci differed regarding topology, hence we considered each locus as a single partition in phylogenetic reconstruction (Supplementary data Fig. S1).

We applied the Bayesian phylogenetic reconstruction implemented in BEAST 2.0, which uses a Markov chain Monte Carlo (MCMC) method to optimize phylogenetic trees (Drummond and Rambaut, 2007). Instead of assuming substitution models a priori, we applied a reversible-jump MCMC to use different substitution models (~30) over simulations, allowing a more extensive search on the tree space (Bouckaert and Drummond, 2017). We set a relaxed log-normal molecular clock for each locus, using hyperparameters to estimate substitution rates (Drummond *et al.*, 2006). We assumed the calibrated Yule model for tree topology, and we set two secondary calibration points by Gavrutenko (2020): (1) the last common ancestor of *Eriocnema*+*Phyeseterostemon*+*Miconia* (14.71–29.9 Mya); and (2) the *Miconia* crown [Miconia IV + Miconia V groups in Goldenberg *et al.* (2008)] (7.05–13.44 Mya). The MCMC lasted 7×10^7 iterations, with sampling every 7×10^4 iterations. We verified the convergence of MCMC and sampling sufficiency (effective sample size, ESS > 200) via Tracer v.1.7 (Rambaut *et al.*, 2018). We generated a mean-valued maximum clade credibility (MCC) after a 20 % burn-in via TreeAnnotator (Drummond and Rambaut, 2007). The MCC tree agreed with previous phylogenetic trees of the *Miconia* supersect. *Discolores* (Goldenberg *et al.*, 2008; Caddah, 2013), but with higher statistical support and greater taxonomic representation (Supplementary data Fig. S2).

To consider the inherent uncertainty of phylogenetic reconstruction, we conducted comparative analyses on a sample of phylogenetic trees. We drew a random sample of phylogenetic trees ($n = 100$) from the burn-in posterior distribution.

Species occurrence dataset

To infer the geographic range and niche breadth of species, we built a taxonomically curated dataset of species occurrences for the *Miconia* supersect. *Discolores*. Taxonomically curated datasets have 24 % fewer misidentifications than non-curated datasets (Freitas *et al.*, 2020). Moreover, taxonomically curated datasets provide equally suitable information for environmental niche modelling compared with more comprehensive datasets, despite their reduced sample sizes (Fourcade, 2016).

We gathered species occurrences while considering taxonomic nomenclature, voucher association and identification by experts. First, we researched all synonyms for each species (106 names; Supplementary data List S1; Meirelles, 2015;

Caddah *et al.*, 2020; Goldenberg and Bacci, 2020), in order that occurrences could reflect the geographical range of species despite their different naming among countries or research groups. Second, we downloaded occurrences (latitude and longitude) representing herbarium vouchers in the SpeciesLink (splink.org.br) and PBI:Miconiae (sweetgum.nybg.org/melastomataceae) databases. We did not consider GBIF a suitable source of species occurrence for the AF, because three-quarters (75 %) of GBIF entries hold invalid spatial data for this domain (Colli-Silva *et al.*, 2020). Third, we retained only occurrences identified by an expert on *Miconia* taxonomy (68 experts in Supplementary data List S2). We recognized taxonomic expertise when the researcher had published monographs on *Miconia* groups, floras of Melastomataceae including *Miconia*, or descriptions of new *Miconia* species. We also recognized taxonomic expertise when the researcher had authored unpublished floras of poorly known localities, such as some areas of Amazonia. Our initial effort resulted in 9724 occurrences.

Afterwards, we conducted procedures to improve dataset quality. First, we excluded same-voucher occurrences within species and occurrences with low geographical precision or erroneous placement (e.g. municipality centroids and sea). Second, we assigned geographical coordinates to incomplete occurrences, following a standardized dataset of Neotropical localities (available from the first author upon request). Finally, to avoid spatial pseudo-replication, we conducted spatial thinning over occurrences using the *thin* function in the 'spThin' package (Aiello-Lammens *et al.*, 2015). We excluded same-species occurrences <7 km apart, the greatest distance within a 5 km × 5 km site. For eight species known from few populations (*Miconia angelana*, *M. capixaba*, *M. dura*, *M. kollmannii*, *M. kriegeriana*, *M. mellina*, *M. penduliflora* and *M. suberosa*), we considered that same-site occurrences were not pseudo-replicates but rather a rough approximation of abundance. After improvement, our dataset comprised 5521 species occurrences.

Nonetheless, herbarium-based datasets might reflect the sampling bias by taxonomists rather than species distributions, a known pattern in the AF domain (Ostroski *et al.*, 2020). Hence, to detect spatial sampling bias, we applied a normal kernel density estimation to species occurrences with the *kde2d* function in the 'MASS' package (Venables and Ripley, 2002). We found that sampling was five times denser towards the southeastern AF (Supplementary data Fig. S3). To avoid the effect of sampling bias, we applied the background-group strategy to environmental niche modelling (for further explanation, see the *Environmental niche modelling* section).

Geographical distribution of species

To assess species geographical distributions, we quantified species occurrences over Neotropical domains. We considered eight Neotropical domains: Amazonia, Andes, Atlantic Forest, Caatinga, Cerrado, Chaco, Mesoamerica and Pampa, whose boundaries were based on the shapefile of Olson *et al.* (2001) (Supplementary data Fig. S4). We overlapped species occurrences in the shapefile to quantify their absolute presence in each domain (Supplementary data Table S2). Most species (45 spp.) were in more than one domain, and the most frequent distributions were as follows: AF + Cerrado (eight spp.); Amazonia + Cerrado (six spp.); AF + Caatinga + Cerrado (four spp.); and

AF + Amazonia + Caatinga + Cerrado (four spp.). Another 17 geographical distributions including more than one domain had low frequencies (three or fewer spp.) (Supplementary data Table S2). The remaining species (21 spp.) had single-domain distributions: AF (17 spp.); Amazonia (three spp.); and Cerrado (one sp.).

However, absolute presence is misleading when defining endemism because it is sensitive to erroneous records and does not consider biological processes that can revoke endemism temporarily, such as peripheral shrinking populations (Lima *et al.*, 2020). Hence, we followed Lima *et al.* (2020) in defining optimal thresholds to detect endemic plant species in the AF domain based on their percentage presence. We assigned species to three geographical distributions based on their percentage presence in the AF domain: 'AF-endemic', ≥90 % of occurrences inside the AF domain; 'outside the AF domain', ≤10 % of occurrences inside the AF domain; 'AF and other domains', between 10 and 90 % of occurrences inside the AF domain. The percentage presence in the AF domain had a bimodal distribution, peaking at 10 and 90 % (Supplementary data Fig. S5), indicating these values as non-arbitrary divisors for discrete states.

We did not use each domain and their combinations as geographical distributions for different reasons. First, our objective was to understand the underlying processes of endemism in the AF, because this domain contains most endemic species in our study system. Hence, geographical distribution coding should reflect the degree of restriction to the focal area (e.g. Vasconcelos *et al.*, 2020). Second, historical biogeographical analyses have already been conducted by Caddah *et al.* (2022), which indicated an Amazonian origin for our study system. Third, in our study system, non-endemic species can occupy two or more domains in different combinations, rendering 22 types of geographical distribution in ancestral reconstructions. Given that geographical distributions are treated as evolutionary regimes (see the *Evolutionary scenario inference* section), our phylogenetic sampling would not have the statistical power to infer parameters for many regimes.

Environmental heterogeneity estimates

To estimate the environmental heterogeneity, we applied Rao's Q index over environmental raster layers using the *paRao* function in the 'rasterdiv' package (Rocchini *et al.*, 2021). The Q index is the average dissimilarity between a focal site and other sites within a given spatial frame (Rocchini *et al.*, 2017). To calculate the Q index, we measured dissimilarity among sites as the Euclidean distance based on the four environmental raster layers. We scaled environmental values to z-scores to avoid overweighting attributable to different scales. We considered a spatial frame including the eight immediate neighbours of each site, hence Q-values would approximate the environmental heterogeneity found during dispersal events, the relevant scale for the heterogeneity–specialization model (Brown and Pavlovic, 1992). After calculating the Q raster (Supplementary data Fig. S6), we used species occurrences to extract their respective Q-values. The Q-value distributions of species often departed from normality (Supplementary data Fig. S7); therefore, we considered the median Q-value as the proxy for the overall environmental heterogeneity faced by a species.

