

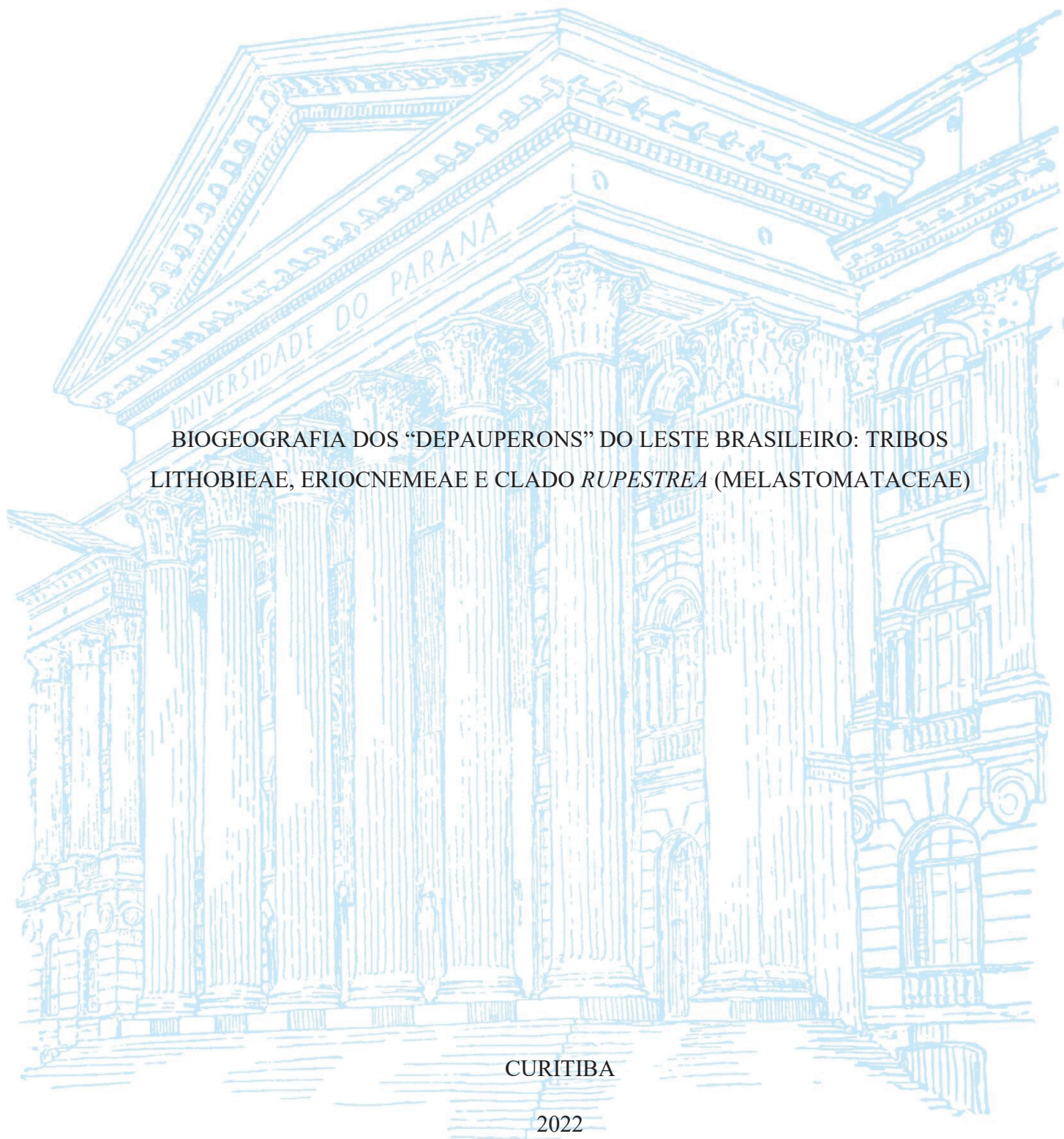
UNIVERSIDADE FEDERAL DO PARANÁ

BRUNO BASTOS DE OLIVEIRA

BIOGEOGRAFIA DOS “DEPAUPERONS” DO LESTE BRASILEIRO: TRIBOS
LITHOBIEAE, ERIOCNEMAE E CLADO *RUPESTREA* (MELASTOMATACEAE)

CURITIBA

2022



BRUNO BASTOS DE OLIVEIRA

BIOGEOGRAFIA DOS “DEPAUPERONS” DO LESTE BRASILEIRO: TRIBOS
LITHOBIEAE, ERIOCNEMEAE E CLADO RUPESTREA (MELASTOMATACEAE)

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Orientador: Prof. Dr. Renato Goldenberg
Coorientador: Dr. Lucas F. Bacci
Coorientador: Prof. Dr. Marcelo Reginato
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RESUMO

A diversidade de espécies evidentemente não é distribuída igualmente no espaço, no tempo, nem entre grupos taxonômicos. Esse é um tema que desperta curiosidade e impulsiona diversos estudos em áreas como a biogeografia, biologia evolutiva, ecologia e outras. Enquanto algumas linhagens contêm ampla riqueza, diversidade e vêm sendo identificadas com altas taxas de diversificação (balanço entre especiação e extinção), outras apresentam padrões opostos. Esses últimos clados podem apresentar ainda origem antiga e serem isolados filogeneticamente (geralmente como grupo irmãos de linhagens megadiversas). As linhagens que possuem estas características são conhecidas como "depauperons" e explicar como elas persistem através do tempo ainda é um desafio. Dentre as plantas, a família Melastomataceae apresenta linhagens com ampla diversidade (como a tribo Miconieae com quase 2000 espécies) e também contém exemplos de depauperons como é o caso das tribos Eriocnemeae, Lithobieae e o clado *Rupestrea* (com 7, 1 e 2 espécies, respectivamente). Essas três linhagens são restritas ao leste do Brasil, com poucas coletas e ausência de informações sobre aspectos biológicos; além disso, os processos que determinam sua diversidade e distribuição restrita atual, não foram estudados até o momento. Por esta razão, estruturamos essa dissertação em um capítulo único integrando diferentes abordagens relacionadas à capacidade de dispersão, modelos de distribuição de espécies (SDMs) para diferentes períodos (passado, presente e futuro) e compilação de dados de história natural para descobrir se esses depauperons em Melastomataceae compartilham padrões comuns entre si, além de apontarmos preocupações sobre a conservação dessas linhagens. A capacidade de dispersão estimada foi ainda integrada com modelos de distribuição previstos de cenários futuros para avaliar deslocamentos e/ou retrações em áreas adequadas. Por fim, comparamos as tolerâncias climáticas dos depauperons com suas tribos irmãs megadiversas através de envelopes climáticos. Em geral, nossos resultados indicam capacidade de dispersão limitada, dependência da água para dispersão (exceto para Lithobieae), e nicho restrito como características comuns para todas as nove espécies em Eriocnemeae, Lithobieae e *Rupestrea*. Nossas análises também apontam que os ciclos glaciais ocorridos durante o Quaternário não afetaram amplamente os grupos. Além disso, verificamos que o espaço de nicho climático dos depauperons é limitado e totalmente incluído dentro do espaço de nicho de suas tribos irmãs. Coletivamente, nossos resultados sugerem que os níveis de ameaça nesses grupos até 2050 serão elevados, principalmente considerando a incapacidade de dispersão a longas distâncias, nichos restritos e aumento contínuo na fragmentação de habitats.

Palavras-chave: depauperons; dispersão; hidrocoria; Melastomataceae; SDMs.

ABSTRACT

Species diversity is evidently not distributed evenly in through space, time, or among taxonomic groups. This is a topic that arouses curiosity and drives many studies in areas such as biogeography, evolutionary biology, ecology, and others. While some lineages are very rich and diverse, and have been identified with high rates of diversification (balance between speciation and extinction), others show opposite patterns. These latter clades can still have ancient origins and be phylogenetically isolated (usually as sister lineages of megadiverse groups). Lineages with these characteristics are known as "depauperons" and explaining how they persist through time is still a challenge. Among the plants, the family Melastomataceae presents lineages with ample diversity (such as the tribe Miconieae with almost 2000 species) and also contains examples of depauperons as is the case of the tribes Eriocnemeae, Lithobieae and the *Rupestrea* clade (with 7, 1 and 2 species, respectively). These three lineages are restricted to eastern Brazil, with few collections and lack of information on biological aspects; moreover, the processes that determine their diversity and current restricted distribution have not been studied so far. For this reason, we structured this dissertation in a single chapter integrating different approaches related to dispersal ability, species distribution models (SDMs) for different periods (past, present and future) and compilation of natural history data to find out if these depauperons in Melastomataceae share common patterns among themselves, as well as pointing out conservation concerns on these lineages. The estimated dispersal ability was further integrated with predicted distribution models of future scenarios to assess shifts and/or retractions in suitable areas. Finally, we compared the climatic tolerances of depauperons with their megadiverse sister tribes via climate envelopes. Overall, our results indicate limited dispersal ability, dependence on water for dispersal (except for Lithobieae), and restricted niche as common features for all nine species in Eriocnemeae, Lithobieae, and *Rupestrea*. Our analyses also suggest that glacial cycles that occurred during the Quaternary did not largely affect the groups. Furthermore, we find that the climatic niche space of the depauperons is limited and fully included within the niche space of their sister tribes. Collectively, our results suggest that threat levels in these groups by 2050 will be high, especially considering the inability to disperse over long distances, restricted niches, and continued increase in habitat fragmentation.

Keywords: depauperons; dispersal; hydrochory; Melastomataceae; SDMs.

