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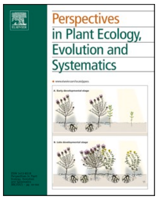

Limited dispersal ability and restricted niche characterize “depauperons” in Melastomataceae

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ABSTRACT

The asymmetric pattern in species richness is a notable feature across different lineages and geographic regions. While some lineages have high richness, diversity and wide distribution, others have the opposite. Despite low rates of diversification, the latter might also be phylogenetically isolated. Lineages that accumulate these characteristics are known as “depauperons’’ and explaining their existence and persistence through time is still a challenge. The plant family Melastomataceae contains both megadiverse lineages (such as the tribe Miconieae, with around 1900 species) and groups with few species (such as the tribes Eriocnemeae, Lithobieae, and Rupestreeae with 7, 1 and 2 species, respectively). These three clades are restricted to eastern Brazil, where they have been seldom studied. The lack of information about their basic biology as well as which processes determine their distribution have not been previously studied. Here we integrated metrics of dispersal ability, species distribution models (SDMs) and natural history data compilation in order to uncover common patterns shared by these depauperons in Melastomataceae and raise conservation concerns. For all nine species we estimated the dispersal ability and generated SDMs in different time-periods (past, present and future). Dispersal ability was associated with predicted distribution models under future scenarios to evaluate shifts and/or retractions in suitable areas. In addition, we compared the climatic tolerances of the depauperons with their megadiverse sister tribes via climatic envelopes. Overall, our results indicate limited dispersal ability, dependency on water for dispersal, and restricted niche as common characteristics for all species in the deupauperon tribes Eriocnemeae, Lithobieae and Rupestreeae. Our analyses also show that the climatic niche spaces of the depauperons are limited and totally included within the niche space of its sister tribes. Based on our findings, the level of threat in these groups can be potentiated by rapid climate change, mainly due to their inability to spread over long distances, restricted niches and increased habitat fragmentation. We suggest that future conservational actions prioritize these unique taxa in Melastomataceae, especially if a phylogenetic diversity perspective is taken into account.

1. Introduction

The disparity in species richness among lineages and between geographic regions is a pervasive feature across the tree of life (Rabosky, 2009). Among plants, we can observe lineages with great diversity and species richness while others show reduced numbers (Magallón et al., 2019). Interestingly, some groups with restricted diversity can be isolated phylogenetically, usually with one or a few species positioned sister to highly diverse groups (Sauquet and Magallón, 2018). These lineages that show low rates of diversification have been defined as branches that differentiated before the evolution or during the assembly of traits or conditions associated with the increased diversification of the speciose sister clade and are known as “depauperons” (Donoghue and Sanderson, 2015). Depauperons are common across the tree of life. In angiosperms, for example, Amborellaceae (*Amborella trichopoda* Baill.), is sister to the ~300,000 remaining angiosperm species; *Acorus* (2–6 spp.) is sister to the monocots (~60,000 spp.); and *Ceratophyllum* (2 spp.) is sister to the eudicots (~200,000 spp; Donoghue and Sanderson,

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2015; Magallón et al., 2019). Understanding the persistence of these relictual lineages is still a puzzle. Some hypotheses have been proposed, such as a putative higher diversity in the past, which has been eroded through time due to successive extinctions (Donoghue and Sanderson, 2015; Vasconcelos et al., 2020).

Richness patterns arise through the processes of speciation, extinction and dispersal (Wiens, 2011a). Dispersal influences spatial patterns and can add lineages to a given region or habitat (Pontarp and Wiens, 2017). In plants, dispersal is facilitated by the transport of seeds or diaspores away from the parent plant, usually by some type of vector, such as animals, wind, water, among others (van der Pijl, 1982). Dispersal ability in plants may impact several population-level processes, including geographic isolation, adaptive divergence, and extinction probability (Levin et al., 2003; Willis et al., 2014). Thus, dispersal range is an important parameter to predict future distributions, especially for rare species with small and isolated populations (Morgan and Venn, 2017). In this context, integrating dispersal ability with species distribution models can be also useful to predict a more reliable future scenario (Di Musciano et al., 2020).

Species distribution models (SDMs) are tools frequently used to predict suitable locations for species by associating occurrence records and environmental variables (Soberón and Nakamura, 2009). These correlative models can be applied for a number of other purposes, including estimating biological invasions (Qin et al., 2015), predicting climate change impacts and possible losses of suitable areas (Trisurat et al., 2011; Fois et al., 2016), in addition to identifying areas for conservation including rare and endemic species (Dagnino et al., 2020). However, these models seldom incorporate the dispersal ability of the species, and, therefore, threats and extinction risk may be underestimated (Vittoz and Engler, 2007). Thus, in a world of accelerated climate change, future scenarios for groups with restricted distribution may be even worse than has already been estimated (Bitencourt et al., 2016; Zhang et al., 2017).

One important aspect of SDMs is that they can also be used in historical approaches (Nyari and Reddy, 2013). For instance, they can aid to uncovering distribution patterns over time, through the identification of refugia (Keppel et al., 2018; Moritz and Agudo, 2013). Refugia can be understood as places that provide spatial and/or temporal protection for lineages against long-term disturbances (Keppel et al., 2018). They have been historically described as limited geographic extensions that sheltered and favored the survival of different organisms during and after the glaciations that occurred in the Quaternary period (Haffer, 1969; Bennett and Provan, 2008). Some studies indicate that certain regions were not directly affected by ice sheets, but rather by aridity (Arctander et al., 1999; Gathorne-Hardy et al., 2002; Byrne, 2008). In the Neotropical region including the Atlantic Forest and Cerrado domains (especially *campos rupestres)* refugia have already been estimated for some endemic groups (Barres et al., 2019; Bonatelli et al., 2014; Carnaval and Moritz, 2008). These refugia related to vegetational contractions and expansions have influenced the distribution of endemic lineages of these regions (e.g., Ramos et al., 2007; Thode et al., 2014), including possibly some depauperons that also occur in these areas (Vasconcelos et al., 2020).

With around 5850 species, Melastomataceae is among the richest angiosperm families in eastern Brazil, as well in the Neotropics, with species distributed mostly in tropical and subtropical regions around the world (Michelangeli et al., 2020; Penneys et al., 2022). These species are common in savannas and tropical forests (Renner, 1993; Reginato et al., 2020) and, specifically in eastern Brazil, it has around 554 species in the Atlantic Forest and 513 in the Cerrado (Goldenberg et al., 2022). More than half of the species of Melastomataceae belong to few megadiverse and broadly distributed lineages, such as tribes Miconieae (ca. 1900 spp., all neotropical; Michelangeli et al., 2019) Sonerileae (ca. 1080 spp; pantropical; Liu et al., 2022), and Melastomateae (ca. 820 spp., pantropical; Veranso-Libalah et al., 2022). On the other hand, some lineages have few known species, are poorly sampled and also poorly known regarding natural history, ecology and biology in general. This is the case of the tribes Eriocnemeae, Lithobieae (Penneys et al., 2020) and Rupestreeae (Goldenberg et al., 2015; Penneys et al., 2022). These lineages are known only from eastern Brazil, and apart from their low richness, their species also have restricted distributions. In addition, each one of them are phylogenetically positioned as sister groups of megadiverse lineages in Melastomataceae (Goldenberg et al., 2015; Penneys et al., 2020; Reginato et al., 2020). Since these features are similar to the ones described above for other angiosperm depauperons (Donoghue and Sanderson, 2015), we have adopted this term here to refer to these lineages. Thus, Melastomataceae, with its contrasting sister lineages with disparate richness, is an interesting group to explore variation based on unique characteristics, such as climatic niches and dispersal ability, and related natural history data. Moreover, these depauperons are especially important for conservation, since the extinction of these lineages can lead to the loss of genetic uniqueness and also of important components of functional diversity.

In this study, we focused on modeling the climatic niche of three depauperon lineages of Melastomataceae from eastern Brazil. Models were generated to assess past, current and future climate scenarios, in order to check possible refuges (in the past), but also assessing possible losses and/or spatial shifts of suitable climatic areas (in the future). In addition, we combined the estimated dispersal ability of the species in these groups with future niche models, in order to compare the effect of dispersal on the prediction of suitable areas generated by the forecasts. Finally, aiming to verify whether or not there are particularities in the current climate tolerances of these depauperons, we compiled distribution data for their megadiverse sister tribes to conduct a pairwise comparison of climate envelopes. In summary, we aimed to answer the following questions: (1) How is the dispersal ability of the species in these depauperate lineages? (2) What might have been the influence of the Quaternary climatic oscillations on the currently restricted distribution of these lineages? (3) How does the dispersal ability affect the putative suitable areas in future predictions for the depauperons? (4) Are there differences in the climatic tolerances between the depauperons and their sister groups?