To evaluate whether species with different geographical distributions faced distinct environmental heterogeneity, we applied a phylogenetic generalized least squares (PGLS) model using the *gls* function in the 'nlme' package (Pinheiro *et al.*, 2021). We considered the species Q-value as the response variable and species geographical distribution as a fixed factor. Given that species can inherit occupied sites from ancestors, we sought to estimate phylogenetic inheritance of environmental heterogeneity. We fitted the Brownian motion (BM) and the Ornstein–Uhlenbeck process (OU) models to species median Q-values by using the *fitContinuous* function in the 'geiger' package (Harmon *et al.*, 2008). The OU model had the best fit according to the AICc; therefore, BM-based methods, such as phylogenetic independent contrasts, were considered unsuitable (Díaz-Uriarte and Garland, 1996). Based on the OU model, we calculated the variance–covariance matrix of species Q-values and implemented this matrix into the PGLS models to correct residual variation. We ln-transformed Q-values because the relationship between variables was exponential.

We also applied PGLS modelling to assess whether montane landscapes would influence the environmental heterogeneity faced by species. In this second model, we considered the species Q-value as the response variable and species median elevation as the predictor variable. The variance–covariance matrix calculation and data transformation proceeded as described above.

Environmental niche modelling

Niche modelling is a proxy for the overall environmental conditions occupied by a species. At a finer spatial scale, each species occupies a relative position along each environmental gradient within a given community, the alpha niche, which changes across communities owing to abiotic and biotic factors (Ackerly *et al.*, 2006). At a coarser spatial scale, each species experiences environmental variation across its geographical range, the beta niche, which changes with evolutionary processes acting upon the whole species (Ackerly *et al.*, 2006). Geographically referenced data, such as those applied to niche modelling, can approximate the beta niche scale (Ackerly *et al.*, 2006). Hence, we used occurrences on raster layers to extract environmental values occupied by species, and we considered niche models as a proxy for the environmental niche at a beta scale.

Niche modelling should also indicate unoccupied environmental values, which are provided by absence records. Data derived from scientific collections lack absence records (Ponder *et al.*, 2001); therefore, their application to niche modelling requires strategies that take this limitation into account. The background-group strategy assigns virtual absences of a given focal species based on presences of other spatially related species (Ponder *et al.*, 2001). This strategy assumes that sampling effort is equally effective in detecting the focal species and the spatially related species, hence the presence of the latter without the presence of the former is considered an absence of the focal species (Ponder *et al.*, 2001). Consequently, this strategy incorporates spatial bias from presence records into absence records, avoiding the problem that niche inferences reflect sampling bias (Phillips *et al.*, 2009). We considered this strategy suitable for the *Miconia* supersect. *Discolores* because

the group has been subject to taxonomic studies that have surveyed all species simultaneously (Caddah *et al.*, 2022). Hence, we defined the background group of each modelled species as the occurrences of all other species, except sites where the modelled species occur.

To infer species environmental niche, we applied the hypervolume modelling method to species environmental values. The hypervolume method applies kernel functions to observed environmental values to infer the probability density function over *n* environmental variables (Blonder *et al.*, 2014). The inferred probability functions delimit an *n*-dimensional volume, the hypervolume, whose size is a proxy for the overall niche breadth (Blonder *et al.*, 2014). Hence, we performed environmental niche modelling using functions from the 'hypervolume' package (Blonder *et al.*, 2014). We had already scaled environmental values to *z*-scores to avoid overweighting owing to the measurement scale.

To evaluate the predictive performance of hypervolume models, we used a *k*-fold cross-validation procedure under different probability thresholds. We considered environmental values from species occurrences as 'presences' and environmental values from the respective background group as 'absences'. We split presences randomly into three sets ($k = 3$), using two sets (two-thirds) as training and one set (one-third) as testing over three different rounds. For species known from few localities, we validated hypervolume models by using a leave-one-out procedure ($k = n$). We built species hypervolume models based on the training by the *hypervolume_gaussian* function, using a normal bandwidth approximation by the *estimate_bandwidth* function (Blonder *et al.*, 2018). We evaluated the predictive performance of models with the true skill statistics (TSS; sensitivity + specificity − 1) (Allouche *et al.*, 2006), considering different probability thresholds (0.05, 0.25, 0.5, 0.75 and 0.95). Sensitivity was the proportion of the training classified as 'presence', and specificity was the proportion of the background group classified as 'absence'. We averaged same-threshold rounds to evaluate model performance, and we used the maximum TSS value to choose the best threshold to model the species environmental niche.

After model evaluation (Supplementary data Table S3), we applied the hypervolume method to the environmental values of species, using the probability threshold of the maximum TSS value. We retrieved the hypervolume size as a proxy for species environmental niche breadth. Small hypervolumes sizes indicated increased environmental specialization. We calculated the 50 % interquartile range (IQR) over each probability density distribution as a measure of species niche breadth over each environmental gradient.

Nonetheless, specialization inferred from species occurrences can be an artefact of spatial autocorrelation (Cardillo *et al.*, 2018). Under great spatial autocorrelation, distinct environmental values are found only at great distances (Legendre, 1993). Hence, when inferring niche breadth via occurrence-based modelling, specialization can be inferred for small-ranged species only because species occurrences are over regions with great spatial autocorrelation (Cardillo *et al.*, 2018). To assess whether spatial autocorrelation influenced specialization inference, we estimated the local Moran's *I* around species occurrences (Anselin, 1995). We calculated the *I* of environmental variables at a local scale, 3 × 3 sites, using the *MoranLocal*

function in the 'raster' package (Hijmans, 2021). We then extracted the *I*-values from species occurrences, and we considered the median *I*-values of species as an estimate of the spatial autocorrelation in regions occupied by species.

To evaluate whether species with different geographical distributions had distinct niche breadths, we applied a PGLS model using the *gls* function in the 'nlme' package (Pinheiro *et al.*, 2021). We considered the species hypervolume size as the response variable and species geographical distribution as a fixed factor with three levels. We set species median *I*-values as a covariate to evaluate the effect of spatial autocorrelation. We fitted the BM and OU models to hypervolume size by using the *fitContinuous* function in the 'geiger' package (Harmon *et al.*, 2008). The OU model had the best fit according to the AICc. Based on the OU model, we calculated the covariance matrix for species hypervolume size and implemented it into the PGLS model to correct residual variation. We applied square-root transformation to conform residual variation to a normal distribution.

We also applied PGLS modelling to evaluate whether species with different geographical distributions differed regarding niche breadth over each environmental gradient. In each model, we considered the species IQR values for an environmental variable as the response variable and species geographical distribution as a fixed factor with three levels. The variance–covariance matrix calculation proceeded as described above, but without transforming the response variables.

Species geographical range

To infer species geographical ranges, we calculated the area within the minimal convex polygon (i.e. convex hull) delimited by species occurrences. Although less accurate for oddly shaped geographical distributions (Burgman and Fox, 2003), the convex hull is an accurate estimator of range size reduction (Darroch and Saupe, 2018). Given that we sought to evaluate geographical range reduction during the Pleistocene, we considered the convex hull area a reliable proxy for species geographical range. We delimited the convex hulls around species occurrences using the *st_convex_hull* function, and we measured the area (in square kilometres) within the convex hulls using the *st_area* function, with all functions being from the 'sf' package (Pebesma, 2018).

To evaluate whether species geographical range was related to specialization, we applied PGLS models using the *gls* function in the 'nlme' package (Pinheiro *et al.*, 2021). In the first model, we considered the species convex hull area as the response variable and species hypervolume size as the predictor variable. In the second model, we kept the same response variable, but nested species hypervolume size within geographical distribution. We set species median *I*-values as a covariate in all models. We fitted the BM and OU models to the convex hull area using the *fitContinuous* function in the 'geiger' package (Harmon *et al.*, 2008). The OU model had the best fit according to the AICc. Based on the OU model, we calculated the variance–covariance matrix of species convex hull area and implemented it into the PGLS models. We applied a cubic-root transformation to the convex hull area because the relationship between variables was cubic. We selected the best-fitting model by AICc.