Sumário

1. Introdução Geral	9
2. Capítulo 1: Limited dispersal ability and restricted niche characterize “depauperons” in Melastomataceae / Capacidade de dispersão limitada e nicho restrito caracterizam “depauperons” em Melastomataceae	13
2.1 Introduction	16
2.2 Methods	18
2.2.1 Study group	18
2.2.2 Dispersal distance	20
2.2.3 Species occurrences dataset.....	21
2.2.4 Climatic data.....	21
2.2.5 Species distribution models (SDMs)	22
2.2.6 Past refuges and future scenarios	23
2.2.7 Climatic envelopes	24
2.3 Results	24
2.3.1 Dispersal distance	24
2.3.2 Current potential distribution.....	25
2.3.3 Past refuges and future distributions	25
2.3.4 Climatic envelopes	27
2.4 Discussion.....	27
2.4.1 Limited dispersal capacity	27
2.4.2 Potential distribution under climate change	29
2.4.3 Overlapping climatic tolerances	32
2.5 Conclusions	33
2.6 References	34
2.7 Tables	41
2.8 Figures	44
2.9 Supplementary material.....	49
3. Conclusão Geral	53
4. Referências	54

1. Introdução Geral

As espécies não são igualmente distribuídas no espaço, no tempo e entre grupos taxonômicos (Scotland & Sanderson, 2004; Mittelbach et al., 2007; Wiens, 2011). Esse é um dos temas centrais em diferentes áreas do conhecimento como a biogeografia, biologia evolutiva, ecologia, entre outras (Wiens & Donoghue, 2004; Wen et al., 2013). Os estudos produzidos nas últimas décadas que estimam taxas de diversificação ampliaram nosso conhecimento a respeito dos padrões assimétricos na riqueza entre linhagens, porém, os processos que causam esses padrões distintos ainda são difíceis de se explicar (Scholl & Wiens, 2016; Magallón et al., 2019). Dentre as plantas, o grande grupo das angiospermas com aproximadamente 300.000 spp. descritas (Christenhusz & Byng, 2016) e cerca de 350.000 spp. estimadas (Plant List, 2017), contém linhagens com grande riqueza e altas taxas de diversificação (por exemplo, Asterales, Lamiales, Solanales). Por outro lado, outros grupos incluem poucos representantes e baixas taxas de diversificação (por exemplo, Amborellales, Ceratophyllales, Chloranthales; Magallón & Castillo, 2009). Esses últimos grupos com baixa taxas de diversificação, pobres em espécies, isolados filogeneticamente (geralmente como grupos irmãos de linhagens megadiversas) são conhecidos como “depauperons” (Donoghue & Sanderson, 2015). Devido à baixa diversidade esses grupos acabam recebendo relativamente menos atenção dos pesquisadores (Dick & Pennington, 2019).

O surgimento e a perda de espécies em um clado, assim como seus padrões de distribuição espacial são relacionados diretamente aos processos de especiação, extinção e dispersão (Wiens, 2011; Scholl & Wiens, 2016). No caso das plantas, o evento de dispersão é uma etapa fundamental na vida desses organismos, permitindo que os descendentes se afastem da planta-mãe e se estabeleçam em novos locais (Thomson et al., 2010). A distância de dispersão é geralmente atrelada a uma síndrome de dispersão e ocorre através de vetores específicos (animais, vento, água, entre outros; van der Pijl, 1982; Vittoz & Engler, 2007). O processo de dispersão pode afetar a probabilidade de extinção, o isolamento geográfico e em última análise, a dinâmica populacional (Willis et al., 2014). Compreender a capacidade de movimentação dos indivíduos é fundamental para prever respostas das populações às perturbações dos ecossistemas e às mudanças climáticas (Robledo-Arnuncio et al., 2014). Nesse sentido, associar modelos de distribuição de espécies (SDMs) com a capacidade de dispersão pode ser uma saída para medidas de conservação e manejo de populações em risco (Vittoz & Engler, 2007; Di Musciano et al., 2020).

Os SDMs são ferramentas comumente usadas para prever locais adequados às espécies associando registros de ocorrência e variáveis ambientais (Soberón & Nakamura, 2009). Os SDMs são considerados modelos correlativos (Peterson et al., 2015; Sales et al., 2021) e utilizam métodos estatísticos para estimar a adequação de habitat ou probabilidade de ocorrência de uma linhagem no espaço geográfico, usualmente representada através dos mapas de adequabilidade (Sillero et al., 2021). As estimativas desses modelos geralmente são subconjuntos do nicho fundamental conhecidos como “nicho realizado” (Hutchinson, 1957; Colwell & Rangel, 2009) ou “nicho potencial” (Jackson & Overpeck, 2000; Soberón & Peterson, 2005), e, frequentemente, estão envolvidos em questões biogeográficas, dinâmica de distribuição populacional e aspectos históricos (Sillero et al., 2021). Esta abordagem metodológica vem sendo usada para uma série de outros fins, entre eles: estimar invasões biológicas (Qin et al., 2015), prever impactos das mudanças climáticas e possíveis perdas das áreas adequadas (Trisurat et al., 2011; Fois et al., 2016), além de identificar áreas para conservação incluindo espécies raras e endêmicas (Dagnino et al., 2020). No entanto, esses modelos raramente incorporam a capacidade de dispersão das espécies e, portanto, podem acabar subestimando os níveis de ameaça e riscos de extinção (Vittoz & Engler, 2007). Assim, em um mundo de mudanças climáticas aceleradas, os cenários futuros para grupos com distribuição restrita podem ser ainda piores do que as estimativas atuais (Bitencourt et al., 2016; Zhang et al., 2017). Na verdade, as áreas acessíveis a dispersão das espécies (ou “M” do diagrama de BAM, Soberón & Peterson, 2005) podem ser estimadas de várias formas, por exemplo, através de regiões biogeográficas (Barve et al., 2011).

Os SDMs também têm sido associados às abordagens históricas (Nyari & Reddy., 2013) e, com isso, podem ser aplicados para reconhecer padrões de distribuição ao longo do tempo, por meio da identificação de áreas de refúgios nas quais muitas linhagens persistiram durante mudanças climáticas passadas, resultando em alto endemismo (Moritz & Agudo, 2013; Keppel et al., 2018). Os refúgios podem ser entendidos como locais que fornecem proteção espacial e/ou temporal para as linhagens contra diferentes distúrbios (Keppel et al., 2018). Historicamente os refúgios foram descritos como extensões geográficas limitadas que abrigaram e favoreceram a sobrevivência de diversos organismos durante e após as glaciações ocorridas no período quaternário (Haffer, 1969; Bennett & Provan, 2008). Na região neotropical, especialmente para os biomas da Mata Atlântica e Cerrado (incluindo os campos rupestres) já foram estimados refúgios para alguns grupos endêmicos (Carnaval & Moritz, 2008; Bonatelli et al., 2014; Barres et al., 2019; e outros). Esses refúgios relacionados a

contrações e expansões vegetacionais parecem ter influenciado a distribuição de linhagens endêmicas dessas regiões (por exemplo, Ramos et al., 2007; Thode et al., 2014), incluindo possivelmente alguns depauperons que também ocorrem nessas áreas (Fiaschi & Pirani, 2009; Vasconcelos et al., 2020). O leste brasileiro (composto pela Mata Atlântica, Cerrado e Caatinga) é conhecido por possuir uma extraordinária diversidade de espécies e altos níveis de endemismo, principalmente de plantas (Werneck et al., 2011; Morellato & Silveira, 2018; Reginato & Michelangeli, 2020). A Mata Atlântica e o Cerrado são dois dos principais hotspots de biodiversidade do mundo e atualmente encontram-se ameaçados por conta da perda e fragmentação de habitats causados pela ocupação humana e uso desordenado dos recursos naturais (Myers et al., 2000; Mittermeier et al., 2011).

Entre as famílias de angiospermas com maior riqueza de espécies no leste do Brasil, bem como na região neotropical, Melastomataceae tem um total de 5.700 espécies distribuídas principalmente em regiões tropicais e subtropicais ao redor do mundo (Michelangeli et al., 2020). Suas espécies são comuns nas savanas e florestas tropicais (Renner, 1993; Reginato et al., 2020) e especificamente no leste do Brasil, tem cerca de 554 espécies na Mata Atlântica e 513 no Cerrado (Goldenberg et al., 2020). Mais da metade das espécies de Melastomataceae pertencem a poucas linhagens megadiversas e amplamente distribuídas, tais como as tribos Miconieae (ca. 1900 spp., todas neotropicais; Michelangeli et al., 2019) Sonerileae (ca. 1020 spp.; pantropical; Liu et al. no prelo), e Melastomeae (ca. 870 spp., pantropical; Michelangeli et al., 2013; Veranso-Libalah et al., 2017). Por outro lado, algumas linhagens têm poucas espécies conhecidas com amostragem reduzida e pouco conhecidas no que diz respeito à história natural, ecologia e biologia em geral. É o caso das tribos Eriocnemeae, Lithobieae (Penneys et al., 2020) e do clado *Rupestrea* (Goldenberg et al., 2015). Estas linhagens são conhecidas apenas do leste do Brasil, e além de sua baixa riqueza, suas espécies também têm distribuições restritas. Além disso, todas elas estão filogenicamente posicionadas como grupos irmãos de uma das linhagens megadiversas em Melastomataceae (Goldenberg et al., 2015; Penneys et al., 2020; Reginato et al., 2020). Como estas características são semelhantes às descritas acima para outros depauperons em angiospermas (Donoghue & Sanderson, 2015), decidimos adotar este termo aqui para nos referirmos a estas três linhagens. Assim, Melastomataceae, com linhagens com ampla assimetria na riqueza de espécies, é um grupo interessante para explorar a diversificação baseada em características únicas, tais como nichos climáticos, capacidade de dispersão e dados relacionadas a história natural.

Neste estudo, nos focamos em realizar a modelagem de nicho climático e estimar a capacidade de dispersão de três depauperons em Melastomataceae do leste do Brasil. Produzimos modelos de distribuição de espécies (SDMs) para avaliar cenários climáticos passados, atuais e futuros, a fim de verificar possíveis refúgios (no passado), mas também avaliar possíveis perdas e/ou mudanças nas áreas climáticas adequadas (no futuro). Além disso, combinamos a capacidade de dispersão estimada para as linhagens com modelos dos cenários futuros, a fim de comparar o efeito da dispersão sobre a previsão de áreas adequadas preditas pelos SDMs. Finalmente, com o objetivo de verificar se existem ou não particularidades nas tolerâncias climáticas atuais desses depauperons, compilamos dados de distribuição para suas tribos irmãs megadiversas para comparar os envelopes climáticos aos pares. Resumidamente, tentamos responder as seguintes perguntas: (1) Qual a capacidade de dispersão dessas linhagens? (2) Qual foi a influência das oscilações climáticas durante o Quaternário na distribuição atualmente restrita desses grupos? (3) Como a capacidade de dispersão afeta as áreas adequadas nas previsões futuras para os depauperons? (4) Existem diferenças nas tolerâncias climáticas entre os depauperons e seus grupos irmãos? Estruturamos esta dissertação em um único capítulo apresentado em forma de artigo científico e formatado conforme as normas do periódico: *Perspectives in Plant Ecology, Evolution and Systematics (PPEES)* - ISSN: 1433-8319.