2. Methods

2.1. Study group

The lineages selected here belong to three tribes, totaling four genera with nine species in Melastomataceae. Tribe Eriocnemeae (Penneys et al., 2020) currently has two genera, *Eriocnema* and *Physeterostemon*, with one and five species, respectively. Tribe Lithobieae (Penneys et al., 2020) has only a single species, while tribe Rupestreeae has a single genus with two species (Goldenberg et al., 2015; Penneys et al., 2022). All these lineages are endemic to Minas Gerais and Bahia states in eastern Brazil, and occur within the limits of two distinct domains, the *campos rupestres* in Cerrado (*Rupestrea* and *Lithobium*) and the Atlantic Forest (*Eriocnema* and *Physeterostemon*). Information on vegetation and habitat, as well as the respective references, are detailed in Table 1.

The plants in the four genera are small (0.05–3 m), ranging from lithophytic herbs (*Eriocnema acaulis* and *Lithobium cordatum*), rhizomatous subshrubs (*Physeterostemon aonae*, *P.jardimii* and *P. thomasii*) to small shrubs (*P. fiaschii*, *P. gomesii*, *Rupestrea carvalhoana* and *R. johnwurdackiana*, Goldenberg and Amorim, 2006; Amorim et al., 2009; Amorim et al., 2014; Goldenberg et al., 2015; Goldenberg et al., 2016; Penneys et al., 2020), see Table 2. Their flowers show a similar pattern, with no prominent specializations: they are all medium-sized (7–16.1 mm), the petals are either white (*Eriocnema*, *Physeterostemon*) or pink to light purple (*Rupestrea* and *Lithobium*), the stamens are twice the number of the petals, isomorphic, with the connective not prolonged, and lacking glands or complex appendages (present in *Rupestrea* and *Lithobium*, but very small), with neither too long nor too short (1–2.2 mm long) yellow, small-pored anthers (Andrade et al., 2007;

Table 1
All taxa selected for this study, with ecological information corresponding to the places of occurrence and references used.

Tribes	Species	Phytophysiognomy	Habitat	Altitude	References
Eriocnemeae	*Eriocnema acaulis* (Chamisso) Triana.	Semideciduous seasonal forest	Shaded areas on rock walls along stream banks	730–1348 m	Andrade et al. (2007); Penneys et al. (2020)
Eriocnemeae	*Physeterostemon aonae* Amorim, Michelangeli & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	800–1275 m	Goldenberg et al. (2016)
Eriocnemeae	*Physeterostemon fiaschii* Goldenberg & Amorim.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	444–520 m	Goldenberg and Amorim (2006)
Eriocnemeae	*Physeterostemon gomesii* Amorim & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	250–450 m	Amorim et al. (2014)
Eriocnemeae	*Physeterostemon jardimii* Goldenberg & Amorim.	Ombrophilous forest / "mata higrófila"	Shaded places along rivers or streams	850–1050 m	Goldenberg and Amorim (2006)
Eriocnemeae	*Physeterostemon thomasii* Amorim, Michelangeli & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shaded places on riverbanks	40–100 m	Amorim et al. (2009)
Lithobieae	*Lithobium cordatum* Bongard.	*Campos rupestres*	Fissures, ledges and cavities in rock outcrops	554 m	Silva and Romero (2008); Penneys et al. (2020)
Rupestreeae	*Rupestrea carvalhoana* (Baumgratz & Souza) Almeda, Michelangeli & Goldenberg.	*Campos rupestres*	Seasonally dry grasslands	850–1080 m	Goldenberg et al. (2015); Penneys et al. (2022)
Rupestreeae	*Rupestrea jonhwurdackiana* (Baumgratz & Souza) Michelangeli, Almeda & Goldenberg.	*Campos rupestres*	Seasonally dry grasslands	850–1200 m	Goldenberg et al. (2015); Penneys et al. (2022)

Table 2
Habit, flower and fruit information for each of the studied lineages. The size of the flowers is twice the average length of the petals. The parameters used for dispersal analyses were growth form (GF), dispersal syndrome (DS), seed release height (RH).

Species	GF	Diameter of flowers (mm)	Petals length (mm)	Anthers length (mm)	Fruits	Seeds	DS	Height (m)	RH (m)
Eriocnema acaulis	herb	10	5	–	dehiscent	ovoid	abiotic	0.05	0.05
Physeterostemon aonae	subshrub	16.1	7.7–8.4	2–2.1	dehiscent	not seen	abiotic	0.12–0.20	0.16
Physeterostemon fiaschii	shrub	9.4	3.7–5.7	1.6–1.9	dehiscent	cuneate	abiotic	0.40–1	0.7
Physeterostemon gomesii	shrub	9.2	4.5–4.7	1.7–2	dehiscent	cuneate	abiotic	0.40–1.40	0.9
Physeterostemon jardimii	subshrub	14	7	1.3–1.6	dehiscent	cuneate	abiotic	0.20–0.40	0.3
Physeterostemon thomasii	subshrub	14	6.8–7.2	1.3–1.5	dehiscent	cuneate	abiotic	0.15–0.25	0.2
Lithobium cordatum	herb	7	3–4	1	dehiscent	ovoid	abiotic	0.03–0.07	0.05
Rupestrea carvalhoana	shrub	9.6	4.6–5	1.7–2	indehiscent	elliptic	abiotic	2	1
Rupestrea jonhwurdackiana	shrub	13.4	5.7–7.7	1.7–2.2	indehiscent	elliptic	abiotic	0.50–3	1.5

Silva and Romero, 2008; Goldenberg et al., 2015; Penneys et al., 2020). These features indicate a classic example of buzz-pollination (Renner, 1989), as seems to be the bauplan in the family (Dellinger et al., 2022), and somewhat contrasting with specialized features in larger lineages, such as the bigger flowers with dimorphic, long-connective bearing stamens in Microlicieae and Melastomateae (Velloso et al., 2018; Telles et al., 2020; Brito et al., 2021) or the purple corollas with food bodies, visited by birds in Merianieae (Dellinger et al., 2019), neither the dense inflorescences with small flowers and wide anther pores pollinated by small, non-buzzing insects in some Miconieae (Goldenberg et al., 2008). Among the four genera there is only one record for pollinators in *Eriocnema acaulis*, whose flowers provide only pollen as a resource for buzzing bees (Andrade et al., 2007).

The seed dispersal in these groups is abiotic, and hydrochory appears to be the predominant syndrome among them, maybe except for *Lithobium* (Table 2). All have dry and dehiscent capsules containing small and numerous seeds (Fig. 1), except for *Rupestrea*, which has a unique feature in the family: the fruits are dry and indehiscent, with only one or two large seeds > 2 mm long (Goldenberg et al., 2015). In *Eriocnema*, dispersal occurs close to the mother plant due to the folding of the infructescence peduncle and fruit pedicel downwards to the substrate, with gradual release of the seeds. Another possibility is ballistic dispersal by raindrops. Furthermore, the seeds have a translucent structure similar to an "air bag" that may help the seed to float on water (Andrade et al., 2007). We have no information regarding dispersal in *Physeterostemon*, but the extended branches of the inflorescences, the morphology and position of the fruits and the fact that these small plants inhabit shaded and very wet areas in the forest understory, suggest seed dispersal through raindrops, similar to the mechanism described for *Bertolonia* (Pizo and Morellato, 2002). There is no published information on the seed dispersal of *Lithobium*, but we suspect that the pedicel extends while the fruits mature, so that the fruits are directed to rock crevices where these plants grow (Fig. 1I), in a mechanism similar to the one explained above for *Eriocnema*; once inside the crevices, the fruits seem to be ready to release the seeds (i.e., a possible autochory). Unlike the other groups, the indehiscent fruits of *Rupestrea* (Fig. 1L) seem to be carried by the water, with the seeds inside them; furthermore, the pericarp around the seeds has a layer of turgid cells that may also be related to floating (Goldenberg et al., 2015).