Evolutionary scenario inference

To assess when endemism to the AF domain had evolved, we conducted an ancestral reconstruction of species geographical distribution using the 'BioGeoBEARS' package (Matzke, 2013). We applied the dispersal–extinction–cladogenesis (DEC) model, which represents the evolution of species geographical distribution via random dispersal and local extinction, while considering different modes of geographical area inheritance (Ree and Smith, 2008). We considered two geographical areas, AF and other domains, consequently allowing three geographical distributions: 'AF-endemic', 'AF and other domains' and 'outside the AF domain'. We did not use time-structured transition rates because the AF domain is much older than our study system. We fitted the DEC model to our sample of phylogenetic trees ($n = 100$), and we used the maximum marginal likelihood at each node to assign ancestral species to a geographical distribution on each phylogenetic tree.

To infer the most likely evolutionary scenario of niche breadth and geographical range, we applied a model-fitting approach to species hypervolume size and convex hull area, considering species geographical distributions as evolutionary regimes. We used evolutionary models for continuous-scaled phenotypes based on the Brownian motion (BM) and the Ornstein–Uhlenbeck (OU) process. Under the BM models, phenotypic divergence results solely from an evolutionary rate (σ) representing stochastic variation through time (Felsenstein, 1988). In turn, under OU models, phenotypic divergence results not only from a an evolutionary rate (σ) but also from an attraction force (α) towards some optimum value (Θ) (Hansen, 1997). As a general interpretation, BM models would represent evolution under genetic drift and mutation or fluctuating directional selection, whereas OU models would represent evolution under consistent stabilizing selection or constraints (Beaulieu *et al.*, 2012).

Based on this approach, we contrasted seven evolutionary models with a different number of parameters (i.e. complexity) implemented in the 'OUwie' package (Beaulieu *et al.*, 2012). The simplest model (BM1) assumed a single σ value for all evolutionary regimes, and the most complex model (OUMVA) assumed variable σ, Θ and α values for each evolutionary regime. The other models had an intermediate number of parameters (Table 1). We applied all evolutionary models to species hypervolume size and convex hull area, considering different phylogenetic trees ($n = 100$). For each phylogenetic tree, we evaluated model fit by the AICc and ranked models by delta AICc (ΔAICc). When the lowest ΔAICc model was more complex than the second lowest ΔAICc model, we chose the more complex model only if it scored more than two over the simpler model.

After model fitting, we assessed whether evolutionary regimes departed from expectations under neutral evolution. We first estimated σ in BM1 for species hypervolume size and convex hull area on each phylogenetic tree by the *Ouwie* function in the 'OUwie' package. Using the estimated σ values, we simulated the evolution of hypervolume size and convex hull area under the BM model by the *fastBM* function in the 'phytools' package. We ran 100 simulations on each phylogenetic tree, randomly setting an observed value as a possible ancestral state (z_0) at each simulation. We calculated the mean value of each simulation to produce a null distribution ($n = 10\ 000$) for each trait. Finally, we compared the mean

TABLE 1. *Description of evolutionary models applied to species hypervolume size and convex hull area. Parameters represent different aspects of evolutionary regimes (σ, evolutionary rates; Θ, optimum value; and α, attraction force). 'Single' indicates that parameter values were the same for evolutionary regimes, whereas 'variable' indicates that parameter values could vary among evolutionary regimes*

Model	Parameters		
	σ	Θ	α
BM1	Single	–	–
BMS	Variable	–	–
OU1	Single	Single	Single
OUM	Single	Variable	Single
OUMV	Variable	Variable	Single
OUMA	Single	Variable	Variable
OUMVA	Variable	Variable	Variable

values in each evolutionary regime with the null distributions to assess whether evolutionary regimes would be expected under neutral evolution.

Ancestral reconstruction of geographical range

To evaluate the effect of Pleistocene climatic shifts on species geographical range, we reconstructed ancestral convex hull areas using our sample of phylogenetic trees ($n = 100$). We estimated ancestral values based on the best-fitting evolutionary models using the *OUwie.anc* function in the 'OUwie' package. From each phylogenetic tree, we retrieved the convex hull area, geographical distribution based on DEC, and age for every inner node (i.e. ancestral species). Then we compared mean ancestral values in each geographical distribution across ages, and we evaluated visually whether ancestral values underwent a reduction during the Pleistocene. We acknowledge that OU-based reconstructions have limited interpretation at deep nodes of phylogenetic trees (Royer-Carenzi and Didier, 2016); therefore, we have focused our discussion on relative rather than absolute values of convex hull area.

It is noteworthy that geographical range size is an emergent species-level trait, meaning that it is absent at the organism level, albeit affected by organism-level processes (Grantham, 1995). Species geographical range derives from heritable components, mostly organismal requirements, tolerances and dispersal mode, and non-heritable components, broadly including geographical features and historical processes (Sheth *et al.*, 2020). These heritable components would provide some theoretical basis to infer ancestral geographical ranges based on evolutionary models for heritable phenotypes. Supporting this approach, the fossil records of some taxonomic groups display a positive relationship between ancestral and descendant range sizes (Jablonski, 1987). Moreover, based on *in silico* simulations, medium to large heritability values can produce the typical distribution of geographical range values observed in most taxonomic groups (Borregaard *et al.*, 2012). Hence, we treated species geographical range as an evolving phenotype, but we also
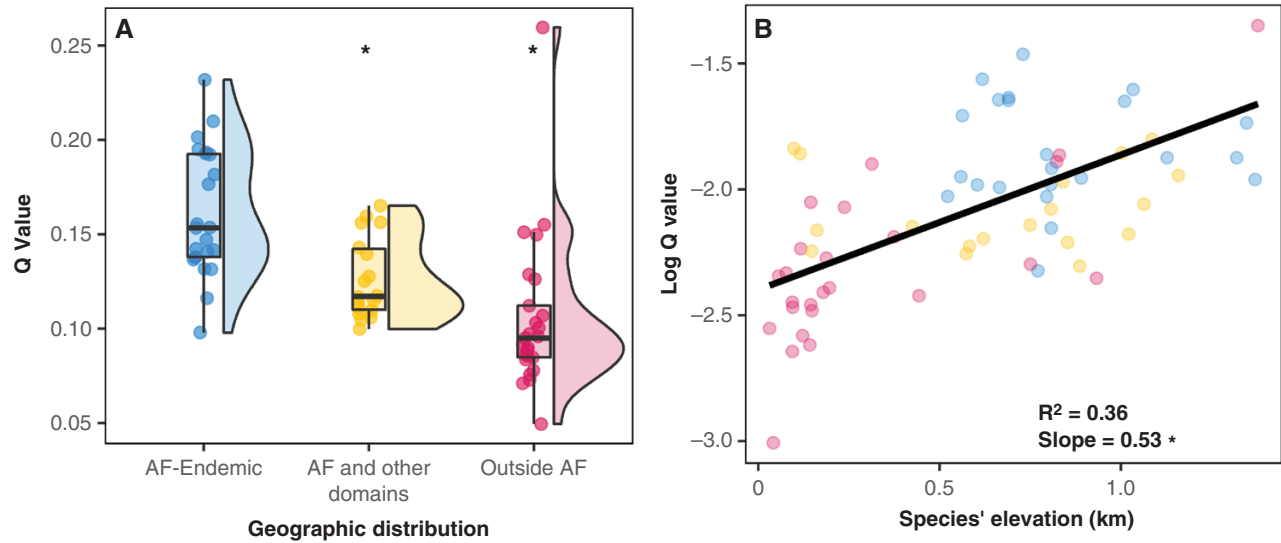
Fig. 2. Rao's *Q*-value, representing environmental heterogeneity faced by species, and its relationship with species geographical distribution and elevation. (A) Species *Q*-value and its relationship with species geographical distribution. Box-and-whisker plots represent the 50 and 95 % interquartile ranges, and violin plots represent density distributions. *Significant differences from AF-endemic species. (B) Log species *Q*-value and its relationship with species elevation (in kilometres). The line represents the inferred relationship based on a phylogenetic generalized least squares (PGLS) model. The slope value indicates the inferred effect of species elevation, and the *R*² value indicates model fit. *Significant effect of the predictor variable.

acknowledged effects from non-heritable components of geographical range.

RESULTS

Our sampling included 66 species of the *Miconia* supersect. *Discolores*: 23 species were AF-endemic and 33 non-endemic. Among the non-endemic species, 18 were spread in the AF and other domains, and 25 were outside the AF domain. The AF-endemic species had fewer occurrences (41 ± 63, mean ± s.d.) overall than species spread in the AF and other domains (181 ± 276) and species outside the AF domain (53 ± 46).