2. Capítulo 1

**LIMITED DISPERSAL ABILITY AND RESTRICTED NICHE CHARACTERIZE
“DEPAUPERONS” IN MELASTOMATACEAE**

**CAPACIDADE LIMITADA DE DISPERSÃO E NICHOS RESTRITOS CARACTERIZAM
“DEPAUPERONS” EM MELASTOMATACEAE**

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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 the genus *Rupestrea* 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 current diversity and distribution have not been previously studied. Here we address these by integrating different approaches related to 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 species distribution models (SDMs) in different time-periods (past, present and future). Dispersal ability was integrated 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 dispersion (except for Lithobieae), and restricted niche as common characteristics for all species in Eriocnemeae, Lithobieae and *Rupestrea*. Our analyses also show that the climatic niche space of the depauperons is 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 conservation actions prioritize these unique taxa in Melastomataceae, especially if a phylogenetic diversity perspective is taken into account.

Keywords: depauperons; dispersal; hydrochory; Melastomataceae; SDMs.

2.1 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 beside highly diverse groups (Sauquet & Magallón, 2018). These lineages that show low rates of diversification have been explained 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 & Sanderson, 2015). Other hypotheses are that these small clades may be the result of decline past megadiversity or are recovering from a drastic populational reduction (Magallón et al., 2019). Depauperons are common across the tree of life. In angiosperms for example include Amborellaceae (*Amborella trichopoda* Baill.), which is sister to the ~300,000 remaining angiosperm species; *Acorus* L. (2-6 spp.) is sister to the monocots (~60,000 spp.); *Ceratophyllum* L. (2 spp.), and is sister to the eudicots (~200,000 spp.; Donoghue & Sanderson, 2015; Magallón et al., 2019). Understanding the persistency of these relictual lineages is still a puzzle to be solved. 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 & 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 & 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 & 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

& 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 & 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 & Reddy, 2013). For instance, they can aid to uncover distribution patterns over time, through the identification of refuge areas (Moritz & Agudo, 2013; Keppel et al., 2018). Refuges 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 (Haffer, 1969; Bennett & 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 Neotropics including the Atlantic Forest and Cerrado biomes (especially *campos rupestres*) refugia have already been estimated for some endemic groups (Carnaval & Mortiz, 2008; Bonatelli et al., 2014; Barres et al., 2019). These refugia related to vegetational contractions and expansions have influenced the distribution of endemics 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 a total of 5700 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). 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., 2020). 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. 1020 spp; pantropical; Liu et al. in press), and Melastomateae (ca. 870 spp., pantropical; Michelangeli et al., 2013; Veranso-Libalah et al., 2017). On the other hand, some lineages have few known species with scattered sampling, and

are poorly known regarding natural history, ecology and biology in general. This is the case of the tribes Eriocnemeae, Lithobieae (Penneys et al., 2020) and the clade *Rupestrea* (Goldenberg et al., 2015). These lineages are known only from eastern Brazil, and apart from their low richness, their species also have restricted distributions. In addition, all of them are phylogenetically positioned as sister groups of one of the 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 & Sanderson, 2015), we decided to adopt this term here to refer to these lineages. Thus, Melastomataceae, with its contrasting sister lineages with disparate richness, is an interesting group to explore diversification based on unique characteristics, such as climatic niches and dispersal ability, and related natural history data.

In this study, we focused on modeling the climatic niche of three depauperate 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 compare climate envelopes pairwise. In summary, we tried 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?

2.2 Methods

2.2.1 Study group

The lineages selected here belong to two tribes and one clade with no formal taxonomic tribal positioning, totaling four genera with nine species of 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 clade *Rupestrea* has a single genus with two species (Goldenberg et al., 2015).

All these lineages are endemic to Minas Gerais and Bahia states in eastern Brazil, and occur within the limits of two distinct biomes, 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 - 3m), ranging from lithophytic herbs (*Eriocnema acaulis* and *Lithobium cordatum*), rhizomatous subshrubs (*Physeterostemon aonae*, *P. jardimii* and *P. thomasi*) to small shrubs (*P. fiaschii*, *P. gomesii*, *Rupestrea carvalhoana* and *R. johnwurdackiana*, Goldenberg & Amorim, 2006; Amorim et al., 2009; Amorim et al., 2014; Goldenberg et al., 2015; Goldenberg et al., 2016; Penneys et al., 2020). Their flowers show a similar pattern, with no conspicuous specializations: they are all medium-sized, 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 yellow, small-pored anthers (Andrade et al. 2007; 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 (Delinger et al. 2018), and somewhat contrasting with specialized features in larger lineages, such as the bigger flowers with strongly 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 (Delinger 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 are visited by 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 >2mm 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 dispersion by raindrops (Andrade et al., 2007). 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 inflorescence branches, 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 & Morellato, 2002). There is no published information on *Lithobium*'s seed dispersal, 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., in prep.). 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., in prep.). The *Rupestrea* clade 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., in prep.) 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+Henrietteae (~245 spp.; Penneys et al., in prep.) or to Blakeeae (~200 spp.; Maurin et al., 2021).

2.2.2 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), 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 & 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 dispersion of most species was by wind (without special adaptations in the seeds) except for *Eriocnema acaulis* (which may present ballistic dispersion, Andrade et al. 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).

2.2.3 Species occurrences dataset

Occurrence data were compiled from herbarium records available on SpeciesLink (<https://specieslink.net>) and GBIF (<http://gbif.org>) biodiversity databases. 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 and duplicated coordinates; (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 determined to species level.

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), *Phyesterosstemon aonae* (6), *P. fiaschii* (12), *P. gomesii* (7), *P. jardimii* (11), *P. thomasii* (2), *Lithobium cordatum* (19), *Rupestrea johnwurdackiana* (40) e *R. carvalhoana* (6). The other filtered points belong mainly to Miconieae (87,852 records), Melastomateae (28,945), Henrietteae (6,041), Blakeae (5,932), Rhexieae (3,695), and others.

2.2.4 Climatic data

The 19 bioclimatic variables used to generate the species distribution models were taken from WorldClim (<https://www.worldclim.org>) for current (1970-2000) and future (2050) scenarios. Bioclimatic variables from PaleoClim (<http://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 - IGM (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. al., 2017; Fordham et al., 2018; Brown & Carnaval, 2019). Descriptions for all bioclimatic variables used can be found in Table S1.

2.2.5 Species distribution models (SDMs)

In order to estimate the potential distributions of depauperons we used the R package 'ENMTML' to generate, evaluate and design species distribution models (SDMs). 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-

Marssin 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 & 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 (Jiménez-Valverde et al., 2011), we performed a principal component analysis (PCA) to reduce the number of original environmental variables to a smaller set of principal components (PCs). We used the first 5 PCs that captured >95% of the total variance (De Marco & Nóbrega, 2018; Table S2). In the processing stage, we used five different algorithms: Generalized Additive Models (GAM; Hastie & Tibshirani, 1986), Generalized Linear Models (GLM; McCullagh & Nelder, 1989), MaxEnt with default setting (MXD; Phillips et al., 2006), Random Forests (RDF; Breiman, 2001) and Support Vector Machine (SVM; Karatzoglou et al., 2004). In post-processing, we performed an ensemble modeling (EM) approach based on the weighted average of the predictions for each algorithm (Araújo & 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, 2017). Final maps were generated in QGIS v.3.10.13 (<https://qgis.org>). The steps described above are summarized in Fig. 3.

2.2.6 Past refuges and future scenarios

Suitable areas (in km²) 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 refuges) we gathered the maps resulting from the different projections (HLC, LGM, IGM and MIS19) into a consensus map (i.e., summation 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 associate one more scenario to combine dispersal ability with SDMs. This scenario refers to the estimated possibility of maximum dispersion 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 observation), 50 dispersion events were considered for all lineages.

2.2.7 Climatic envelopes

To compare climatic tolerances between the depauperons and their megadiverse sister tribes, we used climatic envelope profiles. 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' 3.4-10 (Hijmans, 2021). The extracted climatic values were summarized using Principal Component Analysis (PCA) with the R package 'ade4' (Dray & Dufour, 2007), while plots were generated using the R package 'factoextra 1.0.7' (Kassambara & Mundt, 2017). Pairwise comparisons were performed based on the tribal relationships described in section 2.1. In this way, we made comparisons between Eriocnemeae vs. Miconieae (sister tribes according to both Penneys et al., in prep. and Maurin et al., 2021), Lithobieae vs. Astronieae+Henrietteae and between *Rupestrea* vs. Rhexieae (according to Penneys et al., in prep.). Given the phylogenetic uncertainty, comparisons of Lithobieae vs. Blakeeae and *Rupestrea* vs. Melastomateae were also performed (sister tribes according to Maurin et al., 2021).

2.3 Results

2.3.1 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, $F = 28.23$, $df = 11.22$, $P < 0.001$).

2.3.2 Current potential distribution

Our dataset ranged from 2 to 40 records per species totaling 137 records for the 9 taxa. As explained above, the small number of records for some species of *Physeterostemon* and *Rupestrea* lead 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. 4: B, E, H and K) show suitable areas close to the real points 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 4). In general, TSS values per individual algorithm were also high (predominantly above 0.5), indicating acceptable to excellent models (Table 4). In the current scenario, the potential distribution area by lineage was, respectively, *Eriocnema* = 58211 km², *Physeterostemon* = 9186 km², *Lithobium* = 18796 km² and *Rupestrea* = 6144 km² (Table 5).

The potential distribution of all lineages under current climatic conditions includes known areas of occurrence, as well as nearby locations with similar phytophysionomies. 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; climatic suitable areas are on the border between the Atlantic Forest and Cerrado biomes, 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.