These clades were estimated to originate in the Neogene (Fig. 2), during the Miocene (23.03 – 5.33 Mya; Reginato et al., 2020; Vasconcelos et al., 2020; Reginato et al., 2022). Eriocnemeae emerged at around 8 Mya, and is sister to Miconieae, with ca. 1900 species (Amorim et al., 2009; Penneys et al., 2020; Maurin et al., 2021; Penneys et al., 2022). Rupestreeae's origin is a bit older, about 14 Mya, and its relationships are less clear: it has been suggested either as sister to tribe Rhexieae (~21 spp.; Penneys et al., 2022) or to Melastomateae (~870 spp.; Maurin et al., 2021). Lithobieae must be at least 20 Mya, and its relationships neither are clear: it may be sister to the tribal pair Astronieae+Henriettaeae (~245 spp.; Penneys et al., 2022) or to Blakeeae (~200 spp.; Maurin et al., 2021).

2.2. Dispersal distance

The dispersal ability of the depauperons was estimated using the "dispeRsal" function (Tamme et al., 2014), which depends on mixed effects models as implemented in the "nlme" package (Pinheiro, 2011). This function uses plant functional traits to estimate species' maximum dispersal distances, among them: growth form (tree, shrub, grass), dispersal syndrome (wind, animals, ballistics and others), seed mass (g),

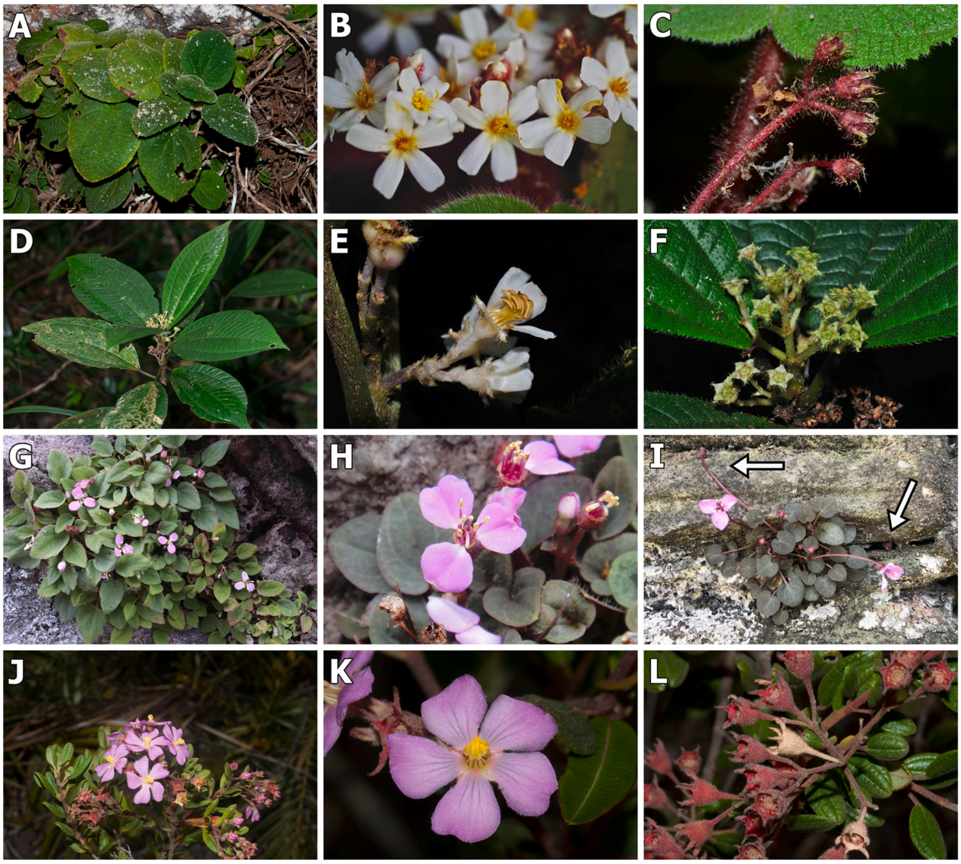

Fig. 1. *Eriocnema*, *Physeterostemon*, *Lithobium* and *Rupestrea*. Habit, flowers and fruits. *Eriocnema acaulis* (A-C), *Physeterostemon gomesii* (D-F). *Lithobium cordatum* (G-I). *Rupestrea johnwurdackiana* (J-L). In I, the white arrows indicate the extension of the pedicel with fruits directed towards the crevices in rocky outcrops. Photos by Fabian Michelangeli (A, D and J), Pedro Viana (B), Erica Borsali (C), Renato Goldenberg (E-F), Devyson Costa (G), Ana Flávia Versiane (H), Renato Ramos (I) and Luciano Pataro (K-L).

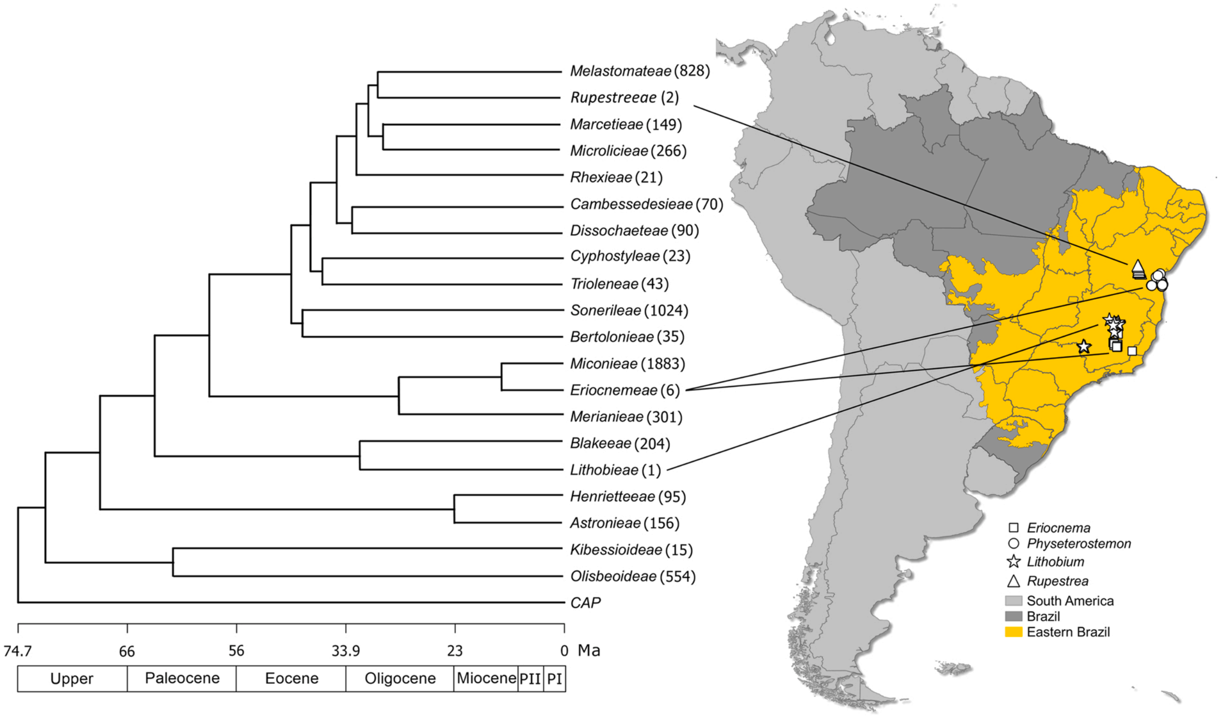

Fig. 2. Distribution of depauperons in eastern Brazil (area used to produce the models). Dated phylogeny of Melastomataceae modified from (Reginato et al., 2020) and based on the phylogenetic relationships of the concatenated tree using RAxML in (Maurin et al., 2021). Geological scale: PI - Pleistocene and PII - Pliocene.

seed release height (m) and terminal velocity (m/s). Among the five models available in the package, we used the ones that were suitable for the data we had available (models 3 and 5). Model 3 considers the dispersal syndrome (DS), the growth form (GF) and the seed release height (RH). Model 5 is simpler and takes into account only DS and GF. The DS and GF characteristics available for the species were obtained from the literature (Goldenberg and Amorim, 2006; Andrade et al., 2007; Amorim et al., 2009, 2014; Goldenberg et al., 2015, 2016; Penneys et al., 2020) and RH was estimated by the average height of the plants (Table 2). This dispersal analysis does not include the direct option for hydrochory and, therefore, the option selected for the dispersal of most species was by wind (without special adaptations in the seeds) except for *Eriocnema acaulis* (which may present ballistic dispersal, Andrade et al., 2007). Other information on terminal velocity and seed mass is absent for all taxa. Differences between models were tested using t-test, while differences in dispersal distance between species were tested through ANOVA (Di Musciano et al., 2020).