Environmental heterogeneity: higher *Q*-values for AF-endemic species and at higher elevations

Following our first prediction, *Q*-values, a proxy for the environmental heterogeneity faced by species, were 33 and 60 % higher for AF-endemic species (0.16 ± 0.03, mean ± s.d.) than for species spread in the AF and other domains (0.12 ± 0.02) and species outside the AF domain (0.10 ± 0.04), respectively ($t = -3.0$ and -6.2, $P = 0.003$ and 0.001, respectively; Fig. 2A). Considering each environmental variable separately, *Q*-values were also higher for AF-endemic species than for non-endemic species (Supplementary data Fig. S8). Species at high elevations, mostly AF-endemic species, had increased *Q*-values (slope = 0.53, $t = 7.0$, $P < 0.001$), and elevation explained about one-third of *Q*-value variation ($R^2 = 0.36$; Fig. 2B).

Environmental niche modelling: smaller hypervolumes among AF-endemic species

Following our second prediction, the hypervolume size, a proxy for species overall niche breadth, was 60 and 59 %
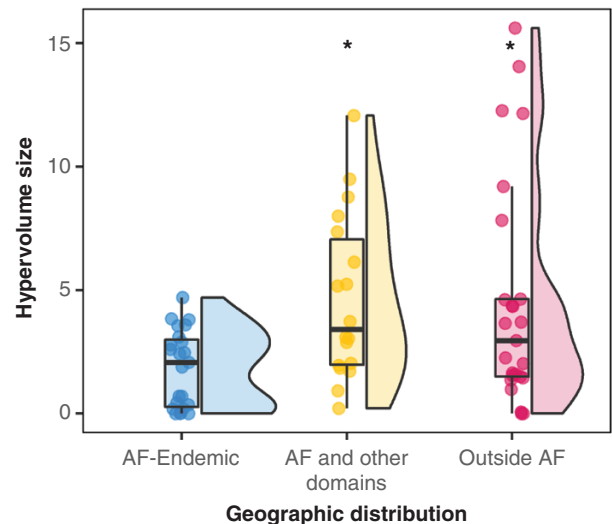

Fig. 3. Hypervolume size, representing species' environmental niche breadth, and its relationship with species geographical distribution. Box-and-whisker plots represent the 50 and 95 % interquartile ranges, and violin plots represent density distributions. *Significant differences from AF-endemic species.

smaller for AF-endemic species (1.84 ± 1.54, mean ± s.d.) than for species spread in the AF and other domains (4.64 ± 3.34) and species outside the AF domain (4.55 ± 4.60), respectively ($t = 2.97$ and 2.03, $P = 0.004$ and 0.046, respectively; Fig. 3). The value of Moran's *I*, a proxy for the spatial autocorrelation in regions occupied by species, did not affect species hypervolume size ($t = 0.88$, $P = 0.37$), indicating that small hypervolume sizes (i.e. specialization) were not associated with highly autocorrelated regions. Interquartile range values calculated over solar radiation and soil pH differed between AF-endemic and non-endemic species, whereas the diurnal

temperature range and precipitation seasonality did not differ (Supplementary data Fig. S9). Interquartile range values over solar radiation were 27 % smaller among AF-endemic species (896) than among species spread in the AF and other domains (1200) and species outside the AF domain (1201) ($t = 2.8$ and 2.7, $P = 0.005$ and 0.006, respectively). Interquartile range values of soil pH were 28 and 47 % smaller among AF-endemic species (0.31) than among species in the AF and other domains (0.43) and species outside the AF domain (0.59), respectively ($t = 2.2$ and 4.1, $P = 0.003$ and 0.001, respectively). Hence, the smaller hypervolume sizes of AF-endemic species reflected a narrow niche breadth over solar radiation and soil pH gradients.

Geographical range: smaller areas with smaller hypervolumes, mostly among AF-endemic species

Convex hull area, a proxy for species geographical range, was 14 and 20 times smaller for AF-endemic species (12 ± 15 km^2, median $\pm$ IQR) than for species spread in the AF and other domains (169 ± 574 km^2) and species outside the AF domain (223 ± 324 km^2), respectively.

Following our third prediction, convex hull area was positively associated with hypervolume size. When comparing PGLS models on the relationship between convex hull area and hypervolume size, the nested model (AICc $= 294$, $R^2 = 0.57$) had a better fit and explained a greater part of convex hull area variation than the simpler model (AICc $= 308$; $R^2 = 0.38$). Under the nested PGLS model, hypervolume size had a great positive effect on convex hull area among AF-endemic species (slope $= 0.73$, $t = 2.6$, $P = 0.009$), but only a moderate effect among species spread in the AF and other domains (slope $= 0.44$, $t = 3.1$, $P = 0.002$) and species outside the AF domain (slope $= 0.31$, $t = 3.6$, $P = 0.001$; Fig. 4).

Evolutionary scenarios: best-fitting OUMV models indicate distinct selective regimes

Phylogenetic reconstruction indicated that the *Miconia* supersect. *Discolores* dates to 8.1 Mya (95 % highest posterior density = 5.9–10.8 Mya; Fig. 5). The last common ancestor of the group was outside the AF domain, and most descendant species remained outside. Endemism in the AF domain has evolved independently three times (numbered squares in Fig. 5). First, a vicariant process originated an AF-endemic lineage between 6.2 and 4.4 Mya, which then diversified in the AF domain. Different dispersal processes to other domains originated non-endemic lineages between 2.4 and 0.1 Mya, during the Pleistocene. Second, a vicariant process originated an AF-endemic lineage between 2.0 Mya and the present, during the Pleistocene. Third, a vicariant process originated an AF-endemic lineage between 0.8 Mya and the present, during the Pleistocene.

Overall, hypervolume size and convex hull area had a similar distribution of values across species, with small values usually co-occurring in AF-endemic species. Nonetheless, this association did not hold mostly among non-endemic species. Species age did not affect either hypervolume size or convex hull area
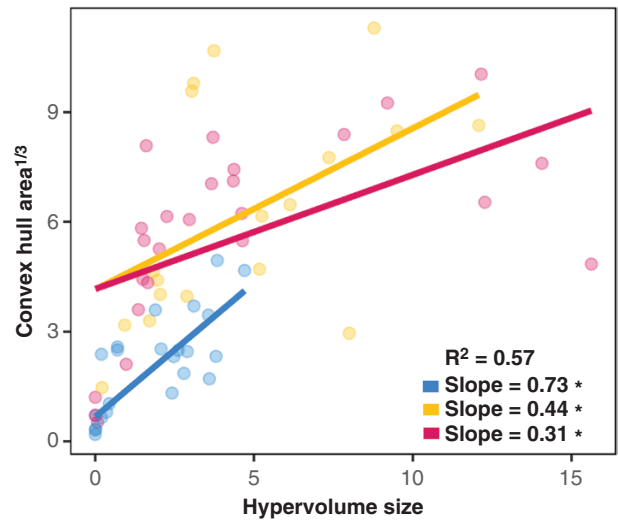

FIG. 4. Convex hull area, representing species geographical range, and its relationship with hypervolume size, representing species' environmental niche breadth. Convex hull area is cubic root-transformed to represent relationships in a linear fashion. Each line represents a relationship between variables according to species geographical distribution based on a nested phylogenetic generalized least squares (PGLS) model. Slope values indicate the inferred effect of species hypervolume size, and the R^2 value indicates the overall model fit. *Significant effects of geographical distribution on the inferred relationship.

because shorter and longer branches had both small and large values for both variables.

The OUMV model had the lowest ΔAICc for hypervolume size and convex hull area across 100 and 74 % of the phylogenetic trees, respectively. Following our fourth prediction, the OUMV represents a selection-driven scenario, in which each geographical distribution (evolutionary regime) has its own Θ and σ values but has a single α value (Table 1).

Considering the OUMV estimates for hypervolume size, Θ values of AF-endemic species ($\Theta = 1.8 \pm 0.03$, mean $\pm$ s.d.) were three times smaller than those of species spread in the AF and other domains ($\Theta = 4.4 \pm 0.10$) and species outside the AF domain ($\Theta = 4.6 \pm 0.08$) (Fig. 6A). The σ values of AF-endemic species ($\sigma = 5.1 \pm 3.8$) were two and three times smaller than those of species spread in the AF and other domains ($\sigma = 11.2 \pm 8.5$) and species outside the AF domain ($\sigma = 15.5 \pm 12$), respectively (Fig. 6B). The mean hypervolume size in all geographical distributions was smaller than BM expectations ($P < 0.05$), but deviation from BM expectations was greater for AF-endemic species (Fig. 6C).