2.3.3 Past refuges and future distributions

The SDMs under current conditions were projected for the different periods in the past (HLC, LGM, IGM, MIS19) and future (2050), and the potentially suitable areas were compared. The extent of coverage areas (in km²) and the projections indicated in the projected maps for each lineage in each estimated past period are described in the Supplementary Material (Table S3 and Fig. S1). The regions predicted for depauperons in past periods indicated larger

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 (IGM ~130ka). Already between the IGM 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 IGM periods, a significant increase in the IGM 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* = 41793Km², *Physeterostemon* = 14865Km², *Lithobium* = 38032Km² and *Rupestrea* = 9531Km². Beyond the oscillations identified over the different periods (areas 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 refuges) in the near of the current occurrence of the groups (Fig. 3: A, D, G and J). 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 S3). 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 potentially suitable areas for the depauperons when compared to the current scenario (Fig. 4: C, F, I and L). These areas were 26010 km² (*Eriocnema*), 5150 km² (*Physeterostemon*), 15757 km² (*Lithobium*) and 1943Km² (*Rupestrea*). The proportional loss of potentially suitable areas in the future, when compared to the current conditions (Table 5), were 55.31% (*Eriocnema*), 43.93% (*Physeterostemon*), 17.13% (*Lithobium*) and 7.01% (*Rupestrea*). Taking into account the maximum dispersal distance (MDD) scenario, it is possible to notice an even greater decrease in potentially suitable areas for those lineages (Table 5). In this scenario, the coverage areas for the groups were 2,666 km² (*Eriocnema*), 3,593 km² (*Physeterostemon*), 0,149 km² (*Lithobium*) and (15,880 km²) *Rupestra*. In this case, the proportion of accessible areas ranged from approximately 96 to 99% when 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.

2.3.4 Climatic envelopes

The first PCA comparing climate tolerances between tribes Eriocnemeae and Miconieae (Fig. 5A) had 83.07% 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 tribes Lithobieae and Astronieae+Henrietteae (Fig. 5B) 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 the clade *Rupestrea* and tribe Rhexieae (Fig. 5C) 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, and between *Rupestrea* and Melastomateae can be found in the supplementary material (Fig. S2A, S2B). The complete overlap of climatic envelopes of the depauperons and their sister tribes is evident, except for tribe Lithobieae, with only a partial (Fig. S2A) or no overlap in relation to its sister lineages (Fig. 5B).

2.4 Discussion

2.4.1 Limited dispersal capacity

The dispersal distances estimated by different algorithms (Tamme et al., 2014) predict reduced dispersal capacity for all depauperons, since none of the nine species in Eriocnemeae, Lithobieae and *Rupestrea* showed potential ability to disperse their seeds beyond 10 meters. Most angiosperms disperse their seeds between 10-1500m from the parent plant (Corlett & Westcott, 2013) with few cases above that (Vittoz & Engler, 2007) and with distances seldom greater than 100m for most dispersal modes, including water and wind (Thomson et al., 2011). Information on dispersal through falling raindrops is scarce, but the distances are shorter or

close to 1m (Vittoz & Engler, 2007). The idea of phylommatry in plants contemplates intrinsic and extrinsic factors related to limited dispersal, such as the morphological characteristics of the diaspores themselves and the local environmental conditions, respectively. 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, 2021). 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, short statured species are more likely to be phyllomatric than taller species (Cheplick, 2021). The nine species studied here are herbs or small shrubs and disperse their seeds/fruits at heights <1m. On the other hand, there are lineages in their sister tribes ranging from lianas and epiphytic shrubs in Blakeeae (Penneys & Judd, 2011) to large trees >20m in Astronieae (Mancera et al., 2017). Dispersal capacity can be estimated by other characteristics, for example, the speed at seed fall (Tamme et al., 2014), but we don't have this information for the depauperons; fieldwork on dispersal distance would improve the predictions in these groups (Di Musciano et al., 2020).

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). Although 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 all dry fruits, some of the groups treated here show a wide range of specialized features related to dispersal, such as those related to hydrochory.

Different fruits with similar dispersal mechanisms may come from different morphological backgrounds, 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., 2019). Water dispersal in herbaceous melastomes have been detailed

for species in Bertoloniaeae, and this has been also invoked to explain patterns of diversity and endemism in this group (Bacci et al., 2019). The mechanism involved in seed dispersal in this lineage is related to the triangular shape of their fruits (“squirt-corner seed dispersal”, Pizo & 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., 2019), 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 Bertoloniaeae 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 dispersion (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 & 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.

2.4.2 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), 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. 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 Bertoloniaeae (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 & 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 &

Peterson, 2005). This niche dimension is also known as “potential niche” or “existing fundamental niche” (Peterson et al., 2012), and lineages may not occur in these areas due to several factors, including physical barriers, habitat loss, intrinsic physiological limitations, and limited dispersion (Rabosky & Hurlbert, 2015; Wiens, 2011b). 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 different time periods, with expansions for the taxa from *campos rupestres* between the Last Interglacial (IGM) 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 refuges 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* (Carnaval & Moritz, 2008; D'Horta et al., 2011; Bonatelli et al., 2014; Barbosa et al., 2015; Barres et al., 2019), as well as in other 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 (*campo rupestres* and Atlantic Forest) instead of the species themselves. During Pleistocene glaciations, the northern part of the Atlantic Forest did not undergo major vegetational changes (Carnaval & Mortiz, 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 refuges 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 organisms in the same

period of time, including plants (Velazco et al., 2019; Evangelista-Alves et al., 2021; Wan et al., 2021) and animals (Pietro-Torres et al., 2020; Gonçalves et al., 2021). For rare species, future scenarios may be even worse (Ledig et al., 2010; Vincent et al., 2020; Di Musciano 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 state. For the Atlantic Forest, estimates of area loss can be even more severe (about 88%) and the remaining vegetation may range from approximately 11% to 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 & Prevedello, 2019; Lourenço-de-Moraes et al., 2019; De Lima et al., 2019).

Dispersal capacity plays a key role in reliable future predictions of plant species distribution (Di Musciano et al., 2020). Overlapping the estimates of maximum dispersion 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 & 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 & Venn, 2017). We consider the inclusion of future geological and pedological data can complement our findings and improve our understanding of the edaphic endemism behind each group (Corlett & Tomlison, 2019).

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 (Wiens et al., 2010; Crisp & Cook, 2012) 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 & 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; Luzuriaga et al., 2018).

2.4.3 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 making 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., 2018; Slatyer et al., 2013; Vincent et al., 2020). In fact, some species in the sister tribes, e.g., *Miconia albicans*, *Miconia calvescens*, *Clidemia hirta*, among others, are widely distributed (Murphy et al., 2008; Le et al., 2018; Paz et al., 2021) 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 (Whittaker, 1972; Clarke & Gaston, 2006). 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 & 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. Since most depauperons seem to rely on water to disperse their seeds, the effects of precipitation at smaller scales should be further investigated. Other factors must be taken into account in order to explain diversity reduction in the family, for example, ecological (pollination, competition, predation, etc...), morphological (growth form), physiological (stress tolerance), genetic (polyploidy and drift) factors, among others events (Wisz et al., 2013; Wiens, 2017). In addition to the influence of climate predictors, the supposed higher rate of extinction in lineages with abiotic dispersal (Reginato et al., 2020), associated with the other factors discussed above (limited dispersion

capacity and restricted niche) may help to explain, at least in part, the existence of these species-poor lineages today.

2.5 Conclusions

Our findings indicate that the depauperons potential niche is reduced (in restricted geographic ranges) and possibly conserved over time for at least 700k years. 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 can further enhance the threat levels of these taxa in the face of rapid global climate change. Other studies that manage to incorporate physiological traits for these lineages may improve our predictions about their potential distribution limits and also test whether these taxa are preadapted and whether they will survive the sharp temperature increase in the coming decades. 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). Expanding the number of accurate occurrence records with field collections would also help improve the quality of the data available in databases. As a result, biased patterns, such as model over-prediction, may be minimized through increasingly accurate predictions.

Depauperons are ancient, species-poor, phylogenetically isolated lineages that, to date, are treated as survivors (or relict taxa) from previous 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. On the other hand, we suggest that the limited dispersal ability and the restricted niche are common to these depauperons, and may be important to explain the low diversity in these groups. The same factors may also reflect the richness asymmetry among other lineages in Melastomataceae, such as other species-poor and phylogenetically isolated groups that occur outside eastern Brazil, including tribe Cyphostyleae, and the genera *Loricalepis*, *Ochtephilus*, *Dinophora*, *Feliciadamia*, among others. These other depauperons would open space for new studies that can further expand our knowledge about diversity in Melastomataceae. 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. We believe that the suitability maps prepared here can guide choices of potential areas for reintroduction of species and identification of populations at risk.

Author contributions

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 Bochorhy:** Conceptualization, Investigation, Validation, Writing - review & editing.

Declaration of Competing Interest

No conflict of interest.

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2.7 Tables

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

Tribes/clade	Species	Phytophysiology	Habitat	Altitude	References
Eriocnemeae	<i>Eriocnema acaulis</i> (Chamisso) Triana.	Semideciduous seasonal forest	Shaded areas on rock walls along stream banks	730 - 1348m	Andrade et al., 2007; Penneys et al., 2020
Eriocnemeae	<i>Physeterostemon aonae</i> Amorim, Michelangeli & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	800-1275 m	Goldenberg et al., 2016
Eriocnemeae	<i>Physeterostemon fiaschii</i> Goldenberg & Amorim.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	444-520 m	Goldenberg & Amorim, 2006
Eriocnemeae	<i>Physeterostemon gomesii</i> Amorim & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shaded areas in moist forests	250 - 450 m	Amorim et al., 2014
Eriocnemeae	<i>Physeterostemon jardimii</i> Goldenberg & Amorim.	Ombrophilous forest / "mata higrófila"	Shaded places along rivers or streams	850 - 1050 m	Goldenberg & Amorim, 2006
Eriocnemeae	<i>Physeterostemon thomasii</i> Amorim, Michelangeli & Goldenberg.	Ombrophilous forest / "mata higrófila"	Shady places on the riverbanks	40 - 100 m	Amorim et al., 2009

Lithobieae	<i>Lithobium cordatum</i> Bongard.	<i>Campos rupestres</i>	Fissures, ledges and cavities in rock outcrops	554 m	Penneys et al., 2020
<i>Rupestrea</i>	<i>Rupestrea carvalhoana</i> (Baumgratz & Souza) Almeda, Michelangeli & Goldenberg.	<i>Campos rupestres</i>	Seasonally dry grasslands	850–1080 m	Goldenberg et al., 2015
<i>Rupestrea</i>	<i>Rupestrea johnwurdackiana</i> (Baumgratz & Souza) Michelangeli, Almeda & Goldenberg.	<i>Campos rupestres</i>	Seasonally dry grasslands	850–1200 m	Goldenberg et al., 2015

Table 2. Values of dispersal characters for the investigated species. Growth form (GF), dispersal syndrome (DS), seed release height (RH).