2.3. *Species occurrences dataset*

Occurrence data were compiled from herbarium records available in biodiversity databases obtained from SpeciesLink (specieslink.net) and GBIF.org (22 August 2021) GBIF Occurrence Download (doi.org/10.15468/dl.4w8d59). We followed standard steps and procedures in filtering data to minimize the use of incorrect and inaccurate records. Our final database only included records with valid and complete coordinates. This involved removing: (1) records without coordinates; (2) non-numeric coordinates and duplicated; (3) non-terrestrial areas and corresponding to country/state/municipal centers; (4) records close to biodiversity institutions and not corresponding to the distribution pattern of the lineages (outliers). All the above data cleaning steps were carried out through R package 'CoordinateCleaner' (Zizka et al., 2019). From the filtered records, we kept only those that could be associated with herbarium vouchers and were identified. Because of the few records for depauperons, we manually checked all points and determined coordinates whenever possible from descriptions of the localities of occurrence.

The cleaning procedure started with a database with 802,165 records for the depauperons and their sister tribes, representing approximately 50% of the records available for Melastomataceae. After data filtering, there were 132,856 points with reliable occurrences, i.e., with valid coordinates and identifications. The number of records filtered for the depauperons totaled 137: *Eriocnema acaulis* (34 records), *Phyesterostemon aonae* (6), *P. fiaschii* (12), *P. gomesii* (7), *P. jardimii* (11), *P. thomasii* (2), *Lithobium cordatum* (19), *Rupestrea johnwurdackiana* (40) e *R. carvalhoana* (6). Most clean points belong to megadiverse sister tribes, Miconieae (87,852 records), Melastomateae (28,945), Henrietteeae (6041), Blakeeae (5932), Rhexieae (3695) and Astronieae (288). The records of occurrences at different cleaning stages can be found on the distribution maps in the supplementary material (see Fig. S1, S2).

2.4. *Climatic data*

The 19 bioclimatic variables used to generate the species distribution models were taken from WorldClim (worldclim.org) for current (1970–2000) and future (2050) scenarios. Bioclimatic variables from PaleoClim (paleoclim.org) were used for past distribution estimates. The past periods selected for this study were Late Holocene - HLC (ca. 4.2–0.3ka), Pleistocene during the Last Glacial Maximum - LGM (ca. 21ka), Late Interglacial - LIG (ca. 130ka) and Marine Isotope Stage 19 - MIS19 (ca.787 ka). Paleoclimate simulations are based on the UK Met Office's Unified General Circulation Model (GCM) (HadCM3) and the National Center for Atmospheric Research's (NCAR) Community Climate System Model (CCSM). Future climate layers are based on three Atmosphere-Ocean Global Circulation Models (AOGCMs), namely BBC-CSM1, CCSM4 and MIROC-ESM. Due to uncertainties in future climate change (Meinshausen et al., 2011) we apply a precautionary approach and for all scenarios we use the most severe/pessimistic carbon dioxide emission perspective ("Representative Carbon Pathway" – RCP 8.5) defined by the latest IPCC report on world climate (IPCC 2013). In this scenario, global average temperatures are expected to rise by 3.7 °C (ranging from 2.6° to 4.8°C) in 2080–2100 (Taylor et al., 2012; IPCC 2017), with constant carbon dioxide emission and intense changes in land use. The projections for the three global circulation models were summarized in a single consensus map, and this map was used in comparisons with the current scenario. Spatial resolutions selected for all time periods are 2.5 arc-minutes (~4.5 km) for the sake of standardization (Otto-Bliesner et al., 2006; Hill, 2015; Dolan et al., 2015; Karger et al., 2017; Fordham et al., 2018; Brown and Carnaval, 2019). Descriptions for all bioclimatic variables used can be found in Table S1.

2.5. *Species distribution models (SDMs)*

In order to estimate the potential distributions of depauperons we used the R package 'ENMTML' to generate, evaluate and design SDMs (Andrade et al., 2020). In the pre-processing stage, we thinned the filtered occurrence data to reduce sampling bias associated with spatial clustering, whereas we kept only occurrence points at least 5 km apart to minimize spatial autocorrelation (R package 'spThin', (Aiello-Lammens et al., 2015). Some species had fewer occurrence points (<19) than predictors, and therefore some models could not be adjusted. Therefore, we decided to gather the species records and produce genus-level models for *Physeterostemon* and *Rupestrea*, while models for *Eriocnema* and *Lithobium* were generated at species level. Modeling above species level is detailed in (Smith et al., 2019), and takes into account that species in each of these genera occur in close proximity and in similar habitats under equivalent climatic conditions (which is the case for those genera). The number of unique occurrences for each group was *Physeterostemon* (38) and *Rupestrea* (46). The models were fitted and cross-validated using spatial blocks (Roberts et al., 2017; Valavi et al., 2018). We used a number of pseudo-absences 100 times the number of presences (Barbet-Massin et al., 2012), which were randomly generated within the calibration area. The latter was defined based on the area accessible to the groups in the eastern region of Brazil (Reginato and Michelangeli, 2020). This approach takes into account the bioregions available to the lineages over time (Barve et al., 2011). To decrease the collinearity of the environmental variables and the overprediction of the model, we performed a principal component analysis (PCA) to reduce the number of original environmental variables to a smaller set of principal components (PCs) according to De Marco and Nóbrega (2018). We used the first 5 PCs that captured $> 95\%$ of the total variance (Table S2). In the processing stage, we used five different algorithms: Generalized Additive Models (GAM; Hastie and Tibshirani, 1987), Generalized Linear Models (GLM; McCullagh and Nelder, 1983), MaxEnt with default setting (MXD; Phillips et al., 2006), Random Forests (RDF; Breiman, 2001) and Support Vector Machine (SVM; Karatzoglou et al., 2006). In post-processing, we performed an ensemble modeling (EM) approach based on the weighted average of the predictions for each algorithm (Araújo and New, 2007; Marmion et al., 2009). Evaluation of the models was performed using the TSS (True Skill Statistic) metric. TSS values range from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate performance no better than random. Values of 0.5 or greater are generally considered acceptable, and values above 0.7 indicate the good predictive ability of a modeling method in this evaluation metric (Allouche et al., 2006). The final set models were binarized through the TSS maximization threshold (MAX_TSS), which uses the suitability value that gives the highest TSS value to create binary maps. The manipulation of spatial data was done with the R package 'raster' (Hijmans, 2021). Final maps were generated in QGIS v.3.10.13 (qgis.org). The steps described above are summarized in Fig. S3.

2.6. Past refuges and future scenarios

Suitable areas (in km^2) in the binarized model projections for the different time-periods (past and future) were compared to evaluate the differences in potential distribution for each lineage. To estimate past stable areas (or climate refugia) we gathered the maps resulting from the different projections (HLC, LGM, LIG and MIS19) into a consensus map (i.e., summation of the suitable areas in the output maps for each period) for each group. For the future scenario (2050), in addition to the consensus map between the different GCMs (BBC-CSM1, CCSM4 and MIROC-ESM) we evaluated one more scenario, the dispersal ability with the SDMs. This scenario refers to the estimated possibility of maximum dispersal distance (MDD), whereas only the areas present within a circular buffer established around the points from the consensus map generated for the future were kept. The MDD takes into account the greater distances estimated from the dispersal ability from the "disperSal" models (Section 2.2). We used the estimated maximum dispersal value (including the highest confidence limit) and multiplied it by the number of blooms in a 50-year interval (time difference between current and future scenarios, 2000–2050). As the evaluated taxa flower once a year (Goldenberg, personal communication), 50 dispersal events were considered for all lineages.

2.7. Climatic envelopes

To compare climatic tolerances between the depauperons and their megadiverse sister tribes, climatic envelope profiles were used. The climate variables were the same from the WorldClim dataset mentioned above (Section 2.3). Filtered occurrence records for the three lineages were cross-referenced with all environmental layers through the R package 'raster' (Hijmans, 2021). The extracted climatic values were summarized using Principal Component Analysis (PCA) with the R package 'ade4' (Dray and Dufour, 2007), while plots were generated using the R package 'factoextra 1.0.7' (Kassambara and Mundt, 2017). Pairwise comparisons were performed based on the tribal relationships described in Section 2.1. In this way, we made comparisons between the Eriocnemeae vs. Miconieae (sister tribes according to both Penneys et al., 2022 and Maurin et al., 2021), Lithobieae vs. Astronieae+Henriettaeae and between Rupestreeae vs. Rhexieae (according to Penneys et al., 2022). Given the phylogenetic uncertainty, comparisons of Lithobieae vs. Blakeeae and Rupestreeae vs. Melastomateae were also performed (sister tribes according to Maurin et al., 2021).