Considering the OUMV estimates for convex hull area, Θ values of AF-endemic species ($\Theta = 19.4 \pm 7.3$) were 20 and 15 times smaller than those of species spread in the AF and other domains ($\Theta = 369.2 \pm 358.9$) and species outside the AF domain ($\Theta = 283.3 \pm 11.91$), respectively (Fig. 6D). The σ values of AF-endemic species ($\sigma = 98 \pm 110$) were 13 and eight times smaller than those of species spread in the AF and other domains ($\sigma = 1339 \pm 1574$) and species outside the AF domain ($\sigma = 795 \pm 905$), respectively (Fig. 6E). The mean convex hull area in all geographical distributions was smaller than BM expectations ($P < 0.05$), but deviation from BM expectations was greater for AF-endemic species (Fig. 6F).
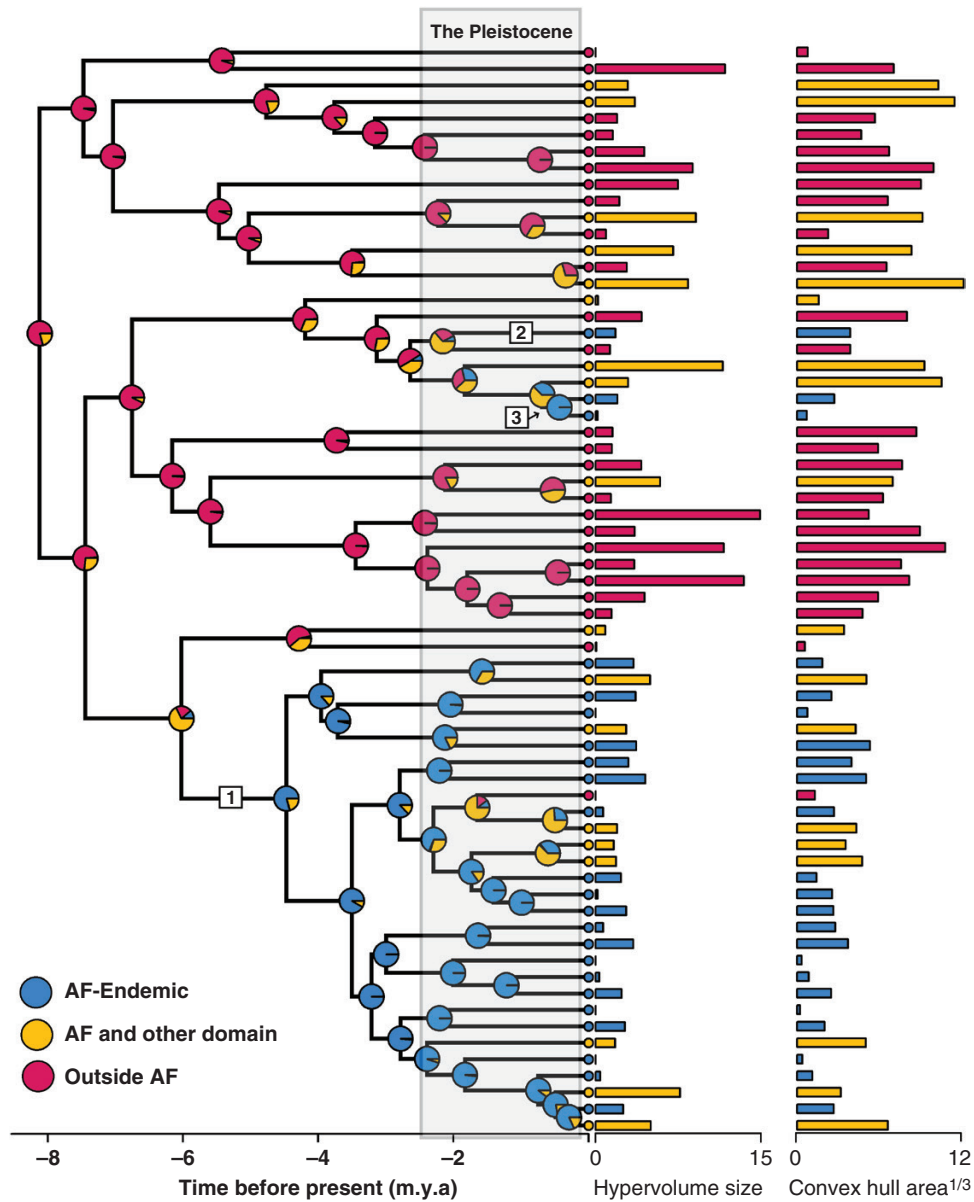
FIG. 5. Phylogenetic reconstruction of *Miconia* supersect. *Discolores*, inferred ancestral geographical distributions, and their hypervolume sizes and convex hull areas. Phylogenetic relationships are represented by the maximum clade credibility tree. Pie charts at nodes represent the proportional likelihood of ancestral species geographical distributions based on the DEC model, and pie charts at tips indicate geographical distributions of extant species. Numbered squares at branches indicate the origin of Atlantic Forest (AF)-endemic lineages. Bars at the tips represent hypervolume sizes and convex hull areas for extant species. The convex hull area is cubic root-transformed to highlight the overall linear relationship between variables among AF-endemic species. The scale at the bottom represents the time before the present (in millions of years ago). The grey band highlights the Pleistocene. Throughout, colours indicate geographical distributions as follows: blue, AF-endemic; yellow, AF and other domains; red, outside the AF domain.

Ancestral reconstruction of geographical range: AF-endemics rapidly reduced their geographical ranges after their evolution

Ancestral reconstructions of convex hull area indicated greater values at older than at more recent ages (Fig. 7). The last common ancestral of AF-endemic species had a greater convex hull area than same-age non-endemic species, but this difference rapidly inverted after the evolution of AF-endemic species. Between 8 and 6 Mya, ancestral AF-endemic species had a 52 % reduction of convex hull area, while species spread in the AF and other domains and species outside the AF domain had 23 and 0.5 % reduction of convex hull area, respectively. After this rapid inversion, ancestral AF-endemic species retained smaller convex hull areas than ancestral non-endemic species during the following ages. Other changes of convex hull area occurred during the Pleistocene. During this period, AF-endemic species and species outside the AF domain had a 1.3 and 22 % reduction of convex hull area, respectively, whereas species spread in the AF and other domains had an 8 % increase.
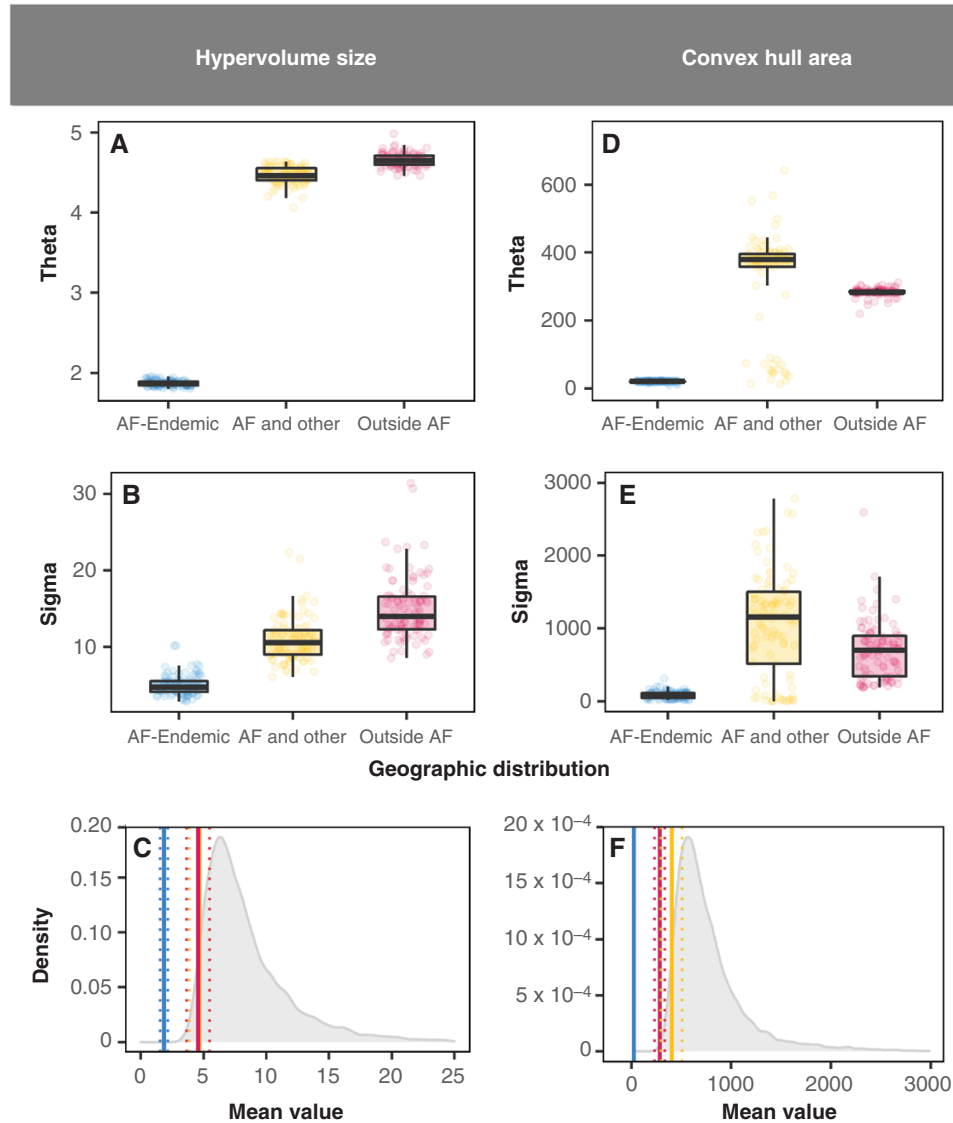
FIG. 6. OUMV model estimates for hypervolume size and convex hull area considering species geographical distribution as evolutionary regimes. The Θ (A) and σ (B) estimates for hypervolume size. The Θ (D) and σ (E) estimates for convex hull area. Observed means (continuous lines) of hypervolume size (C) and convex hull area (F) and associated standard errors (dotted lines) for each geographical distribution and the expected means (grey distributions) under the Brownian motion (BM) model. Throughout, colours indicate geographical distributions: blue, AF-endemic; yellow, AF and other domains; red, outside the AF domain.