Species	GF	Fruits	Seeds	DS	Height (m)	RH (m)
<i>Eriocnema acaulis</i>	herb	dehiscent	ovoid	abiotic	0.05	0.05
<i>Physeterostemon aonae</i>	subshrub	dehiscent	not seen	abiotic	0.12 - 0.20	0.16
<i>Physeterostemon fiaschii</i>	shrub	dehiscent	cuneate	abiotic	0.40 - 1	0.7
<i>Physeterostemon gomesii</i>	shrub	dehiscent	cuneate	abiotic	0.40 - 1.40	0.9
<i>Physeterostemon jardimii</i>	subshrub	dehiscent	cuneate	abiotic	0.20 - 0.40	0.3
<i>Physeterostemon thomasii</i>	subshrub	dehiscent	cuneate	abiotic	0.15 - 0.25	0.2
<i>Lithobium cordatum</i>	herb	dehiscent	ovoid	abiotic	0.03 - 0.07	0.05
<i>Rupestrea carvalhoana</i>	shrub	indehiscent	elliptic	abiotic	2	1
<i>Rupestrea johnwurdackiana</i>	shrub	indehiscent	elliptic	abiotic	0.50 - 3	1.5

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 growth form, dispersal syndrome and seed release height. Model 5 only considers the growth form and the dispersal syndrome.

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

Table 4. Values of True Skill Statistic (TSS) obtained for each lineage modeled by different algorithms. In parentheses, standard deviation (SD) values. MXD = Maxent; RDF = Random Forest; SVM = Support Vector Machine; GAM = Generalized Additive Models; GLM = Generalized Linear Models; ENS = Ensemble.

Lineage	MXD	SVM	RDF	GAM	GLM	ENS
<i>Eriocnema</i>	0.864 (0.077)	0.302 (0.257)	0.716 (0.305)	0.571 (0.528)	0.247 (0.350)	0.802 (0.011)

<i>Physeterostemon</i>	0.973 (0.021)	0.577 (0.585)	0.986 (0.007)	0.980 (0.021)	0.495 (0.700)	0.985 (0.009)
<i>Lithobium</i>	0.944 (0.027)	0.972 (0.010)	0.828 (0.143)	0.882 (0.130)	0.295 (0.417)	0.931 (0.027)
<i>Rupestrea</i>	0.992 (0.011)	0.997 (0.003)	0.977 (0.010)	0.994 (0.001)	0.984 (0.015)	0.997 (0.003)

Table 5. Suitable areas (km²) estimated by the niche models in different scenarios, under current conditions, future projections (2050) and the maximum dispersal distance (MDD) scenario, based on number of occurrence records (total and filtered), and TSS values (with standard deviation - SD) of the set models.

Lineage	Records			Current	Future	Fut/Cur (%)	MDD
	Total	Unique	TSS (SD)				
<i>Eriocnema</i>	183	23	0.802 (0.011)	58211	26010	-55.31	2.666
<i>Physeterostemon</i>	251	37	0.985 (0.009)	9186	5150	-43.93	3.593
<i>Lithobium</i>	95	19	0.931 (0.027)	18796	15757	-17.13	0.149
<i>Rupestrea</i>	169	40	0.997 (0.003)	6144	1943	-7.01	15.880

Table 6. Loadings of Principal Component Analysis (PCA) of the first 3 components (PC1, PC2 and PC3) for the comparisons of climatic envelopes between the depauperons and their sister tribes. The highest values in each component are in bold, and values less than 0.1 have been removed.

Climate Variables	Eriocnemeae x Miconieae			Lithobieae x Astronieae + Henrietteae			<i>Rupestrea</i> x Rhexieae		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
bio1	0.845	0.523	-	-	0.186	-	0.283	0.198	-
bio2	-	0.262	-	0.106	0.156	-	-	0.214	-
bio3	0.551	-	0.504	-	-	0.255	0.288	-	0.151
bio4	-	0.258	-	-	0.186	-	-	-	-
bio5	0.702	0.674	-	-	0.275	-	-	0.303	-
bio6	0.925	0.282	0.232	-	-	0.199	0.311	-	-
bio7	-	0.398	-	0.125	0.260	-	-	-	-
bio8	0.751	0.600	-	-	0.200	-	0.157	0.286	-
bio9	0.898	0.399	0.150	-	0.146	-	0.239	-	-
bio10	0.767	0.601	-	-	0.210	-	-	0.282	-
bio11	0.891	0.415	0.142	-	0.152	0.116	0.307	0.128	-
bio12	0.824	-	-	-	-	-	0.266	-	-
bio13	0.750	-	-	-	-	-	0.286	-	-
bio14	0.653	-	-	-	-	-	-	-	-
bio15	-	0.567	-	-	0.311	-	0.182	0.303	0.307
bio16	0.768	-	-	-	-	-	0.288	-	-
bio17	0.681	-	-	-	-	-	-	-	-
bio18	0.325	-	-	-	-	-	0.183	-	-

bio19	0.779	-	-	-	-	-	0.198	-	-
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2.8 Figures

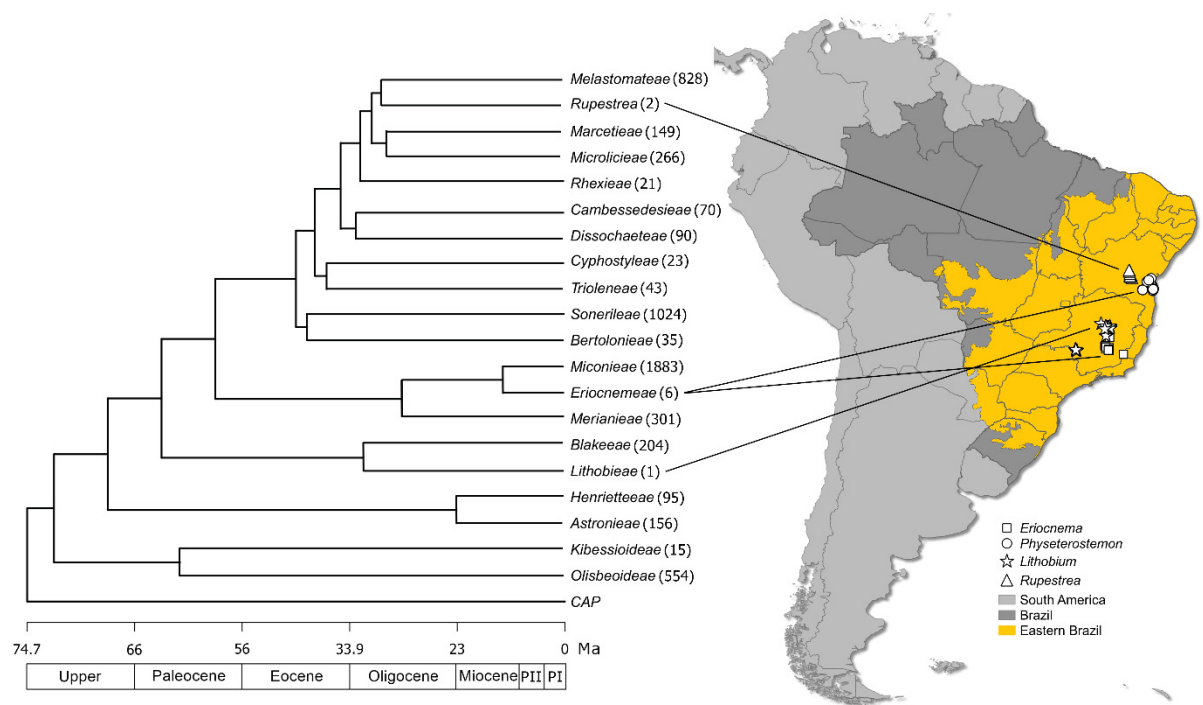
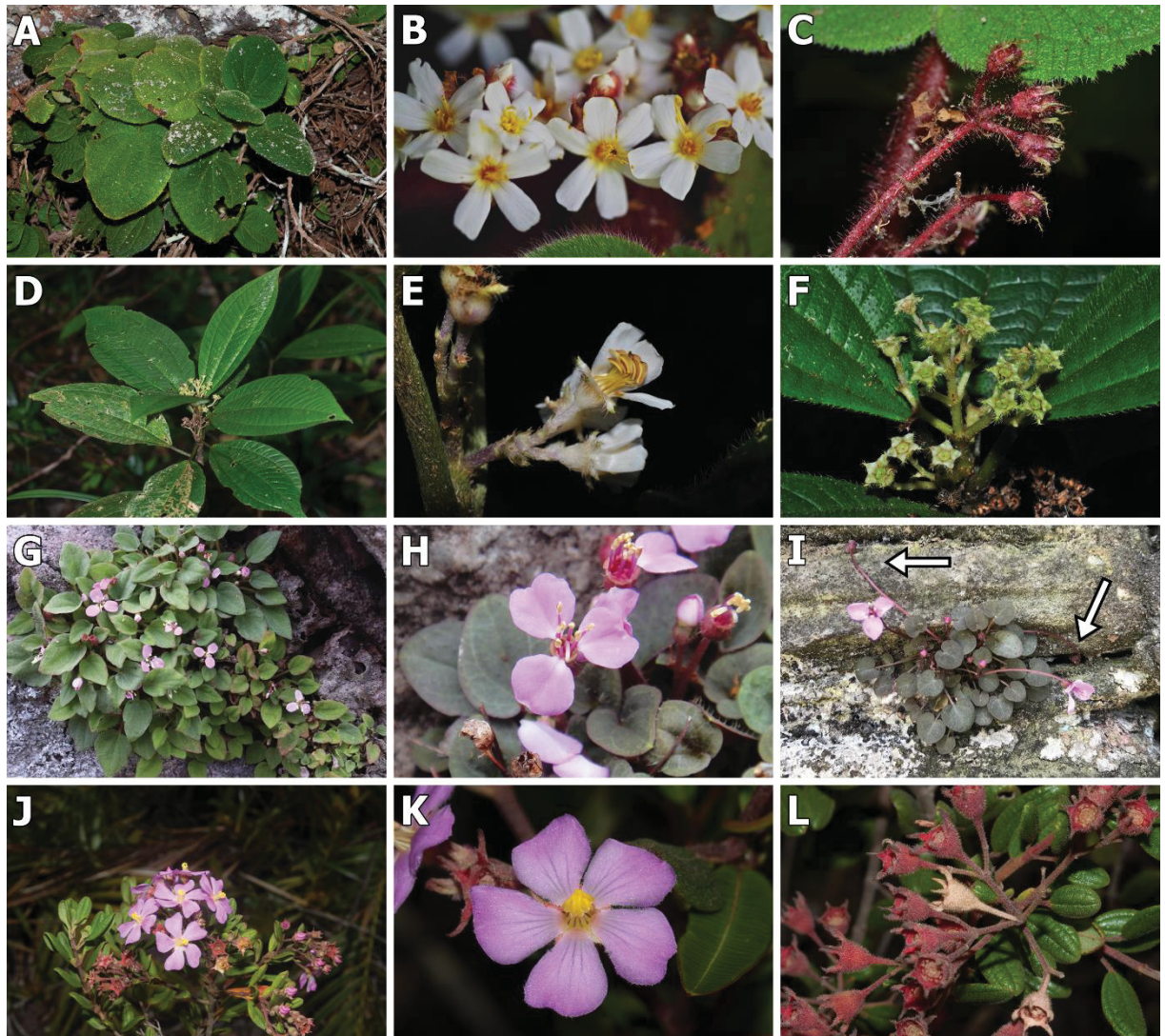
Figure 1. *Eriocnema*, *Physeterostemon*, *Lithobium* and *Rupestrea*. Habit, flowers and fruits (left to right column, respectively). *Eriocnema acaulis* (A-C), *Physeterostemon gomesii* (D-F). *Lithobium cordatum* (G-I). *Rupestrea johnwurdackiana* (J-L). In I, the white arrows indicate the extension of the pedicel with fruits directed towards the crevices in the rocks. 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).

