HERVAL VIEIRA PINTO JUNIOR

PADRÕES DE DIVERSIDADE, MODELOS DE NICHO ECOLÓGICO E ISOLAMENTO BIOGEOGRÁFICO EM INSELBERGS NEOTROPICAIS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientadora: Andreza Viana Neri

VIÇOSA - MINAS GERAIS
2021

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T
P659p
2021

Pinto Junior, Herval Vieira, 1987-
Padrões de diversidade, modelos de nicho ecológico e isolamento biogeográfico em inselbergs neotropicais / Herval Vieira Pinto Junior. – Viçosa, MG, 2021.
1 tese eletrônica (142 f.): il. (algumas color.).

Texto em inglês.
Orientador: Andreza Viana Neri.
Tese (doutorado) - Universidade Federal de Viçosa, Departamento de Biologia Vegetal, 2021.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2021.233
Modo de acesso: World Wide Web.

1. Afloramentos (Geologia). 2. Nicho (Ecologia). 3. Filogenia. 4. Biodiversidade. 5. Mudanças climáticas. 6. Ecossistemas - Conservação. 7. Ecologia das paisagens. 8. Ecologia vegetal. I. Neri, Andreza Viana, 1977-. II. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. III. Título.

CDD 22. ed. 581.753

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APROVADA: 20 de outubro de 2021.

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Herval Vieira Pinto Junior
Autor

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Orientadora

Para os entusiastas dos ecossistemas rupestres...

AGRADECIMENTOS

Aos Coordenadores, Professores e Funcionários do Programa de Pós-Graduação em Botânica, à Universidade Federal de Viçosa por ceder toda a estrutura para realização deste trabalho.

A Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de pós-graduação. Ao Neotropical Grassland Conservacy (NGC) pelo apoio financeiro para a realização dos trabalhos de campo.

Ao Professor Tillmann Buttschardt, Cornelia Steinhäuser e Jan Lehmann pelo apoio e experiência proporcionado em Münster. A todos os colegas do Institute of Landscape Ecology (ILÖK). Ao Deutscher Akademischer Austauschdienst (DAAD) pela bolsa fornecida como pesquisador visitante no Institute of Landscape Ecology (ILÖK) da University of Münster (WWU).

Ao Instituto Estadual de Meio Ambiente e Recursos Hídricos do Espírito Santo (IEMA) pela autorização de pesquisa nas Unidades de Conservação da APA Pedra do Elefante, Parque Estadual Forno Grande e Parque Estadual da Pedra Azul, aos funcionários das UC's pela atenção e gentileza em que éramos recebidos.

A todos os moradores que permitiram nossas coletas em suas propriedades, obrigado pela hospitalidade e alegria.

A minha orientadora Andreza Viana Neri, obrigado por ter aceitado e acreditado no meu projeto, muitíssimo obrigado pelo aprendizado, pela confiança e credibilidade depositada em mim.

Aos meus ex-orientadores e agora parceiros, Luis Fernando e Miriam Cristina pelo apoio logístico nas coletas no Espírito Santo, agradeço também pelas conversas e a motivação em continuar estudando os Inselbergs Capixabas.

A todos que ajudaram de certa forma nos trabalhos de campo, principalmente Larissa Müller, Fernanda Favoreto, Thais Sperandio e José Eduardo Falcon, a sua ajuda foi fundamental! Muito obrigado!

Ao queridíssimo Celso, sempre disposto a ajudar todos (e demais) do LEEP, e é claro sem deixar faltar café!

Aos colegas do Laboratório de Ecologia e Evolução de Plantas (LEEP) Larissa, Alex, Alice, Écio, Nayara Smith, Cecília, Wendelo, Neil, Miguel, Pedro, Gustavo, Fernando, Nayarinha, Evandro, Daniela, Flávia, Prímula, Clara, Rodrigo, Lhoraynne, Bruna, Elielson, Carlos, Maribel, Aloirta, Josi e Nathalia, agradeço pela recepção em Viçosa e pelos excelentes momentos de alegria.

A todos os colegas de pós-graduação, obrigado pela amizade e conhecimentos compartilhados.

Aos ex Pos-Docs do LEEP, Marcelo Bueno, Vanessa Pontara e Gustavo Heringer e ao atual Pedro Villa pela disposição em ajudar sempre que era preciso.

Aos Herbários VIC e SAMES pela disponibilidade e ajuda no tombamento do material botânico.