3. Results

3.1. Dispersal distance

All taxa evaluated here are small herbs or shrubs (< 1.5 m tall), with abiotic, predominantly hydrochoric dispersal. The dispersal distance was shorter than 6 m for all taxa in both different scenarios tested here (Table 3). The longer dispersal distances were estimated for *Rupestrea johnwurdackiana* (5.74 m) and *Eriocnema acaulis* (2.99 m), while the shorter dispersal distances were predicted in both models for *Lithobium cordatum* (0.10 in model 3; 0.99 m in model 5). For most taxa, model 3 provides longer estimates than model 5, except for the three species with the lowest release heights (*Eriocnema acaulis*, *Physeterostemon aonae* and *Lithobium cordatum*). Nevertheless, estimates from the two models do not differ (t-test, $t = 0.791$, $df = 9$, $P = 2.26$), while the relationship between dispersal distance and seed release height was positive for all species (ANOVA, $F = 28.23$, $df = 11.22$, $P < 0001$).

3.2. Current potential distribution

Our dataset ranged from 2 to 40 records per species totaling 137 records for the 9 taxa. As previously explained, the small number of records for some species of *Physeterostemon* and *Rupestrea* led us to model each genus, instead of species, respectively with 38 and 46 records each. The ensemble models produced for each species/genus in the current period (Fig. 3: B, E, H and K), show suitable areas close to the points known of presence of the groups and had an excellent performance, indicating good predictability (TSS > 0.80, ranging from 0.802 in *Eriocnema* to 0.997 in *Rupestrea*; Table S3). In general, TSS values per individual algorithm were also high (predominantly above 0.5), indicating acceptable to excellent models (Table S3). In the current scenario, the potential distribution area by lineage was, respectively, *Eriocnema* = 58,211 km^2, *Physeterostemon* = 9186 km^2, *Lithobium* = 18,796 km^2 and *Rupestrea* = 6144 km^2 (Table S4).

The potential distribution of all lineages under current climatic conditions includes known areas of occurrence, as well as nearby locations with similar phytophysiognomies. Suitable areas for *Eriocnema* are mainly distributed in the state of Minas Gerais, but also in some places in Rio de Janeiro and São Paulo states; climatic suitable areas are on the border between the Atlantic Forest and Cerrado domains, especially along the southern portion of the Espinhaço Range (in the "Iron Quadrangle"). *Lithobium*'s suitable areas are predominantly concentrated within the limits of Minas Gerais, along the *campos rupestres*, mainly in central portions of the Espinhaço Range (including Serra do Cipó, Planalto de Diamantina and Serra do Cabral), and also to the west, in Serra da Canastra. *Rupestrea*'s suitable areas are also in *campos rupestres* on the Espinhaço Range, but northwards (Chapada Diamantina) within the limits of the Caatinga, in the state of Bahia. *Physeterostemon*'s predicted localities are also in Bahia, but in the Atlantic Forest, from coastal areas close to Serra do Conduru State Park towards the interior, including the limits of Boa Nova National Park and Wenceslau Guimarães State Ecological Station (see Fig. 3).

3.3. Past refuges and future distributions

The SDMs under current conditions were projected for different periods in the past (HLC, LGM, LIG, MIS19) and future (2050), and the potentially suitable areas were compared. The extent of coverage areas (in km^2) in the maps for each lineage in each estimated past period are described in the Supplementary Material (Table S5 and Fig. S4). The regions predicted for depauperons in past periods indicated larger

Table 3

Dispersal distances estimated by two models for each of the depauperon species. Mean distances (DM), lower-upper confidence limits (LC). Model 3 considers the form of growth, dispersal syndrome and seed release height. Model 5 only considers the form of growth and the dispersal syndrome.

Species	DM (m)	Model 3	LC (%)	Model 5	LC (%)
Eriocnema acaulis	1.55	0.107	0.091–0.054	2.995	1.619–5.541
Physeterostemon aonae	2.25	2.103	0.335–13.195	2.403	1.084–5.324
Physeterostemon fiaschii	3.10	3.806	0.732–19.775	2.403	1.084–5.324
Physeterostemon gomesii	3.10	3.806	0.732–19.775	2.403	1.084–5.325
Physeterostemon jardimii	2.59	2.788	0.492–15.790	2.403	1.084–5.326
Physeterostemon thomasii	2.36	2.325	0.385–14.029	2.403	1.084–5.327
Lithobium cordatum	0.55	0.107	0.091–0.053	0.998	0.707–1.409
Rupestrea carvalhoana	3.59	4.786	0.961–23.833	2.403	1.084–5.324
Rupestrea johnwurdackiana	4.07	5.741	1.176–28.019	2.403	1.084–5.324

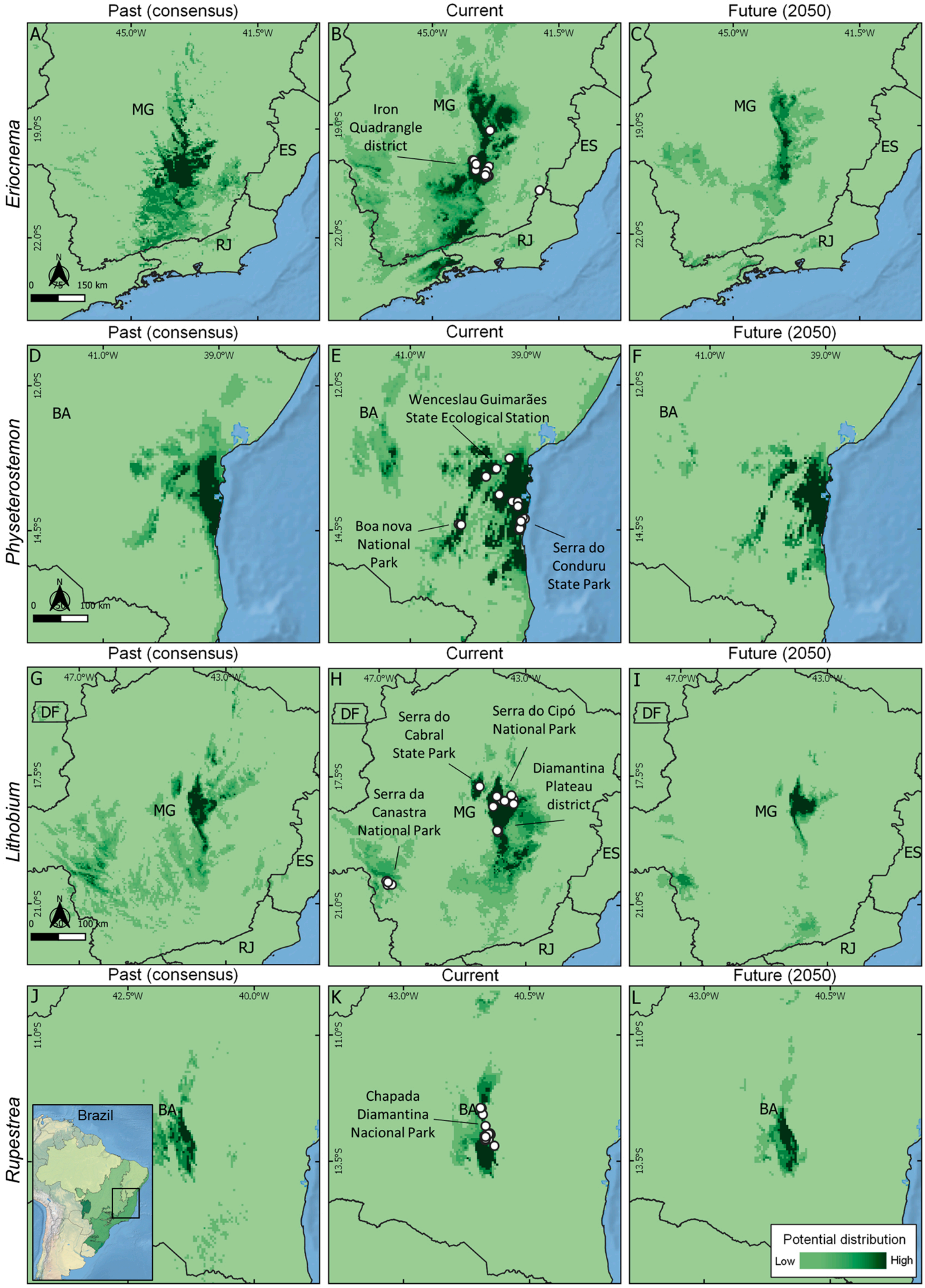

Fig. 3. Potential distribution obtained from ensemble models for the depauperons in the different scenarios under current conditions (central column), past (left column) and future (right column) projections. The maps for the lineages are *Eriocnema* (A-C), *Physeterostemon* (D-F), *Lithobium* (G-I) and *Rupestrea* (J-L), respectively. Dark green regions indicate climatically suitable regions (high potential) and light green regions indicate unsuitable areas (low potential). The white circles indicate the locations of occurrences. MG - Minas Gerais state and BA - Bahia state. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