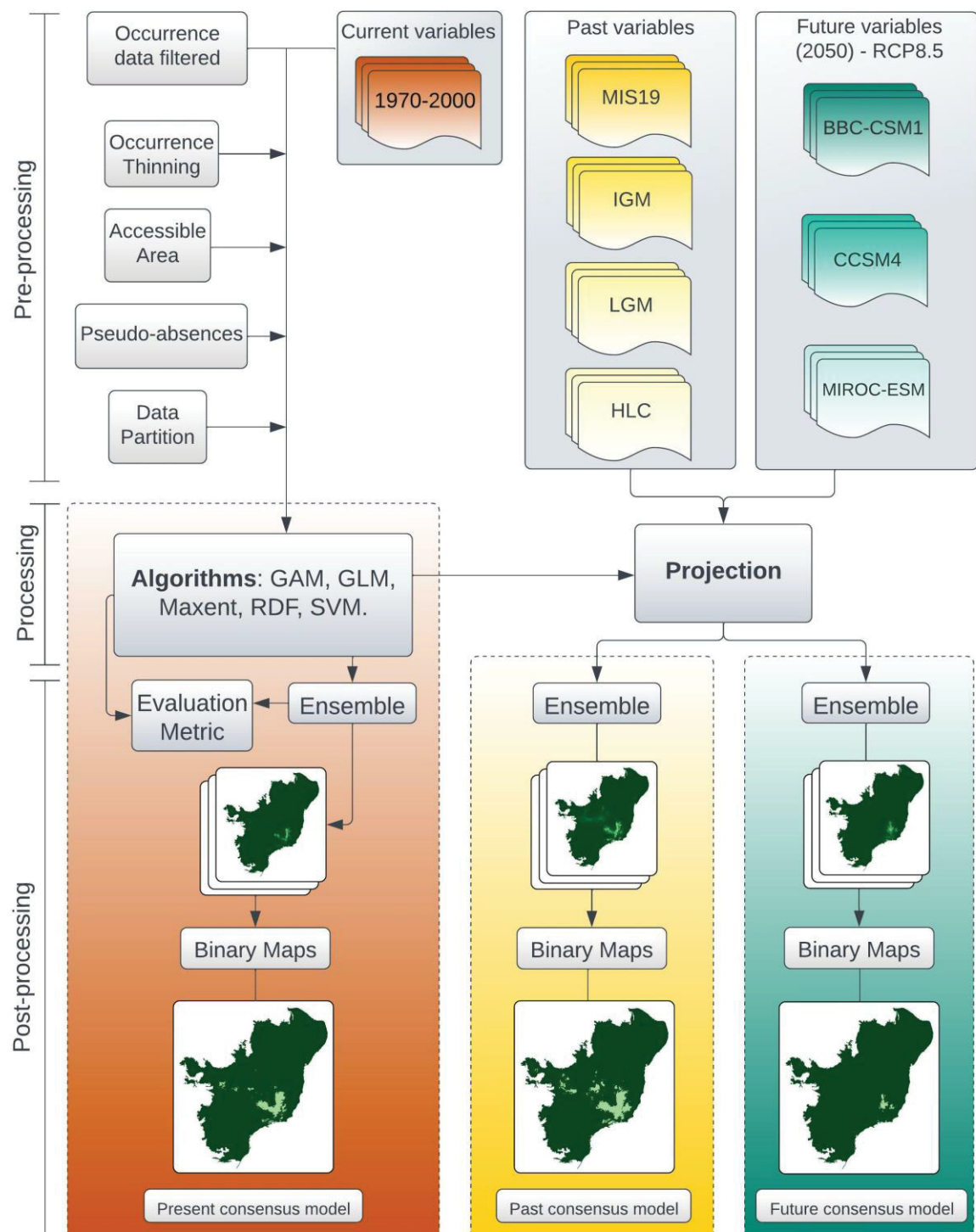
Figure 2. Distribution of depauperons in eastern Brazil. Eriocnemeae - *Eriocnema* (squares) and *Physeterostemon* (circles), Lithobieae - *Lithobium cordatum* (stars) and *Rupestrea* (triangles). Dated phylogeny of Melastomataceae modified from Reginato et al. (2020) and based on the phylogenetic relationships of the concatenated tree using RAXML in Maurin et al. (2021). Geological scale: PI - Pleistocene and PII - Pliocene.

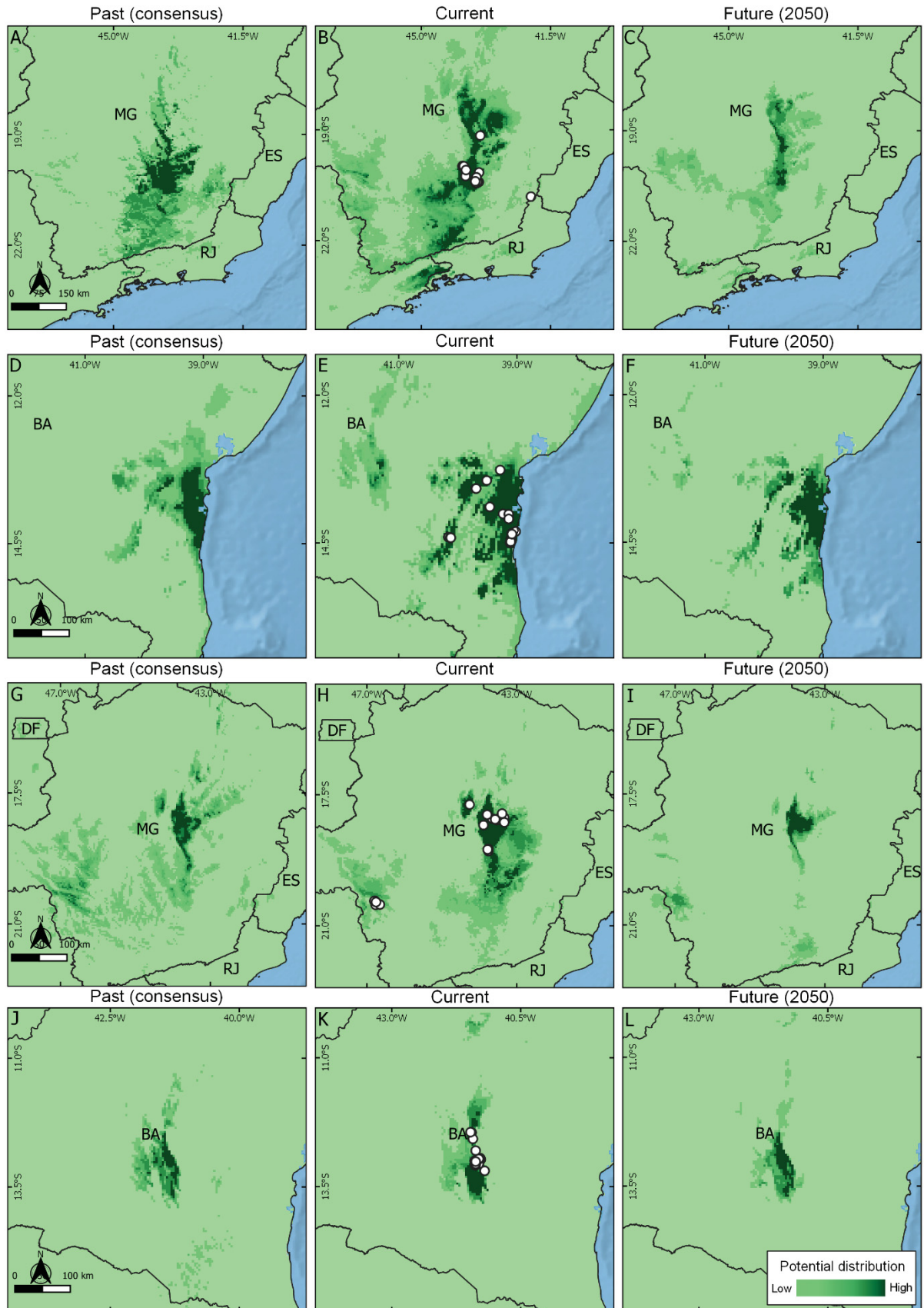
Figure 3. Flow diagram summarizing the structure implemented to produce the species distribution models for depauperons under current (red), past (yellow) and future (blue) conditions.