Aos colegas de república, José Eduardo, Lucas, Felipe, Larissa e Paula pelos momentos de alegria e descontração. Um agradecimento em especial aos eternos republicanos e amigos

Vinicius Taquetti, Ítalo Câmara e Marcos Vinícius que sempre me acolheram nas idas a Alegre. Sem deixar de esquecer a importantíssima acolhida pela família de Izabela Ribeiro e Fernanda Favoreto em São Mateus, sem vocês não teria terminado meus campos!

A todos os Botânicos que auxiliaram nas identificações das espécies.

A todos os meus amigos e familiares que mesmo distantes torciam por mim.

Aos meus irmãos Saulo e Lívia que me incentivaram a vencer mais uma vez esta etapa da minha vida.

A minha companheira Larissa Müller e sua família pela ajuda e incentivo em todos os momentos compartilhados. Obrigado pelas conversas motivadoras e confortantes. E principalmente aos meus pais Herval e Dirley pelo apoio fundamental e por sempre acreditarem no meu potencial.

E por fim, a todos que mesmo indiretamente ajudaram na realização deste trabalho. Deixo aqui o meu muito obrigado.

RESUMO

PINTO-JUNIOR, Herval Vieira, D.Sc., Universidade Federal de Viçosa, outubro de 2021. **Padrões de diversidade, modelos de nicho ecológico e isolamento biogeográfico em inselbergs neotropicais**. Orientadora: Andreza Viana Neri.

Os ecossistemas de inselbergs constituem afloramentos rochosos isolados de granito ou gnaisse, como ilhas de habitats terrestres, que emergem abruptamente dos ecossistemas circundantes, como savanas e florestas. Caracterizam-se por condições edáficas e microclimáticas extremas, como escassez de água e nutrientes, poucas alternativas para fixação de raízes, sementes e propágulos, além de exposição excessiva ao vento, luz e abrupta variação térmica diária. Tipicamente, paisagens antigas, climaticamente protegidas e inférteis (do inglês OCBILs) como os inselbergs, são hipotetizadas como ricas em número de espécies e endemismo, dispersão reduzida e elevado número de clones em muitas espécies, bem como extinção reduzida, marcado paleoendemismo, pequenas populações isoladas e adaptações a solos de baixa fertilidade. A combinação de todos esses atributos tem sido um desafio para a compreensão dos padrões nos estudos taxonômicos, ecológicos, climáticos e biogeográficos, de restauração e biologia da conservação. Apesar de sua importante biodiversidade, os inselbergs estão entre os ecossistemas mais negligenciados e ameaçados, o que aumenta a urgência de planos prioritários de conservação devido ao atual cenário de rápidas mudanças climáticas globais e de uso da terra. Assim, este estudo visa compreender os processos ecológicos relacionados à diversidade taxonômica, funcional e filogenética de espécies nos ecossistemas de inselberg, bem como avaliar os efeitos das mudanças climáticas por modelos de nicho ecológico e estimar os efeitos do isolamento geográfico na diversidade filogenética de plantas através de modelos de conectividade da paisagem, para gerar estudos que possam compreender os ecossistemas rupícolas associados aos inselbergs Neotropicais brasileiros e assim contribuir para a manutenção e conservação desses ecossistemas. Nossos resultados indicam diferenças na estrutura das comunidades de plantas e diversidade entre as escalas local e regional, revelando maior diversidade β-taxonômica e funcional impulsionada por um maior *turnover* taxonômico e funcional. Além disso, exibe estratégias funcionais conservadoras e altamente tolerantes ao estresse (CSR), mostrando o efeito do ambiente sobre as características funcionais. Revela ainda, perda extrema da adequabilidade, onde todos os cenários apresentaram contrações de áreas que podem atingir perdas de até 86,7% nos próximos 50 anos. Apresentamos ainda que um maior isolamento entre as áreas centrais dos inselbergs do nordeste e do sudeste reflete o

efeito conjunto do isolamento pela resistência e a filtragem ambiental. Este padrão pode criar comunidades mais isoladas, compostas por menor diversidade filogenética de espécies mais próximas e funcionalmente adaptadas às condições ambientais (solos empobrecidos e clima estável), suportando a teoria OCBIL. Portanto, os processos ecológicos que moldam a montagem das comunidades estão ligados ao efeito de escala, o padrão de diversidade β-taxonômica e funcional pode resultar de um forte processo de filtragem de nicho, enquanto a abordagem da relação ambiente-traço, estratégias funcionais e adequabilidade de habitat são impulsionados pela filtragem ambiental. Em uma escala de paisagem, o efeito do isolamento biogeográfico é adicionado à filtragem ambiental em ecossistemas de inselberg. Ressaltamos que as estratégias de conservação devem ser direcionadas à proteção de espécies endêmicas e/ou ameaçadas e à criação de áreas protegidas com foco na proteção principalmente de inselbergs isolados, bem como de grupos de cada uma das áreas núcleo. Por fim, a execução de ações mitigadoras por meio de estratégias eficazes de restauração que minimizem o efeito do isolamento entre as áreas centrais, e que levem em consideração a manutenção de diferentes linhagens filogenéticas e as evidentes especializações das espécies para os microhabitats dos inselbergs.