extensions compared to the areas currently estimated. The periods presented variations of the predicted locations, where expansions and retractions for the different lineages were estimated. Eriocnemeae (*Eriocnema* and *Physeterostemon*) presented a gradual increase in suitable areas in the Mid-Pleistocene (MIS19 ~787ka.) and the Late Interglacial (LIG ~130ka). Between the LIG and the Last Glacial Maximum (LGM ~21ka) we found an expressive reduction in these areas for the same groups. Finally, in the LGM and the late Holocene (HLC ~4ka) the proportion of potentially suitable areas returns to larger extents. For Lithobieae (*Lithobium*) and *Rupestrea* lineages we verified a slight reduction of areas in the MIS19 and LIG periods, a significant increase in the LIG and the LGM, and also a small reduction of areas at the end of the LGM and the HCL (unlike the previous groups). The average of potentially suitable areas (in past periods) for each group was, respectively: *Eriocnema* = 41,793 km^2, *Physeterostemon* = 14,865 km^2, *Lithobium* = 38,032 km^2 and *Rupestrea* = 9531 km^2. Beyond the oscillations identified over the different periods (expansions and retractions) we also elaborated consensus maps (Fig. 3: A, D, G and J) in which it is possible to verify common areas of the different projections for each of the lineages. Beyond the oscillations identified in the different periods, our consensus maps (based on the sum of all periods) indicate common areas and point to climatically stable sites (or climatic refugia) near the current known occurrences. The extension values of the areas in the consensus maps refer to the sum of the places where the probability of occurrence of the lineages is greater (Table S5). At these sites temperature and precipitation conditions have remained constant for the lineages during the glacial cycles of the Quaternary, mainly from the lower Pleistocene to the present day.

The consensus projections for the future (2050) based on the RCP 8.5 scenarios showed a strong reduction in the areas potentially suitable for the depauperons when compared to the current scenario (Fig. 3: C, F, I and L). These areas were respectively 26,010 km^2 (*Eriocnema*), 5150 km^2 (*Physeterostemon*), 15,757 km^2 (*Lithobium*) and 5713 km^2 (*Rupestrea*). The proportional loss of potentially suitable areas in the future, when compared to the current conditions (Table S4), were 55.31% (*Eriocnema*), 43.93% (*Physeterostemon*), 16.16% (*Lithobium*) and 7.01% (*Rupestrea*). Taking into account the maximum dispersal distance (MDD) scenario, it is possible to notice an even greater decrease in the areas potentially suitable for those lineages (Table S4). In this scenario, the coverage areas for the groups were: *Eriocnema* = 2666 km^2, *Physeterostemon* = 3593 km^2, *Lithobium* = 0149 km^2 and *Rupestrea* = 15,880 km^2. In this case, the proportions of accessible areas ranged from approximately 96–99% compared with the current scenario. The abrupt drop in suitable areas as indicated by MDD takes into account the estimated maximum dispersal capacity and is basically restricted to the locations closest to the currently known distribution of the groups.

3.4. Climatic envelopes

The first PCA comparing climate tolerances between tribes Eriocnemeae and Miconieae (Fig. 4A) had 83.06% of the variation explained in the first three components (PC1 = 50.69%, PC2 = 20.82% and PC3 = 11.55%). The bioclimatic variables that contributed most to the variation captured in the first two components (PC1-PC2) were related to temperature, respectively bio1 (72.72%), bio11 (71.17%), bio9 (71.15%), bio10 (70.03%) and bio5 (69.82%). The second PCA comparing the Lithobieae and Astronieae+Henrietteae (Fig. 4B) had 80.04% of the variation captured in the first three components (PC1 = 37.05%, PC2 = 29.95% and PC3 = 13.04%). The most important variables in the first two axes were also related to temperature, respectively bio10 (76.79%), bio1 (76.31%), bio9 (76.20%), bio11 (73.79%) and bio5 (72.14%). Finally, the third PCA that compared Rupestreeae and Rhexieae (Fig. 4C) captured 83.10% of the variation in the first three axes (PC1 = 51.25%, PC2 = 16.84% and PC3 = 15.01%). The variables that contributed most to the first two components (PC1-PC2) were mostly related to temperature, respectively, bio11 (75.15%), bio6 (74.99%), bio1 (70.28%), bio12 (69.94%) and but also one related precipitation, bio4 (68.44%). The other comparisons between tribes Lithobieae and Blakeeae, in and between Rupestreeae and Melastomateae can be found in the supplementary material (Fig. S5A, S5B). The complete overlap of climatic envelopes of the depauperons and their sister tribes is evident, except for Lithobieae, with only a partial (Fig. S5A) or no overlap in relation to its sister lineages (Fig. 4B).

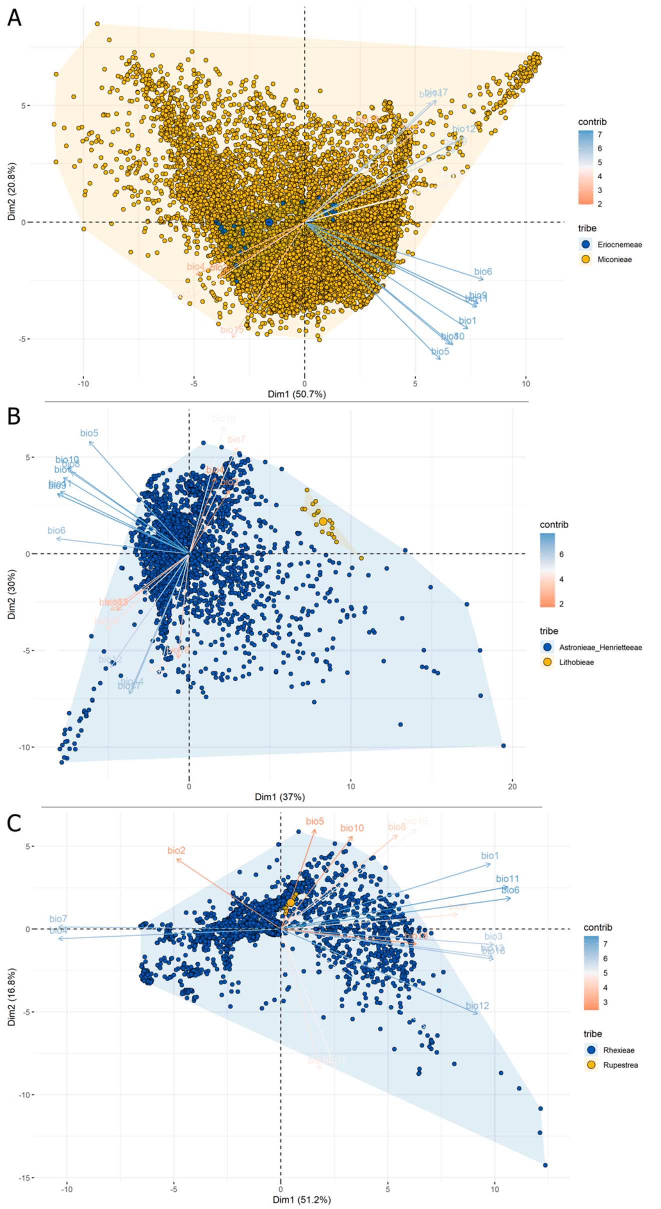

Fig. 4. Comparison of the climatic envelopes of the tribes Eriocnemeae x Miconieae (A), between the tribes Lithobieae and Astronieae+Henrietteae (B) and between Rupestreeae and Rhexieae (C). The climate spaces marked by the “convex hulls” are based on the first two components of the PCA analysis of all 19 WorldClim current bioclimatic variables. The contributions of the variables are proportional to the size of the arrows and their colors (the larger and closer to blue, the greater their contribution).