DISCUSSION

Environmental heterogeneity imposes selective pressures favouring specialization, which, in turn, can constrain geographical range and promote the assemblage of endemic floras. The AF domain is a hotspot that harbours a highly endemic flora, and *Miconia* is the most diverse and remarkably endemic plant genus in this domain. Here, we have hypothesized that *Miconia* species have faced increased environmental heterogeneity and, consequently, have been selected towards increased specialization in the AF domain, and this increased specialization has greatly reduced species geographical range, ultimately promoting endemism. Based on this, we have made five predictions and tested them using geographical, environmental and phylogenetic data on the *Miconia* supersect. *Discolores*, a

major lineage of woody angiosperms that includes AF-endemic and non-endemic species. We have found overall support for all of our predictions, as follows: (1) environmental heterogeneity was 33–60 % higher around AF-endemic species than around non-endemic species; (2) AF-endemic species were overall 60 % more specialized than non-endemic species; (3) specialization strongly predicted smaller geographical ranges among AF-endemic species, but not among non-endemic species; (4) AF-endemic species have evolved towards specialization and small geographical ranges under a selection-driven scenario; and (5) ancestral AF-endemic species underwent a 52 % reduction of geographical range immediately after their evolution, maintaining their small geographical ranges throughout historical periods. The implications of our results are discussed below.
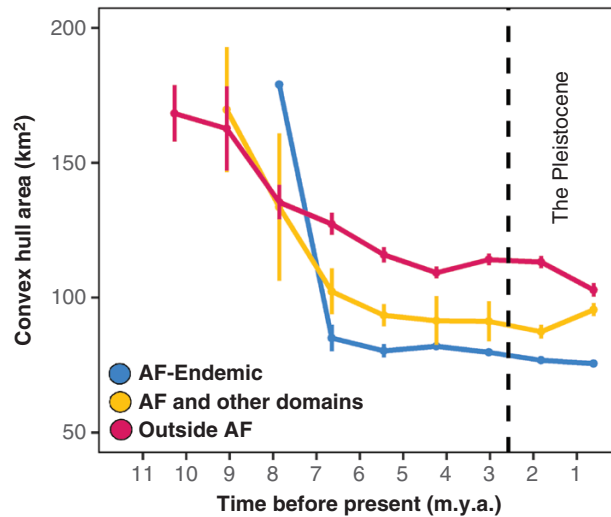
FIG. 7. The convex hull area, a proxy for species geographical range size, in each geographical distribution throughout time. Ancestral values inferred by the OUMV model. Dots represent the mean estimate during a time period, and vertical lines represent the associated standard error. The scale at the bottom represents the time before the present (in millions of years). The dashed line marks the beginning of the Pleistocene. Colours indicate geographical distributions: blue, AF-endemic; yellow, AF and other domains; red, outside the AF domain.

Atlantic Forest-endemic species face great environmental heterogeneity

Environmental heterogeneity was overall 33–60 % greater around AF-endemic species than around non-endemic species (Fig. 2A). Such heterogeneity resulted from greater spatial variation in all analysed environmental gradients (Supplementary data Fig. S4). This pattern supports our first prediction that AF-endemic species should face greater environmental heterogeneity than non-endemic species. Hence, AF-endemic species are more likely to face different environments while dispersing to neighbouring sites (Brown and Pavlovic, 1992). This great environmental heterogeneity around AF-endemic species was considerably associated with elevation (Fig. 2B), indicating that montane landscapes have prompted environmental variation. The spatial complexity in montane landscapes has long been thought to increase environmental heterogeneity (Körner, 2004), and this spatial complexity probably increases with elevation. Other montane features, such as age and position, also contribute to environmental heterogeneity (Perrigo et al., 2020), but their relative roles were not our main focus.

Mountains can shape the regional climate by deflecting radiation and relocating precipitation, and mountain weathering can affect soil composition by moving sediments from highlands to lowlands (Perrigo et al., 2020). In the AF domain, mountain ranges can host more climatic zones than nearby lowland areas, ranging from wet tropical in the foothills to subtropical with short summers at mountain tops (Alvares et al., 2013). Moreover, the mountain ranges of the AF date back to different geological periods and provide different sediment types (Hiruma et al., 2010), such that soil types can vary greatly along mountain slopes (Cunha et al., 2019). These mountain-associated gradients are major drivers of plant distribution in the AF domain, because they underlie distinct vegetation types,

from coastal woodlands (*restingas*) up to cloud dwarf forests (*matinhas nebulares*) (Neves et al., 2017).

Mountains can also explain a major part of the environmental heterogeneity in other Neotropical domains. For instance, the Cerrado domain encompasses a minor portion of the eastern Brazilian highlands, over which annual precipitation and soil types vary the most (Sano et al., 2019). Likewise, the *Campos rupestres* province displays a significant elevational variation that underlies steep gradients of drought severity and temperature oscillation (Bueno et al., 2021). Aside from mountains, environmental heterogeneity around non-endemic species can also result from the Amazon basin, which can concentrate different soil patches into relatively small areas (Quesada et al., 2020). Nonetheless, these different geological and edaphic features are not as spatially close in extra-Andean Neotropical domains as mountain ranges in the AF domain, granting the latter a higher environmental heterogeneity.

Atlantic Forest-endemic species are environmentally specialized

Specialization was 60 % greater overall among AF-endemic species than among non-endemic species (Fig. 3), reflecting a narrower niche breadth over solar radiation and soil pH (Supplementary data Fig. S6). This pattern supports our second prediction that AF-endemic species should be more specialized than non-endemic species. Increased specialization among AF-endemic species is likely to be a response to their immediate surroundings with great environmental heterogeneity. As environments become more different, they impose contrasting challenges that can necessitate trade-offs by organisms (Levins, 1962). Hence, when different environments are spatially close (i.e. great environmental heterogeneity), organisms are more likely to experience reduced fitness when dispersing to their surroundings (Brown and Pavlovic, 1992). Consequently, in an environmentally heterogeneous background, optimally exploring fewer similar environments would lead to greater fitness than exploring several different environments (Brown and Pavlovic, 1992).