Palavras-chave: Afloramentos rochosos. Beta diversidade. Traços funcionais. Resistência da paisagem. Conectividade. Conservação da biodiversidade. Mata Atlântica. Caatinga.

ABSTRACT

PINTO-JUNIOR, Herval Vieira, D.Sc., Universidade Federal de Viçosa, October, 2021. **Diversity patterns, ecological niche models and biogeographic isolation in Neotropical inselbergs**. Adviser: Andreza Viana Neri.

The inselbergs ecosystem constitutes isolated rocky granite or gneiss outcrops, as terrestrial habitats islands, that emerge abruptly from their surrounding ecosystems, such as savannah and forests. They are characterized by extreme edaphic and microclimatic conditions, such as the scarcity of water and nutrients in the soil, few alternatives for fixing roots, seeds, and propagules, in addition to excessive exposure to wind, light, and abrupt daily thermal variation. Typically, old, climatically buffered, infertile landscapes (OCBILs) as inselbergs are hypothesized to be rich in species and endemics, low dispersability, and high clonality in many plants, as well as reduced extinction, marked palaeoendemism, small isolated populations, and adaptations to low-fertility soils. The combination of all these attributes has been a challenge for the understanding of patterns of taxonomic, ecological, climate, and biogeographical, restoration and conservation biology studies. Despite its importance in biodiversity, inselbergs are one of the more neglected and threatened ecosystems, which raises the urgency for conservation priority plans due to the current fast global climate and land-use change scenario. Thus, this study aims to understand the ecological process related to taxonomic, functional, and phylogenetic diversity of species at inselberg ecosystems, as well as evaluate the effects of climate change by ecological niche models and estimate the effects of geographic isolation on the phylogenetic diversity of plants through landscape connectivity models, to generate studies that can understand the rupicolous ecosystems associated with Brazilian Neotropical inselbergs and thus contribute to the maintenance and conservation of these ecosystems. Our results indicating differences in plant community structure and diversity among local and regional scale reveal higher taxonomic and functional β-diversity driven by higher taxonomic and functional turnover component, exhibits highly stress-tolerant and conservative functional strategies (CSR) showing the effect of environment on functional traits, extreme loss of suitable area, where all scenarios showed range contraction that can achieve losses up to 86.7% in the next 50 years and greater isolation between the northeastern and southeastern inselbergs core areas reflecting the joint-effect of isolation by resistance and environmental filtering. This pattern can create more isolated communities, composed by less phylogenetic diversity of closer species and functionally adapted to environmental conditions (impoverished soils and

buffered climate), supporting the OCBIL theory. Therefore, the ecological process that shapes the community assembly is linked to the scale effect, the pattern of taxonomic and functional β-diversity could result from a strong niche filtering process, while environmental-trait approach, functional strategies, and habitat suitability are drives by environmental filtering. On a landscape scale, the effect of biogeographical isolation is added to environmental filtering in inselberg ecosystems. We highlighting that the conservation strategies should be directed towards the protection of endemic and/or threatened species and the creation of protected areas with a focus on protecting mainly isolated inselbergs, as well as groups from each of the core areas. Finally, the implementation of mitigating actions through effective restoration strategies that minimize the effect of isolation between the central areas, and that take into account the maintenance of different phylogenetic lineages and the evident specializations of species for microhabitats of inselbergs.

Keywords: Rock outcrop. Beta diversity. Functional traits. Landscape resistance. Connectivity. Biodiversity conservation. Atlantic Forest. Caatinga

SUMÁRIO

Introdução Geral

Grande parte da pesquisa em ecologia de comunidades refere-se aos padrões de diversidade de espécies e como esses padrões variam no tempo e no espaço (Rosenzweig, 1995). Além disso, é de fundamental importância entender como os múltiplos fatores determinantes para a diversidade de espécies agem e regulam esta diversidade, principalmente para a ecologia de comunidades e biogeografia de ilhas (MacArthur & Wilson, 1967; Leibold et al., 2004). Diversos impulsionadores (*drivers*) tem sido demonstrados como importantes para a riqueza de plantas em manchas de vegetações (*patch*) (Henneron et al., 2019), como os inselbergs, podendo existir efeitos e compensações (*tradeoffs*) entre estes *drivers*. Assim, estas informações podem ser utilizadas para estudar a organização das comunidades e para entender a perda acelerada de biodiversidade frente às mudanças antropogênicas ambientais (Ohlemüller et al., 2008). Portanto, o conhecimento da distribuição espacial da riqueza de espécies é de suma importância para priorizar esforços de conservação tanto em escala global como em escalas regionais e locais (Begon et al., 2007).