4. Discussion

4.1. Limited dispersal capacity

The dispersal distances estimated by different algorithms (Tamme et al., 2014) predicted reduced dispersal capacity for all depauperons, since none of the nine species in Eriocnemeae, Lithobieae and Rupestreae showed potential ability to disperse their seeds beyond 10 m. Most angiosperms disperse their seeds between 10 and 1500 m from the mother plant, with few cases above that. Long-distance dispersal can be favored by large birds, fruit bats, and megaherbivores (Corlett and Westcott, 2013). According to Thomson et al. (2011), dispersal distances rarely exceed 100 m for most dispersal modes, including water and wind. Information on dispersal through falling raindrops is scarce, but the distances are shorter or close to 1 m (Vittoz and Engler, 2007). The idea of philomatry in plants contemplates intrinsic and extrinsic factors related to limited dispersal, such as the morphological characteristics of the diaspores and the local environmental conditions, respectively (Cheplick, 2022). While the disadvantages of restricted dispersal include the inability to migrate to new habitats and may lead to inbreeding depression, on the other hand, remaining close to the maternal habitat may reduce the energetic costs of producing accessory structures necessary for dispersing the diaspores (Cheplick, 2022). The height at seed release seems to play a determining role in the dispersal ability (Tamme et al., 2014), due to the simple idea that seeds released from greater heights can reach greater distances than seeds released close to the ground (Thomson et al., 2011; Tovar et al., 2020). In this sense, smaller species are more likely to be philomatric than taller species (Cheplick, 2022). The nine species studied here are herbs or small shrubs and disperse their seeds/fruits at heights < 1 m. On the other hand, there are lineages in their sister tribes ranging from lianas and epiphytic shrubs in Blakeeae (Penneys and Judd, 2011) to large trees > 20 m in Astronieae (Mancera et al., 2017). Although dispersal capacity across the megadiverse tribes has not been addressed so far in the same way we did here, there are studies that have evaluated dispersal in megadiverse lineages, mainly with emphasis on the genus Miconia (Messeder et al., 2021). The various groups of frugivorous animals that consume the fleshy fruits of this lineage, such as birds and monkeys, may end up dispersing the seeds over long distances (Fuzessy et al., 2017). In some cases, even dispersal by ants can move diaspores for distances greater than 40 m (Lima et al., 2013). Dispersal capacity can be estimated by other characteristics, for example, the speed at seed fall (Tamme et al., 2014), but this information is lacking for the depauperons; fieldwork on dispersal distance would improve the predictions in these groups (Di Musciano et al., 2020). More natural history data should be gathered to further investigate dispersal ability, especially in the seldom studied abiotic dispersing lineages (Messeder et al., 2022).

All depauperons we studied here have dry fruits with abiotic dispersal, which seems to be a plesiomorphic character within Melastomataceae (Reginato et al., 2020). Although no direct association was found between the mode of dispersal (biotic vs. abiotic) and diversification in the family, extinction rates appear to be higher among lineages with abiotic dispersal (Reginato et al., 2020). According to Givnish et al. (2005), the association between dispersal mode and light availability (sun vs. shade) shows a strong correlation and seems to be a clear pattern of evolutionary convergence among monocots. Even though the relationship between dried fruit/open areas has been traditionally assumed for Melastomataceae (Renner, 1989), the association between dispersal mode and richness among different habitats (open/savanna and closed/forest) was also not confirmed for the family (Reginato et al., 2020). Among the depauperons, *Eriocnema* and *Physeterostemon* occur in closed habitats while *Lithobium* and *Rupestrea* in open habitats; which means that the habitat apparently plays no role here. Despite having dry fruits, some of the groups treated here show a wide range of specialized features, such as those related to hydrochory.

Different fruits with similar dispersal mechanisms may come from different morphological background and differences between types of dry fruits in Melastomataceae depend on the shape of the mature hypanthium and dehiscence type of the actual fruits (i.e., the mature ovary; Bacci et al., 2020). Water dispersal in herbaceous melastomes have been detailed for species in Bertolonieae, and this has been also invoked to explain patterns of diversity and endemism in this group (Bacci et al., 2020). The mechanism involved in seed dispersal in this lineage is related to the triangular shape of their fruits ("squirt-corner seed dispersal"; Pizo and Morellato, 2002), and results in small average distances of only a few centimeters. In fact, several species of *Bertolonia* occupy similar habitats in the Atlantic Forest understory (Bacci et al., 2020), in areas close to the occurrence of *Physeterostemon*; seed dispersal in *Physeterostemon* may occur in a similar way, since its fruits also have an angulose apex like those in Bertolonieae and Trioleneae. The other lineages of "depauperons" do have different fruit morphology and, consequently, a different seed dispersal mechanism. In *Rupestrea*, the seeds are much larger (> 2 mm long) compared with the usual Melastomataceae range (from 0.4 to 2 mm long; Silveira et al., 2013). In addition, seeds in this genus are surrounded by a layer of turgid cells belonging to the pericarp and which may possibly be related to water dispersal (Goldenberg et al., 2015). It is common for species growing on swampy areas to have light diaspores capable of floating on water, such as some lineages of monocots (*Alisma* L., *Iris* L. and *Carex* L., Vittoz and Engler, 2007). Both species of *Rupestrea* grow on shallow soils that overflow in the rainy season (Goldenberg et al., 2015), becoming swampy during part of the year; nevertheless, dispersal in *Rupestrea* should be further investigated in the field.

4.2. Potential distribution under climate change

The current potential distribution estimated for the depauperons by species distribution models (SDMs) showed areas with high climatic suitability in eastern Brazil, mainly along the Cerrado (in the *campos rupestres* of the Espinhaço Range) and north of the Atlantic Forest (on the coast of Bahia state), where there are currently known occurrences for these lineages (Goldenberg et al., 2015; Penneys et al., 2020). Although the models have pointed to regions that are geographically restricted, the suitable locations were not limited to the areas where the taxa were recorded. Therefore, we believe that new field surveys can be directed to discover putative new populations in regions that have not yet been explored, in order to expand sampling, which would improve the robustness of the data, and consequently subsequent models (Moudrý and Šímová, 2012). Restricted dispersal patterns and niche conservatism are eminent features in the flora of the *campos rupestres* (Conceição et al., 2016; Rapini et al., 2021). Some studies in the Atlantic Forest also recovered conserved climatic niches for lineages as *Leandra* Raddi s.s. (Reginato, 2014), Cambessedesieae (Bochorny et al., 2019) and *Bertolonia* (Bacci et al., 2021). Some plant lineages (mainly herbaceous) can show these same patterns in locations distant from each other, for example, regions of the Andes (Tovar et al., 2020) and southeastern Australia (Morgan and Venn, 2017). The places in the geographic space where a species is not observed but has conditions favoring its survival (including climatic conditions), are described as one of the dimensions of the species' fundamental niche (Hutchinson, 1957; Soberón and Peterson, 2005). This niche dimension is also known as "potential niche" or "existing fundamental niche" (Peterson and Soberón, 2012), and lineages may not occur in these areas due to several factors, including physical barriers, habitat loss, intrinsic physiological limitations, growth form and limited dispersal (Smith and Beaulieu, 2009; Wiens, 2011b; Rabosky and Hurlbert, 2015). Although information about ecological interactions for the groups is unknown, the low dispersal capacity may be playing a determining role in these cases.

There are marked differences in suitable areas between the different periods, with expansions for the taxa from *campos rupestres* between the Last Interglacial (LIG) and the Last Glacial Maximum (LGM), concomitantly with the contraction of Atlantic Forest taxa in the same time interval. Collectively, past projections showed stable areas in different periods (see Fig. 3: A, D, G and J) that may have acted as climatic refugia for the depauperons. These findings agree with other studies that also predict past refuges during the Quaternary for other organisms (including plants and animals) both in the Atlantic Forest and in the *campos rupestres* (Barbosa et al., 2015; Barres et al., 2019; Bonatelli et al., 2014; Carnaval and Moritz, 2008; D'Horta et al., 2011), as well as in other similar regions of the world described in the OCBILS theory (Hopper, 2009; Hopper et al., 2016; Silveira et al., 2021). However, the variation found in past models may be related to the places where the groups occur (*campos rupestres* and Atlantic Forest) instead of the species themselves. During the Pleistocene glaciations, the northern part of the Atlantic Forest did not undergo major vegetational changes (Carnaval and Moritz, 2008), whereas the Cerrado (including the *campos rupestres*) expanded into forest areas between the late Miocene and early Pliocene (Azevedo et al., 2020). Some studies suggest that the *campos rupestres* could also have functioned as refugia for fire-sensitive lineages since the expansion of the Cerrado in the late Tertiary (Conceição et al., 2016; Rapini et al., 2021). In this sense, the effect of past climate oscillations may not have had such an impact on the lineages in the different regions (Leite et al., 2016; Cabanne et al., 2016; Rapini et al., 2021) and, therefore, this may not be the main factor explaining the persistence of depauperons to the present day. This would be expected since many highly diverse groups from other families occur in these regions (Vasconcelos et al., 2020) and consequently, there are other factors that must act on the diversity and distribution of vegetation in these regions, such as selection and genetic drift, in addition to niche changes (Rapini et al., 2021).