The montane landscapes of the AF harbour different environments that can demand contrasting responses from plant species. Supporting this, environmental gradients predict functional beta-diversity among plant communities in the AF domain, also delimiting different plant physiognomies across montane regions (Silva et al., 2021). For instance, the carbon allocation strategy of woody Rubiaceae species changes with light conditions, varying between valley and ridge areas in the AF domain (Torres-Leite et al., 2019), revealing different plant responses across montane areas. Hence, a single generalist plant strategy would be unlikely to cope with the environmental heterogeneity imposed by the montane landscapes of the AF. Among all environmental gradients, solar radiation and soil pH vary greatly in space owing to montane features. Montane slope and aspect influence solar radiation by changing ground inclination and orientation for sunlight (Martin et al., 2019). Likewise, the montane slope influences soil pH by changing soil material flux (Cunha et al., 2019). As a likely response to this environmental variation, AF-endemic *Miconia* species displayed increased specialization regarding solar radiation and soil pH (Supplementary data Fig. S9). The effect of this

specialization on species functional traits must be addressed elsewhere. Other environmental gradients might also favour specialization in the AF domain because they predict functional variation across plant assemblages (Silva *et al.*, 2021), but assessing their role requires studies in other plant lineages structured by them.

Consequently, specialization can be a frequent, but still overlooked, pattern among endemic plant lineages in the AF domain. In support of this, the phylogenetic turnover of plant communities strongly follows mountain gradients (Mariano *et al.*, 2020), indicating that closely related plant lineages are specialized to different environments. Moreover, phylogenetic endemism overall increases over the montane regions of the AF (Brown *et al.*, 2020), reflecting a spatial accumulation of divergent plant lineages, a likely effect of specialization. Indeed, environmental gradients predict phylogenetic endemism in different taxonomic groups, including plants, in the AF domain (Paz *et al.*, 2021), thus highlighting that endemic plant lineages are associated with specific environmental conditions. Based on this, the high plant endemism in the AF domain could hide a general pattern of plant specialization to different habitats, as recorded in other montane domains (e.g. Casazza *et al.*, 2005; Boulangeat *et al.*, 2012; Buira *et al.*, 2020). Nonetheless, assessing the generality of this pattern requires further studies inferring specialization on other endemic plant systems in the AF domain.

Specialization leads to small geographical ranges, mostly for AF-endemic species

The geographical range of species was positively correlated with their niche breadth, most strongly among AF-endemic species (Fig. 4). This pattern supports our third prediction that specialization should lead to smaller geographical ranges. Specialization can decrease species geographical range by limiting suitable conditions and, consequently, reducing the inhabited areas (Brown, 1984). This process is pervasive, because specialization predicts smaller geographical ranges across different taxonomic groups, especially when related to environmental tolerances (Slatyer *et al.*, 2013). Given that plants have low mobility during their lifespan, geographical ranges more readily reflect environmental niche breadth among plant species (e.g. Sheth and Angert, 2014). As a result, specialization greatly affects the geographical range of plants among all other range-limiting factors (Sheth *et al.*, 2020). Such a relationship could be an artefact owing to great spatial autocorrelation, under which small-ranged species are considered specialists because their occurrences are over environmentally correlated regions (Cardillo *et al.*, 2018). However, great spatial autocorrelation did not predict great specialization in our study system. Hence, as environmental specialization increased, *Miconia* species had fewer suitable areas to inhabit and, consequently, established small geographical ranges, thus prompting endemism in the AF domain.

Nonetheless, AF-endemic species might also experience other range-limiting factors that are confounded by environmental heterogeneity. The mountains of the AF impose steep environmental gradients that restrict the dispersal of bird species (Thom *et al.*, 2021), which could, consequently, restrict

dispersal of *Miconia* species (Messeder *et al.*, 2021). Based on this, environmental heterogeneity would favour plant specialization and reduce plant dispersal, thus confounding different range-limiting factors. The additive effects of specialization and dispersal limitation could underlie the smaller range sizes of AF-endemic species compared with equally specialized non-endemic species (Fig. 4). However, addressing the role of dispersal limitation in plant endemism requires further investigation. Another possible range-limiting factor are historical processes, and Pleistocene climatic shifts are considered a major driver of small-ranged plant lineages in the AF domain (e.g. Bünger *et al.*, 2016). Nonetheless, AF-endemic species underwent a minor reduction of geographical range during the Pleistocene (Fig. 7; for further discussion, see *Small geographical ranges are a long-standing pattern in the AF domain*. Hence, range size reduction among AF-endemic species is likely to derive from great specialization, possibly coupled with dispersal limitations.

In turn, small geographical ranges were moderately associated with specialization among non-endemic species, indicating a greater effect of different range-limiting factors in other Neotropical domains. Given that non-endemic species overall face less environmental heterogeneity than AF-endemic species, they are more likely to establish themselves successfully on surrounding sites (Brown and Pavlovic, 1992), thus forecasting geographical expansion. Hence, specialization among non-endemic species might not respond to environmental heterogeneity. Specialization is also favoured in extremely limiting but frequent conditions, which provide reduced competition with increased area availability (Futuyma and Moreno, 1988). For instance, flooded plains are typical limiting habitats in the Amazon domain, but floodplain-specialist plant species contribute little to Amazonian endemism, because they are often found in other Neotropical domains (Wittmann *et al.*, 2013). Based on this, limiting but frequent conditions might have allowed specialization among non-endemic species without small geographical ranges. Moreover, as specialization becomes less pronounced, other range-limiting factors are likely to take place (Sheth *et al.*, 2020). For instance, Amazonian rivers are strong dispersal barriers to small-sized birds (Hayes and Sewlal, 2004), which can, consequently, limit *Miconia* fruit dispersal in the Amazon basin. Likewise, short-ranging ant species have a major role as *Miconia* fruit dispersers in the Cerrado domain (Christianini and Oliveira, 2009). These dispersal limitations can impact geographical range size regardless of species niche breadth, which might have led some generalist non-endemic species to have small geographical ranges. Thus, non-endemic species with small geographical ranges might better reflect dispersal limitations rather than specialization.

Specialization and small geographical ranges are adaptive optima for AF-endemic species

The niche breadth and geographical range of *Miconia* species evolved under a selection-driven scenario (the OUMV model), with different optima (Θ) and evolutionary rates (σ) among geographical distributions, but under a single attraction force (Beaulieu *et al.*, 2012). The AF-endemic species have evolved towards more specialized and small-ranged optima

than non-endemic species (Fig. 6A, D). Also, AF-endemic species have evolved under lower rates around their respective optima than non-endemic species (Fig. 6B, E). Observed niche breadths and geographical ranges deviated from expectations under neutral evolution for all geographical distributions (Fig. 6C, F). Accordingly, the single attraction force across geographical distributions indicates that selection intensity upon species niche breadth and geographical range are invariant to biogeographical domains. All these patterns support our fourth prediction that specialization and smaller geographical ranges among AF-endemic species should conform to a selection-driven evolutionary scenario rather than to a neutral evolutionary scenario. Nonetheless, they also indicate that selective pressure in the AF domain, as elaborated further, might also occur in other biogeographical domains, but favouring other niche breadth and geographical range values.

Specialization and small geographical ranges among AF-endemic species are likely to be an adaptative response to the great environmental heterogeneity in AF montane landscapes. With increased environmental heterogeneity, nearby areas are more likely to impose contrasting environmental demands, thus imposing selective pressures favouring repeated dispersal and specialization to a few similar environments (Brown and Pavlovic, 1992). In the AF domain, montane habitats contain locally adapted populations for different plant species (e.g. Brancalion *et al.*, 2018; Feliciano *et al.*, 2022; Vető *et al.*, 2022), thus highlighting selective pressures towards specialization in the montane landscapes of the AF. Hence, AF-endemic species have evolved towards specialization and small geographical ranges probably as an optimal adaptative response to the contrasting environments in the montane landscapes of the AF. Moreover, as environmental heterogeneity increases, selective pressures towards specialization would intensify (Levins, 1962), hence the reduced evolutionary rates for AF-endemic species can reflect a strong selective pressure impairing generalization and geographical range expansion (Beaulieu *et al.*, 2012). Aside from selective pressures, reduced evolutionary rates can also derive from evolutionary constraints. Specialization can lead to evolutionary constraints via accumulation of mutations and antagonistic pleiotropy, and both processes impair phenotypic evolution (Poisot *et al.*, 2011). Hence, as specialization increased, AF-endemic species might have lacked some potential to evolve towards generalization and large geographical ranges (Poisot *et al.*, 2011). We lack the genetic data to infer evolutionary constraints properly, but our results indicate a possibility that deserves further attention. Thus, as dispersal to the AF domain or extinction outside it proceeded, *Miconia* species experienced a novel selective regime favouring specialization and small range sizes, thus promoting endemism.