Inselbergs ou pães de açúcar são afloramentos rochosos isolados que surgem abruptamente acima das planícies que os cercam e são caracterizados por condições edáficas e microclimáticas extremas, tais como a escassez de água e nutrientes no solo, poucas alternativas para fixação de raízes, sementes e propágulos, além de excessiva exposição a ventos, luminosidade e brusca variação térmica diária (Porembski et al., 2000; 2007). Estas regiões montanhosas, estão comumente espalhados pelo mundo, ocorrendo em muitas regiões das Américas, África, Ásia e Austrália (Carlucci et al., 2014) formando importantes elementos paisagísticos que desempenham um papel na geração e manutenção da biodiversidade, além de fornecer serviços ecossistêmicos essenciais (Porembski et al., 2016).

Inselbergs *lato sensu* são encontrados em todo o leste do Brasil, desde o semiárido Nordestino até os altiplanos frios e nebulosos do Rio Grande do Sul (Safford & Martinelli, 2000). Embora esses afloramentos graníticos sejam parte familiar da paisagem de talvez 75% da população brasileira, são pouco estudados e as características florísticas, biogeográficas e ecológicas de sua flora são amplamente desconhecidas (de Paula et al., 2016; Pinto-Junior et al., 2020). Na região sudeste do Brasil, principalmente nos Estados do Rio de Janeiro, Espírito Santo e Minas Gerais, os inselbergs estão em regiões de maior expressão da variabilidade desta vegetação (Safford & Martinelli, 2000). A região estudada é coberta por três grandes domínios vegetacionais brasileiras, Floresta Atlântica, Cerrado e Caatinga. Este mosaico de vegetações, o qual os inselbergs estão inseridos é reflexo de uma herança biológica rica, de um clima dinâmico, onde a união entre fatores bióticos e físicos resultou nos inselbergs mais diversos e heterogêneos (Safford & Martinelli, 2000). Martinelli (2007) ainda indica áreas no sul do Espírito Santo como extremamente importantes para a conservação ambiental, onde faltam parcialmente ou totalmente informações biológicas, e por isso é indicada como ação prioritária, a realização de inventários florísticos.

Dois padrões ecológicos são amplamente reportados devido à diferença na composição de espécies entre áreas, (a) a substituição espacial de espécies (*turnover*) e (b) o aninhamento das assembleias (*nestedness*) (Baselga, 2010). A substituição espacial de espécies é um padrão apresentado por comunidades em que o processo de perda ou ganho de espécies se dá de maneira aleatória. Este padrão segue a teoria neutra, que propõe que a persistência no local está

associada à presença de nichos vagos, e a colonização relacionada à dificuldade de dispersão da espécie ou barreiras ecológicas (Qian et al., 2005).

O aninhamento é um padrão em que as comunidades que apresentam baixos valores de riqueza de espécie são um subconjunto das áreas mais ricas em espécies no que diz respeito à composição específica. Este é resultado de um processo de perda de espécies e está relacionado ao modelo determinístico que dita que os filtros ambientais vão selecionar as espécies com características que são favoráveis àqueles ambientes e, portanto, ambientes que se tornarem mais severos farão com que algumas espécies sejam perdidas (Almeida-Neto et al., 2008; Louzada et al., 2010). É importante salientar que uma comunidade pode ser gerida pelos dois processos, tanto pela perda sequencial quanto pela troca de espécies e estes processos variam entre diferentes grupos taxonômicos (Baselga, 2010; Louzada et al., 2010).