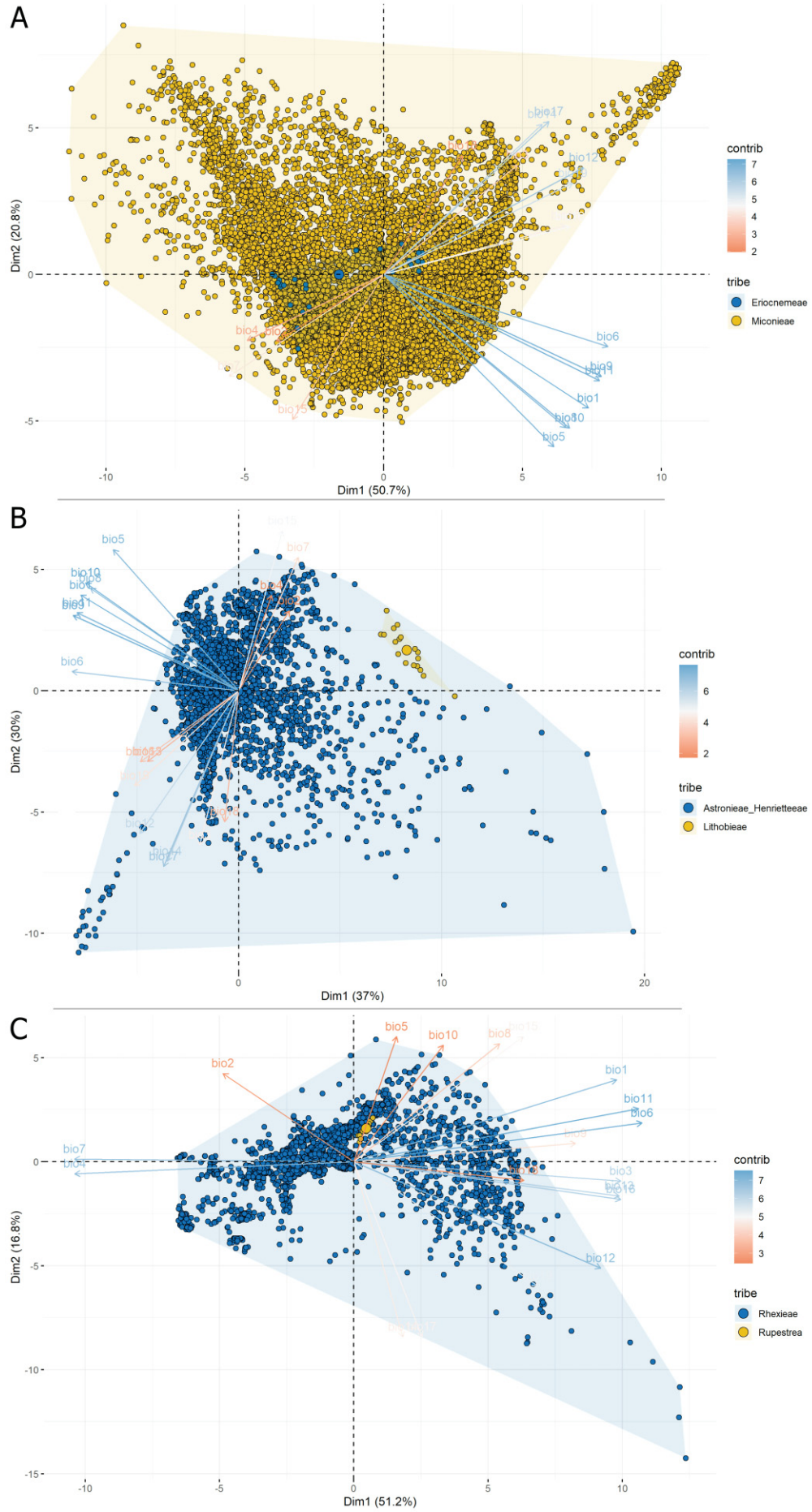
Figure 4. Potential distribution obtained from ensemble models for the depauperons in different scenarios under current conditions (central column) and past (left column) and future (right column) projections. The maps for the lineages are *Eriocnema* (A-C), *Physeterostemon* (D-F), *Lithobium* (G-I) and *Rupestrea* (J-L), respectively. Dark green regions indicate climatically suitable regions and light green regions indicate unsuitable areas. The white circles indicate occurrence locations. MG - Minas Gerais state and BA - Bahia state.

Figure 5. Comparison of the climatic envelopes between tribes Eriocnemeae and Miconieae (A), between tribes Lithobieae and Astronieae+Henrietteae (B) and between *Rupestrea* and Rhexieae (C). The climate spaces marked by the “convex hulls” are based on the first two components of the PCA analysis with all 19 WorldClim current bioclimatic variables. The contribution of each variable is proportional to the size of the arrows and their colors (the larger and closer to blue, the greater their contribution).









2.9 Supplementary material

Table S1. WorldClim bioclimatic variables used in the construction of species distribution models and in the comparisons of climatic envelopes.

Variables (abbreviation)	Description	Units
bio1	Annual Mean Temperature	°C
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C
bio3	Isothermality (BIO2/BIO7) (×100)	°C
bio4	Temperature Seasonality (standard deviation ×100)	%
bio5	Max Temperature of Warmest Month	°C
bio6	Min Temperature of Coldest Month	°C
bio7	Temperature Annual Range (BIO5-BIO6)	°C
bio8	Mean Temperature of Wettest Quarter	°C
bio9	Mean Temperature of Driest Quarter	°C
bio10	Mean Temperature of Warmest Quarter	°C
bio11	Mean Temperature of Coldest Quarter	°C
bio12	Annual Precipitation	mm
bio13	Precipitation of Wettest Month	mm
bio14	Precipitation of Driest Month	mm
bio15	Precipitation Seasonality (Coefficient of Variation)	-
bio16	Precipitation of Wettest Quarter	mm
bio17	Precipitation of Driest Quarter	mm
bio18	Precipitation of Warmest Quarter	mm
bio19	Precipitation of Coldest Quarter	mm

Table S2. Variance and cumulative variance resulting from principal component analysis with WorldClim climate data for the study area. The first five components shown captured >95% of the total variance.

Principal Components	Variance explained for each PC	Cumulative variance explained
1	52.29	52.29
2	19.37	71.66
3	10.90	82.56
4	08.86	91.42
5	03.67	95.10

Table S3. Suitable areas (Km²) in the different periods projected to the past. Marine Isotope Stage 19 - MIS19 (787ka), Last Interglacial - IGM (130ka), Last Glacial Maximum – IGM (21ka), Late Holocene - HLC (4ka), mean and consensus of projections.

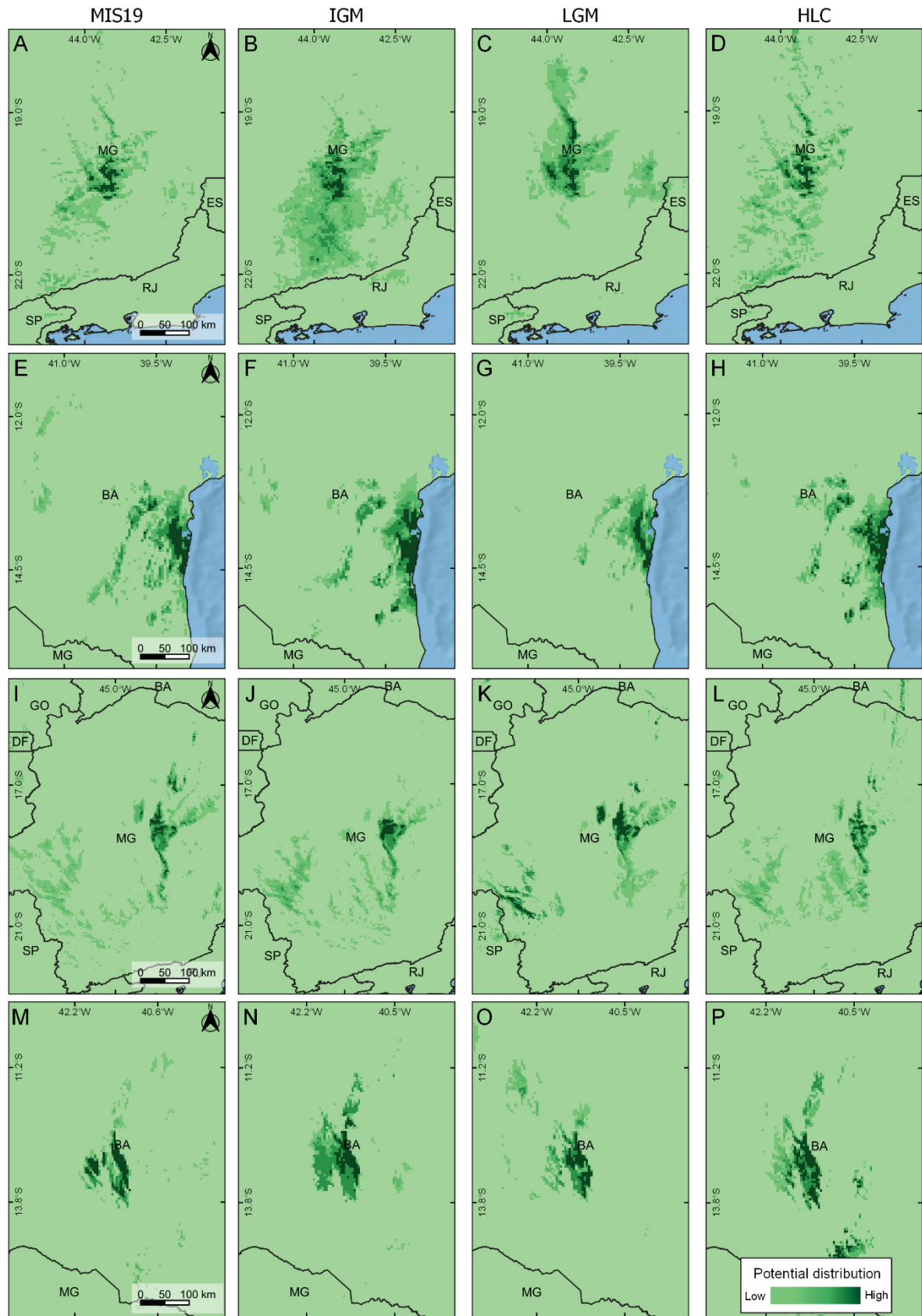
Group	MIS19	IGM	LGM	HLC	PASSADO (CONSENSO)
<i>Eriocinema</i>	44131	53203	26251	43589	11989
<i>Lithobium</i>	33716	30184	58065	30163	10726
<i>Physeterostemon</i>	12988	21205	7577	17692	6268
<i>Rupestrea</i>	5995	3314	14920	13895	2480