Future projections based on the consensus models under the pessimistic scenario (RCP 8.5) showed a sharp drop in the areas predicted as suitable for all depauperons within 50 years (2000–2050). Several studies have shown future area loss for different groups of organisms in the same period of time, including plants (Velazco et al., 2019; Wan et al., 2021) and animals (Gonçalves et al., 2021; Pietro-Torres et al., 2020). For rare species, future scenarios may be even more unfavorable (Di Musciano et al., 2020; Ledig et al., 2010; Vincent et al., 2020). According to the projections by Bitencourt et al. (2016), the *campos rupestres* may lose 10% of their current area by 2050 and about 55% by 2080 in more severe scenarios; the distribution of these losses along the Espinhaço Range will apparently be uneven between different sub-regions, being more accentuated to the north in Bahia when compared to the south in Minas Gerais. For the Atlantic Forest, estimates of area loss can be even more severe (about 88%) and the remaining vegetation may range from approximately 11–16% of the original cover (Ribeiro et al., 2009). Other studies indicate that only 7% of the areas in this hotspot are protected (Lemes et al., 2014) and significant losses of habitat in this biome have already been predicted for several organisms (Alvarenga et al., 2010; De Souza et al., 2011; De Souza and Prevedello, 2019; Lourenço-de-Moraes et al., 2019; De Lima et al., 2019). Among the species evaluated here only four are included in the Red List of the Brazilian "Centro Nacional de Conservação da Flora" (CNCFlora). Currently, *Eriocnema acaulis*, *Lithobium cordatum* and *Rupestrea jonhwurdackiana* are listed as endangered, while *Rupestrea carvalhoana* is assessed as critically endangered (CNCFlora, 2022). Although none of the five species of *Physeterostemon* have been assessed to date, descriptive studies of the species in the genus already point to the threats present where populations have been found and suggest critical threat status (Amorim et al., 2009, 2014; Goldenberg et al., 2016).

Dispersal capacity plays a key role in reliable future predictions of plant species distribution (Di Musciano et al., 2020). Overlapping the estimates of maximum dispersal distance (MDD) and the consensus SDM for future scenarios shows an even stronger and more abrupt decrease in the suitability of the habitats for the depauperons. Other studies linking dispersal ability to species distribution models have also found low dispersal capacity for lineages from mountain regions (Morgan and Venn, 2017; Di Musciano et al., 2020). Species in these areas will most likely suffer from rapid climate change due to the difficulty of colonizing new places because of their low dispersal ability (Morgan and Venn, 2017). We suggest the inclusion of future geological and pedological data to complement our findings and improve our understanding of the edaphic endemism behind each group (Corlett and Tomlinson, 2020).

In most cases, the distribution estimates for all depauperons in the different periods indicate that the realized niche may have remained constant in narrow geographic ranges and close to the already known locations of the groups' presence (although with expansions and contractions over time), mainly due to past climatic fluctuations. These results may be linked to niche conservatism (Crisp and Cook, 2012; Wiens et al., 2010) and so, we expect it to be another limiting factor in lineage dispersal. Niche conservatism states that most species tend to maintain their ancestral niches and therefore have difficulties in developing new physiological tolerances (Wiens and Donoghue, 2004). As a result, species are not expected to reach locations under environmental conditions that are unsuitable for survival due to their intrinsic physiological limitations (Wiens, 2011b). Furthermore, our findings as a whole suggest that the colonization of new areas by the depauperons is unlikely, mainly taking into account their limited dispersal capacity, habitat fragmentation, topographical heterogeneity (inherent in *campos rupestres*), as well as the expansion in land use and human population growth (Di Musciano et al., 2020; Silveira et al., 2016). Although depauperons are not expected to share genes with other species through hybridization and introgression due to their phylogenetic isolation, these lineages may still contain important functional traits that allow them to resist environmental changes, including global temperature increase (Dick and Pennington, 2019).

4.3. *Overlapping climatic tolerances*

There are no marked differences in precipitation and temperature tolerances between the climatic envelopes of the depauperons and their megadiverse sister tribes. In most cases, the depauperons climatic envelopes are within the observed climatic range for the respective sister tribes (except in the particular case of Lithobieae). The broad distribution patterns of the large sister groups (e.g., Miconieae and Melastomateae) across virtually the entire Neotropical region end up obfuscating and also make it difficult to understand and compare the diversity and distribution patterns at smaller scales, such as the ones found for the depauperons. Widely spread lineages experience a wider range of ecological and climatic conditions within their range (Gaston, 2003) and this, in turn, may be related to broader niches, especially among widespread species (Kambach et al., 2019; Slatyer et al., 2013). In fact, some species in the sister tribes, e.g., *Miconia albicans*, *Miconia calvescens*, *Clidemia hirta*, among others, are widely distributed (Goldenberg, 2004; Le et al., 2018; Murphy et al., 2008) and may be influencing much of the variation found when we compared the climatic envelopes. Temperature and precipitation are among the most commonly accepted determinant variables for species distribution and richness at local and global scales (Clarke and Gaston, 2006; Paz et al., 2021; Whittaker, 1972). The predictors that best explain the variation found between the groups are related to temperature. Temperature acts on plant metabolic and growth rates (Went, 1953; Rawson, 1992) and can influence development and reproduction (Hatfield and Prueger, 2015). In addition, temperature appears to be more strongly related to plant traits than precipitation (Moles et al., 2014). Although temperature has more relevance in our case, the effect of precipitation may have been obscured and difficult to interpret, even taking into account seasonal differences. Since most depauperons seem to rely on water to disperse their seeds, the effects of precipitation at smaller scales should be investigated further. Other factors must be taken into account in order to explain diversity reduction in the family, for example, ecological (pollination, competition, predation, etc.), morphological (form of growth), physiological (stress tolerance), genetic (polyploidy and drift), among others events (Wiens, 2017; Wisz et al., 2013).

5. Conclusions

Our findings indicate that the depauperons potential niche is reduced (in restricted geographic ranges) and possibly conserved over time. Given the similarities found between the lineages across the different approaches applied here, it is unlikely that the depauperons may disperse seeds or fruits at medium and long distances, essentially due to limited dispersal ability and niche constraints. We believe that these characteristics associated with habitat fragmentation may further increase the threat levels of these taxons in the face of rapid global climate change, which in turn puts the potential loss of evolutionary diversity at risk. Depauperons are species-poor, phylogenetically isolated lineages that, to date, are treated as survivors (or relict taxa) from subsequent extinction events of groups that may have been diverse in the past. Our findings do not disagree with this scenario, but we cannot be sure whether or not the depauperons have been diverse in the past, given the limited fossil record. In addition, we are aware of methodological aspects that may improve our model predictability, especially regarding sampling, resolution of environmental layers and inclusion of other predictors (e.g., soils, topography, geodiversity, biotic interactions, among others).

The approaches used here could be applied among other lineages in Melastomataceae also poor in species and phylogenetically isolated that occur outside eastern Brazil, including Cyphostyleae, *Loricalepis*, *Ochthephilus*, *Dinophora*, *Feliciadamia*, among others. These other depauperons would open space for new studies that can further expand our knowledge about diversity in this family. We emphasize that estimating the distributions of rare lineages with low sampling and lack of information about their biology proves to be an especially difficult challenge both for modeling and for conservation issues. Most populations of these lineages found so far are mostly within the boundaries of protected areas. However, anthropic actions such as mining, cattle raising, intentional burning, and the introduction of invasive exotic species are among the main threats to these groups, even inside protected areas. In this sense, it is paramount that the conservation units where populations are already established are kept preserved to ensure the quality of their microhabitats. We believe that the suitability maps prepared here can guide choices of potential areas for reintroduction of species and identification of new populations at risk.

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CRediT authorship contribution statement

Bruno Bastos: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing - original draft. **Lucas F. Bacci:** Conceptualization, Investigation, Validation, Writing - review & editing. **Marcelo Reginato:** Conceptualization, Methodology, Investigation, Validation, Writing - review & editing. **Renato Goldenberg:** Conceptualization, Supervision, Investigation, Validation, Funding acquisition, Writing - review & editing. **Thuane Bochorny:** Conceptualization, Investigation, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2022.125701.

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