Outra forma de avaliar a diversidade é a diversidade funcional devido à sua relação com os processos ecossistêmicos (Petchey & Gaston, 2006). A diversidade funcional está ligada à diversidade filogenética devido ao conservantismo de algumas características em linhagens evolutivas (Baraloto et al., 2012). Dessa forma, a diversidade funcional tem como finalidade entender os padrões de dissimilaridade espacial na distribuição de caracteres ou traços (*traits*) dos indivíduos. Como não poderia deixar de ser, a diversidade funcional também pode ser relacionada às funções que cada espécie realiza no ecossistema (Swenson, 2011; Siefert et al., 2012). A relação entre a diversidade funcional e o ambiente é complexa e dependente do contexto. Diferentes traços funcionais podem demonstrar respostas individuais para diferentes gradientes, o que significa que mudanças importantes na diversidade podem ocorrer com mínima mudança na riqueza, podendo explicar variações no ecossistema (*e.g.* produtividade e resiliência) que a riqueza não pode (Cadotte et al., 2011; Mouillot et al., 2013).

Um dos objetivos da ecologia é identificar os mecanismos de montagem das comunidades vegetais e a coexistência de espécies (Tilman & Pacala, 1993; Hubbell, 2001; Webb et al., 2002). De maneira geral, espera-se que espécies proximamente relacionadas sejam mais similares quanto aos atributos ecológicos e condições semelhantes para o seu estabelecimento (Burns & Strauss, 2011). Assim, as afinidades filogenéticas entre as espécies de uma comunidade são o resultado de suas histórias evolutivas e de suas respostas ecológicas às condições ambientais atuais (Pillar & Duarte, 2010). Estas interações ecológicas, sejam bióticas ou abióticas, fazem com que muitas comunidades tenham padrões de parentesco evolutivo não aleatório, de modo que a filogenia seja crucial para o entendimento de como as comunidades são estruturadas (Cavender-Bares et al., 2009; Vamosi et al., 2009).

Dois processos diferentes baseados em nicho são geralmente considerados importantes na montagem das comunidades. A primeira é a exclusão competitiva, que deve impedir a coexistência de espécies cujos nichos se sobrepõem em grande grau (Tilman, 1982; Coomes & Grubb, 2000) e o segundo é a filtragem ambiental, que leva a um aumento na sobreposição de nicho de espécies coexistentes (Weiher & Keddy, 1995; Chase, 2003). Como os nichos tendem a ser conservados dentro de linhagens evolutivas (Harvey & Pagel, 1991; Blomberg et al., 2003), a análise da estrutura filogenética de uma comunidade deve nos ajudar a identificar os processos que organizam a comunidade. A exclusão competitiva, bem como as interações indiretas negativas entre parentes (*e.g.* herbívoros ou patógenos), tenderá a dar origem a um padrão de sobredispersão (*overdispersion*) filogenética, enquanto a filtragem ambiental

restringirá a coexistência com espécies que compartilham algumas características ecológicas, levando a um padrão de agrupamento (*clustering*) filogenético (Webb et al., 2002).

Tendo em vista que as mudanças climáticas podem se tornar um dos principais propulsores do declínio da biodiversidade (Bellard et al., 2012), afetando áreas já fortemente transformadas pelas atividades humanas, bem como ecossistemas naturais e semi-naturais. Os impactos das mudanças climáticas podem ser mascarados ou potencializados por outros impactos antropogênicos diretos e indiretos, como fragmentação da paisagem, conversão de habitats e invasões de espécies.

Os ecossistemas de montanha são provavelmente sensíveis ao aquecimento devido à redução progressiva da área com o aumento da elevação (Guisan et al., 1995; Theurillat et al., 1998; Díaz et al., 2003). Uma avaliação global recente dos impactos das mudanças climáticas nesses ecossistemas sugere que eles devem experimentar, durante o século XXI, taxas de aquecimento duas a três vezes maiores do que observado durante o século XX (Nogués-Bravo et al., 2007). Espera-se que essas rápidas mudanças na temperatura e em outros parâmetros climáticos nos ambientes com elevada altitude tenham fortes efeitos sobre as comunidades vegetais (Beniston et al., 1996; Guisan & Theurillat, 2000; Walther, 2003).

Visando a conservação das comunidades sobre inselberg, uma importante ferramenta que pode permitir avaliar os potenciais impactos das mudanças climáticas sobre a distribuição de espécies são os modelos de nicho ecológico (ou modelos de distribuição de espécies) (Bakkenes et al., 2002; Thomas et al., 2004; Thuiller et al., 2005). Esses modelos permitem relacionar estatisticamente a distribuição atual de uma ou mais espécies com múltiplas informações ambientais (Dormann, 2012) e, desta forma, possibilitam a criação de mapas que exibem as potenciais áreas para sua ocorrência. Assim, através da utilização de previsões para os cenários de mudanças climáticas, é possível fazer projeções sobre a distribuição potencial futura de uma ou mais espécies (Giannini, 2012).