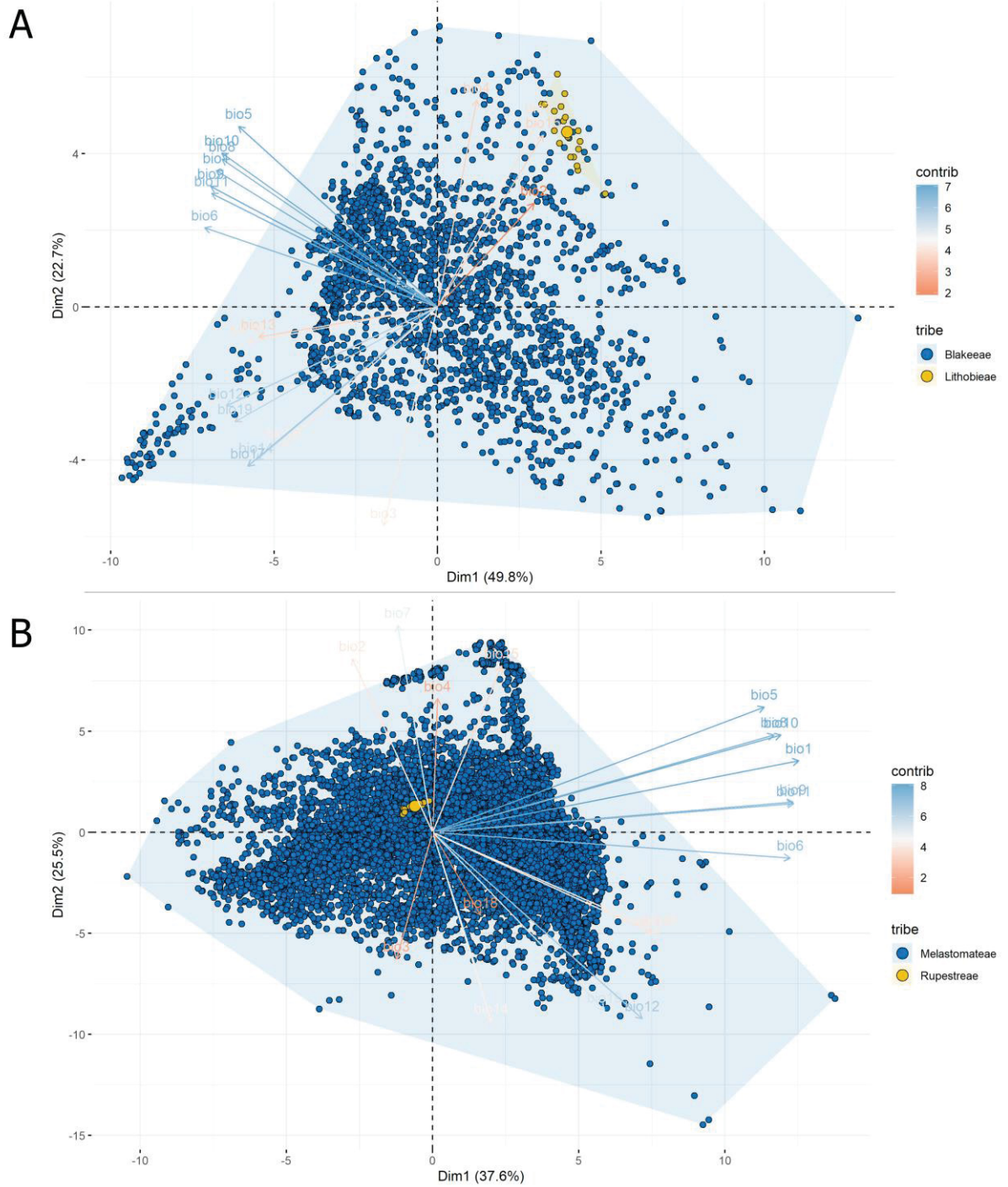
Table S4. Loadings of Principal Component Analysis (PCA) of the first 3 components (PC1, PC2 and PC3) for the comparisons of climatic envelopes between the depauperons and their sister tribes. The highest values in each component are in bold and values less than 0.1 have been removed.

Climate Variables	Lithobieae x Blakeeae			Rupestrea x Melastomateae		
	PC1	PC2	PC3	PC1	PC2	PC3
bio1	-	0,218	0,136	-	-	-
bio2	0,122	0,166	-	0,077	-	-
bio3	-	-	0,329	0,035	0,215	-
bio4	0,049	0,331	-	-	-	0,489
bio5	-	0,289	0,072	-	-	0,054
bio6	-	0,126	0,189	-	0,043	-
bio7	0,128	0,298	-	0,033	-	0,307
bio8	-	0,236	0,121	-	-	0,093
bio9	-	0,193	0,143	-	-	-
bio10	-	0,246	0,101	-	-	0,087
bio11	-	0,181	0,177	-	-	-
bio12	-	-	-	-	0,316	0,149
bio13	-	-	-	-	0,171	0,084
bio14	-	-	-	-	0,321	0,264
bio15	0,133	0,275	-	-	-	-
bio16	-	-	-	-	0,170	0,098
bio17	-	-	-	-	0,340	0,244
bio18	-	-	-	-	0,140	0,375
bio19	-	-	-	-	0,302	-

Figure S1. Potential distribution for depauperons in four Pleistocene (Quaternary) periods. From left to right column, respectively: Marine Isotope Stage 19 - MIS19 (ca. 787 ka), Last Interglacial - IGM (ca. 130ka), Last Glacial Maximum - LGM (ca. 21ka) and Late Holocene - HLC (ca. 4.2-0.3ka). *Eriocnema* (A-D), *Physeterostemon* (E-H), *Lithobium* (I-L) and *Rupestrea* (M-P). Regions in dark green indicate climatically suitable regions (high potential) and regions in light green indicate unsuitable areas (low potential).

Figure S2. Comparisons of climatic envelopes between tribes Lithobieae and Blakeeae (A), and between *Rupestrea* and tribe Melastomateae (B). The climate spaces marked by the “convex hulls” are based on the first two components of the PCA analysis with all 19 current bioclimatic variables from WorldClim. The contributions of each variable is proportional to the size of the arrows and their colors (the larger and closer to blue, the greater their contribution).





3. Conclusão Geral

A partir das lacunas de conhecimento levantadas, as abordagens utilizadas e os dados produzidos aqui, respondemos as principais questões que nortearam nosso estudo. Em primeiro lugar, demonstramos por meio de estimativas de dispersão para todos os nove táxons pertencentes aos clados Eriocnemeae, Lithobieae e *Rupestrea* que a dispersão das sementes se dá a curtas distâncias em poucos metros da planta-mãe via hidrocoria (na maioria dos casos). Em segundo lugar, nossas previsões dos SDMs em diferentes períodos apontam áreas potencialmente adequadas próximas das ocorrências conhecidas tanto nas condições atuais quanto sob condições climáticas passadas e futuras. Através das projeções consenso para o passado verificamos áreas climaticamente estáveis para as linhagens durante o Pleistoceno, sugerindo que os efeitos dos ciclos glaciais que, ocorreram durante o Quaternário, não impactaram amplamente os grupos, embora tenham influenciado a distribuição. Em terceiro lugar, as projeções futuras preveem perdas expressivas de áreas para todos os grupos até 2050 e quando associadas as distâncias de dispersão estimadas (cenário MDD), perdas ainda maiores foram verificadas. Por fim, quando comparados com suas tribos irmãs, os depauperons não mostraram tolerâncias climáticas distintas na maior parte dos casos, mas as variáveis relacionadas a temperatura predizem grande parte da variação encontrada entre os grupos, provavelmente refletindo ao gradiente latitudinal em grande escala, por sua vez, influenciado por linhagens com ampla distribuição. Em conjunto esses achados indicam que o nicho potencial é reduzido em alcances geográficos restritos e possivelmente são conservados ao longo do tempo. Dadas as semelhanças encontradas entre as linhagens através das diferentes abordagens aplicadas aqui, é pouco provável que a dispersão em cada um dos depauperons atinja longas distâncias, essencialmente devido à capacidade limitada de dispersão e as restrições de nicho. Acreditamos que essas características associadas à constante fragmentação de habitat podem potencializar ainda mais os níveis de ameaça desses táxons frente as rápidas mudanças climáticas globais, principalmente levando em conta cenários mais severos com altas emissões de carbono. Além disso, estamos cientes dos aspectos metodológicos que podem melhorar a previsibilidade em nossos modelos, principalmente em relação a amostragem, resolução dos layers ambientais, inclusão de outros preditores, entre outros. Em nosso caso seria essencial ampliar o número de registros de ocorrências com coletas em campo (principalmente com coordenadas geográficas precisas e confiáveis) para melhorar a qualidade dos dados disponíveis em bancos de dados online. Dessa forma, problemas críticos na modelagem como padrões tendenciosos (incluindo a superprevisão dos modelos) podem ser minimizados.

Os depauperons, como conhecidos na literatura, são linhagens antigas, pobres em espécies e isoladas filogeneticamente e que, até o momento, são tratados como sobreviventes (ou táxons relictuais) de eventos subsequentes de extinções de grupos que no passado podem ter sido diversos. Nossos achados com base nos grupos avaliados aqui concordam parcialmente com essas ideias; na verdade, devido à limitação no registro fóssil, não podemos afirmar se a diversidade dos depauperons foi maior no passado. Entretanto, sugerimos que a capacidade de dispersão limitada e o nicho restrito são características comuns aos grupos e podem ter determinado a baixa diversidade até o momento. Além disso, esses fatores podem refletir (pelo menos em partes) na assimetria de riqueza entre os demais grupos em Melastomataceae. Esse é o primeiro estudo que se propôs a estimar a capacidade de dispersão na família utilizando os modelos e métodos detalhados aqui. Existem outras linhagens de Melastomataceae pobres em espécies e isoladas filogeneticamente que ocorrem fora da região leste do Brasil, como é o caso de linhagens em Cyphostyleae, Sonerileae, além de *Lorica lepis*, *Ochtephilus*, *Dinophora*, *Feliciadamia*, entre outras. Essas linhagens abrem espaço a novos estudos que possam ampliar ainda mais nosso conhecimento sobre a diversidade dessa família. Entendemos que essas linhagens podem carregar informações genéticas importantes em Melastomataceae, e, portanto, devem ser priorizadas em ações de conservação. Finalmente, enfatizamos que estimar as distribuições de linhagens com baixa amostragem e falta de informações sobre sua biologia se mostra um desafio especialmente difícil tanto para modelagem quanto para questões da conservação.

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