Environmental heterogeneity has been suggested to promote plant endemism in the AF, but the underlying evolutionary processes have remained mostly assumed. Environmental heterogeneity has long been thought selectively to favour plant specialization, facilitating *in situ* speciation and species accumulation, ultimately promoting endemism (Asthon, 1969; Ricklefs, 1976; Gentry, 1992). For instance, *Protea* species have diversified in the Amazon domain under the repeated evolution of soil specialization, hence sister species are often geographically close but ecologically divergent (Fine *et al.*, 2005). As

a result of evolutionary processes, great environmental heterogeneity can predict high endemism in plant communities across different domains (e.g. Irl *et al.*, 2015; Molina-Venegas *et al.*, 2017; Tordoni *et al.*, 2020). Although environmental heterogeneity has been linked to plant endemism in the AF domain (e.g. Furtado and Menini Neto, 2021), selection-driven plant specialization has been assumed rather than tested. When analysing different AF-endemic plant lineages, Leão *et al.* (2020) found increased diversification rates associated with small geographical ranges, a pattern assumed to reflect specialization-driven speciation. Albeit robust, this study has not inferred specialization and its mode of evolution among endemic plant lineages. As a likely example, endemic bromeliad lineages have evolved towards habitat specificity in the AF domain, and this specificity could have allowed these lineages to occupy overlapping geographical distributions (Maciel *et al.*, 2020). To our knowledge, our study is the first to address environmental heterogeneity and consequent selective pressures favouring specialization as promoters of plant endemism in the AF. Generalizing this explanatory model, of course, requires further studies on other endemic plant systems in the AF domain.

Small geographical ranges are a long-standing pattern in the AF domain

Geographical ranges of the earliest ancestral species were greater than those of extant species regardless of geographical distribution (Fig. 7), indicating widespread ancestral species. However, the earliest ancestral AF-endemic species underwent a sharp reduction of geographical range immediately after their evolution, while ancestral non-endemic species underwent minor reductions in the same time period. After this sharp reduction, ancestral AF-endemic species maintained smaller geographical ranges than ancestral non-endemic species. Hence, this pattern supports our fifth prediction that small geographical ranges among AF-endemic species should date back to the occupation of the AF domain rather than to more recent time periods. This pattern most probably derives from the selective pressures favouring specialization and small geographical ranges in the montane landscapes of the AF, as already discussed. Given that montane ranges are ancient geographical features in the AF domain (145–23 Mya; e.g. Hiruma *et al.*, 2010), this selection-driven reduction of geographical range would have been acting upon *Miconia* species since their establishment in the AF domain. Therefore, the association between specialization and small geographical ranges probably arose with the occupation of the AF domain, lingering throughout historical periods.

Nonetheless, the Pleistocene climatic shifts have probably impacted ancestral *Miconia* species, which underwent changes in geographical range during the Pleistocene (Fig. 7). Glacial–interglacial cycles are thought to have imposed a contraction–expansion dynamic on Neotropical forests during the Pleistocene (Prance, 1982). This historical process has been supported in the AF domain, where climatically stable forest refugia would have sheltered animal taxa during the Pleistocene (Carnaval and Moritz, 2008). Proposed refugia currently harbour greater genetic diversity for different plant species than non-refugial areas (e.g. Turchetto-Zolet *et al.*, 2016; Leal *et al.*, 2018; Mäder *et al.*, 2021), thus supporting their role as climatic

shelters for plants as well. One major refugium is inferred over the montane regions of the Southern AF domain (Porto *et al.*, 2013), where AF-endemic *Miconia* species often occur. In the Southern AF domain, montane plant lineages are thought to have either expanded or displaced their geographical ranges during the Pleistocene (Wilson *et al.*, 2021). These processes might also have occurred with AF-endemic *Miconia* species, but applied reconstruction methods are not sensible to these processes (see the *Materials and Methods* section). Ancestral geographical ranges are better inferred via palaeo-projections of environmental niche models followed by the empirical validation of fossil records (Svenning *et al.*, 2011). Nonetheless, this approach assumes species with non-evolving environmental niches (Soberón and Nakamura, 2009), an assumption that may not hold at the macroevolutionary scale (Donoghue and Edwards, 2014). Despite the limitations, the applied ancestral reconstructions most probably depict group-wise trends in geographical range, whereas palaeo-projections will probably reveal species-specific changes, refining our understanding about the Pleistocene climatic shifts.

In sum, plant endemism in the AF domain most probably derives from the interaction between time-generalized ecological specialization and time-specific environmental changes, but the latter has received far more attention (e.g. Fiaschi and Pirani, 2009). On the one hand, the evolution of ecological specialization depends on spatially variable but temporally steady environmental backgrounds (Sexton *et al.*, 2017), such that natural selection can optimize specialists to a given environment throughout generations (Poisot *et al.*, 2011). Under this perspective, the Pleistocene climatic shifts would immediately have disfavoured ecological specialization by changing environments in the AF domain. On the other hand, geological and climatic changes are known to have increased environmental heterogeneity in the Neotropics, including within the AF domain (Hughes *et al.*, 2013; Palma-Silva *et al.*, 2022). Under this other perspective, the Pleistocene climatic shifts would have favoured ecological specialization by providing novel environmental niches in the AF domain. Understanding this interaction demands further studies on other endemic plant systems in the AF domain, but similar patterns have been recorded in neighbouring biogeographical units. For instance, in the montane *Campos rupestres* province, endemic plant lineages have diversified under different scenarios, both Pleistocene related and unrelated, consequently suggesting specialization and dispersal limitations as endemism drivers as well (Vasconcelos *et al.*, 2020). Indeed, plant endemism is likely to result from the interaction among range-limiting factors (Sheth *et al.*, 2020); therefore, macroevolutionary studies should address the relative roles of factors upon different plant lineages across distinct biogeographical units.

Conclusions

Environmental heterogeneity favours the selection-driven evolution of ecological specialization, constraining the geographical range of organisms and, ultimately, promoting endemism. The AF domain has a highly endemic flora and encompasses distinct environments across its montane landscapes, potentially hiding a plant specialization pattern. Here, we have found that AF-endemic plant species face greater environmental heterogeneity than closely related non-endemic species, probably owing to the montane landscapes of the AF. Furthermore, AF-endemic plant species were more specialized than non-endemic species, a likely response to their contrasting environmental surroundings. We have found a strong association between specialization and small geographical ranges among AF-endemic lineages, supporting specialization as a main range-limiting factor upon endemic lineages. Moreover, AF-endemic plant species have evolved towards specialization and small geographical ranges under a selective regime, probably imposed by the montane landscapes of the AF. We also inferred that small geographical ranges have probably evolved with the occupation of the AF domain. Based on that, we have argued that plant endemism in the AF domain derives mainly from an increased ecological specialization favoured by the great environmental heterogeneity over montane landscapes. Ecological specialization is a time-generalized process driving plant endemism in the AF domain, probably interacting with other time-specific processes.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following.

Fig. S1: principal coordinate analysis of Robison and Foulds' distance among phylogenetic trees based on different loci.

Fig. S2: the mean-valued maximum clade credibility phylogenetic tree.

Fig. S3: total species occurrences and their inferred sampling density.

Fig. S4: Neotropical domains recognized in this study.

Fig. S5: the number of species in each category of percentage occurrence in the Atlantic Forest domain.

Fig. S6: Rao's Q-values over the Neotropics.

Fig. S7: distribution of Rao's Q-value per species.

Fig. S8: species Q-values for different environmental variables and their relationship with species geographical distribution.

Fig. S9: species interquartile range values over different environmental variables and their relationship with species geographical distribution.

List S1: species names researched for the taxonomic database of occurrences.

List S2: acknowledged experts on *Miconia* taxonomy, in alphabetical order.

Table S1: the loci used in the phylogenetic reconstruction and their respective GenBank accession numbers.

Table S2: the total number of occurrences per species and their distribution over different Neotropical domains.

Table S3: predictive performance of hypervolume models per species.

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