Paisagens antigas, climaticamente protegidas e inférteis (OCBILs) (do inglês: old, climatically buffered, infertile landscapes; Hopper, 2021) como os inselbergs, abrigam uma enorme quantidade de espécies exclusivas e endêmicas registradas no Brasil (Brazil Flora G., 2021). No entanto, apesar de sua importância na biodiversidade, este é um dos ecossistemas mais negligenciados e ameaçados, o que torna urgente planos prioritários de conservação (Porembski et al., 2016). A natureza isolada dos inselbergs torna-se interessante para estudos dos processos evolutivos das espécies, principalmente mudanças climáticas de longo prazo (*e.g.* modelos paleoclimáticos) (Svenning et al., 2015), enquanto pode-se investigar os padrões de conectividade da paisagem subjacentes nos cenários passado e atual. Dessa forma, compreender essa conectividade entre inselbergs e populações é vital, uma vez que representa um fator crítico que determina uma ampla gama de fenômenos ecológicos, *e.g.* dinâmica meta-populacional e manutenção da biodiversidade (McRae et al., 2008), e esta é uma questão de grande preocupação no atual cenário de mudanças no uso da terra e de rápidas mudanças climáticas globais (Saura et al., 2014).

Diante dos fatores apresentados o presente estudo tem como proposta central compreender a diversidade taxonômica, funcional e filogenética das espécies associadas aos ecossistemas de inselbergs, assim como avaliar os efeitos das mudanças climáticas através da modelagem de nichos ecológicos e estimar o efeito do isolamento geográfico na diversidade filogenética de plantas através da conectividade da paisagem, a fim de gerar estudos que possam

compreender os ecossistemas rupícolas associados aos inselbergs Neotropicais Brasileiros e com isso contribuir para a manutenção e conservação destes ecossistemas.

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Chapter 1

Taxonomic and functional turnover driven alfa and beta-diversity in Neotropical inselbergs

Abstract

Biodiversity is a multifaceted concept that goes further than simply the number of species present in a given place. Besides local diversity measured by α-diversity, the simplest and most used meaning of measure diversity is the dissimilarity in community composition between two or more sites (taxonomic β-diversity). Despite its importance, α- and β-taxonomic diversities approach are also not sufficient to understand the community assembly rules and their effects on ecosystem process, others facets of biodiversity as trait-based need to be consider. Since sample units distributed in eight inselbergs at Espírito Santo State, we analyzed the plant community structure and α-diversity, as well as linked taxonomic and functional β-diversity and its decomposed component and quantify the contribution of turnover and nestedness-resultant components to each β-diversity index. We still tested whether functional richness was significantly different from null-expectation given the observed patterns of taxonomic richness. The structure and α-diversity showed significantly differences among inselbergs, as well as an evident oligarchic structure in plant communities analyzed. Taxonomic and functional β-diversity and their respective turnover were significantly correlated, with greater contributions of turnover component to β-diversity of each index. This pattern could be the result of a strong niche filtering along historical events, which can afford diversification of several taxa and lineages during the recolonization process, and due to biogeographical isolation that can also impose dispersal limitations to plant species, reflecting in a high taxonomic turnover, speciation, and isolated evolutionary lineages of the inselbergs flora. As investigations on functional β-diversity are scarce compared with taxonomic β-diversity studies, our study demonstrated that these two facets of biodiversity are complementary ecological indicators. Therefore these assessments of taxonomic and functional β-diversity and their components could help to prioritize conservation efforts at inselbergs and other ecosystems.

Keywords: rock outcrop; phytosociological structure; floristic composition; functional traits; functional richness; biodiversity conservation; Atlantic Forest

1. Introduction

The inselbergs ecosystem constitutes isolated rocky granite or gneiss outcrops that emerge abruptly from their surrounding ecosystems, such as savannah and forests (Porembski et al., 2000). They have proven to be useful landscapes for pursuing studies of biogeographical patterns and processes (Barthlott & Porembski, 2000), and are hypothesized to be rich in species and endemism, resulted in low dispersability and high clonality in many species (Hopper et al., 2021). These ecosystems are important centers of plant diversity and endemism and are among the main "old, climatically buffered, infertile ecosystems" in the world (OCBILs, Hopper et al., 2016; 2021).

Despite its importance in biodiversity, inselbergs are one of the more neglected and threatened ecosystems, which raises the urgency for conservation priority plans (Porembski et al., 2016) due to the current fast global climate and land-use change scenario (Saura et al., 2014). Thus, assessments of taxonomic and functional β-diversity for other ecosystems and taxa as well as their respective turnover and nestedness-resultant components could help to prioritize conservation efforts (McKnight et al., 2007; Devictor et al., 2010).

Biodiversity is a multifaceted concept that goes further than simply the number of species present in a given place (*e.g.* taxonomic α-diversity) (Villéger et al., 2013). Partitioning the diversity into different scales (α, β, and γ) can be an alternative to understanding the community assembly rules behind the taxonomic diversity among communities (de Bello et al., 2010). Besides local diversity measured by α-diversity, the simplest and most used meaning of measure diversity is the dissimilarity in community composition between two or more sites (taxonomic β-diversity) (Koleff et al., 2003; Pinto-Junior et al., 2020b; Villa et al., 2021).

Even as the regional diversity, the taxonomic β-diversity can be decomposed into two components: turnover and nestedness-resultant components (Baselga et al., 2012; Villéger et al., 2013). Turnover component reflects the replacement of some species between communities as a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005; Baselga, 2010), while nestedness-resultant reflect the contrary, the differences occur when the species assemblages of poorer sites are subsets of the richer sites (Ulrich & Gotelli, 2007), reflecting a non-random process of decrease of richness in species assemblages (Villéger et al., 2013).

Frequently α and β-taxonomic diversities have been conducted the multifaceted biodiversity. Despite its importance, this approach is also not sufficient to understand the community assembly rules and their effects on ecosystem process, as biological strategies

(McGill et al., 2006) or trait-based approach (Díaz et al., 2007; Lavorel et al., 2011; Mouillot et al., 2011). Thus, to fill the gap in this field many functional diversity indices have been used to compare the functional dissimilarity among communities (de Bello et al., 2010; Villéger et al., 2013) and emphasize the potential of functional traits to reveal the processes in community assembly (Cornwell et al., 2006; McGill et al., 2006; Ackerly & Cornwell, 2007).

Nevertheless, analyzing taxonomic and functional β-diversity and their respective components can disentangle community assembly rules and offer a unique opportunity to test the ecological processes that structure the communities (Sokol et al., 2011; Stegen et al., 2011; Swenson et al., 2010). For instance, communities with high taxonomic β-diversity jointly to high functional β-diversity can be due to high taxonomic turnover, while high functional β-diversity can have multiple meanings: can be driven by a high functional turnover (species are functionally different), which indicate niche differentiation between communities, or driven by low functional turnover (species represent a small subset of the functional strategies present in the other community), indicating strong niche filtering (Villéger et al., 2013). On the contrary, communities with low functional β-diversity can be driven by the presence of the same functional strategies (showing functional convergence), even though species are different; or by neutral processes, if functional β-diversity does not differ from random expectation (Villéger et al., 2012; 2013).

In this study, we aimed to analyze the plant community structure and α-diversity in eight inselbergs at Espírito Santo State, southeastern Brazil. Furthermore, we linked taxonomic and functional β-diversity and its decomposed component allowing quantify the contribution of turnover and nestedness-resultant components to each β-diversity index. Finally, we tested whether functional richness was significantly different from null-expectation given the observed patterns of taxonomic richness. Thus, we expected that the decomposition of taxonomic and functional β-diversity become a unified framework, which allows the comparison of taxonomic and functional β-diversity patterns and hence testing of ecological processes in inselbergs ecosystems.

2. Materials and Methods

2.1. *Study area*

We selected eight inselbergs inserted in Atlantic Forest matrix and distributed from north to south of Espírito Santo State, southeastern Brazil (Fig. 1; Fig. 4). The rupicolous vegetation in inselbergs can be found between 0 and 1,480 m a.s.l., is mainly associated with plant communities formed by monocotyledonous mats of Bromeliaceae, Cactaceae, Cyperaceae, and Velloziaceae distributed in patches and/or shrubs (Porembski, 2007, Pinto-Junior et al., 2020a) (more details in Table S1).

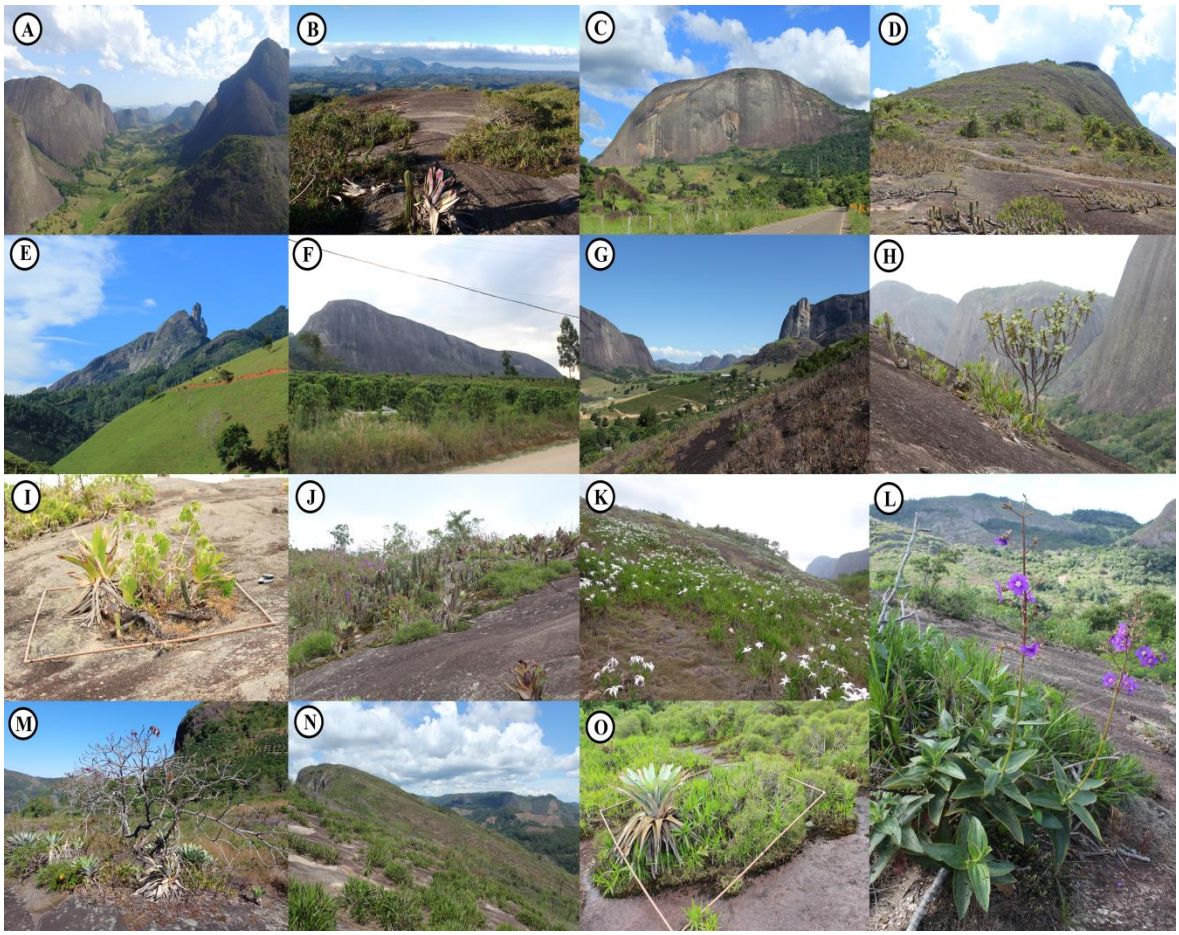

Figure 1 – Granitic inselbergs selected to this study and the rupicolous vegetation (mainly monocotyledonous mats) associated with inselbergs ecosystems. A - aerial view of inselbergs in municipality of Águia Branca, B - monocotyledonous mats in Forno Grande, C – Pedra do Elefante in municipality of Nova Venécia, D – Pedra da Figueira in municipality of Vila Pavão, E – Pedra dos Pontões in municipality of Mimoso do Sul, F – Pedra do Submarino in Brejetuba, G - monocotyledonous mats in Santa Terezinha inselberg, H - monocotyledonous mats in Águia Branca inselberg, I – vegetation patch in sample unit in Pedra do Elefante, J - monocotyledonous mats in Forno Grande, K - synchronized flowering of *Vellozia plicata* Mart. in Águia Branca, L - *Pleroma subsessile* F.S.Mey. & L.Kollmann in Pedra da Lajinha, municipality of Afonso Cláudio, M - monocotyledonous mats in Pedra dos Pontões, N - monocotyledonous mats in Pedra do Submarino and, O - vegetation patch in sample unit in Pedra dos Pontões.

2.2. *Floristic survey and vegetation sampling*

The floristic survey consisted of the collection of fertile specimens and was conducted between April 2017 and February 2021, with successive field expeditions to encompass the different seasons. All fertile botanical material was collected and processed according to the usual techniques for vascular plants (Fidalgo & Bononi, 1989). Taxonomic identification of botanical material was carried out by using the Flora do Brasil 2020 (Brazil Flora G., 2021), taxonomic literature, herbarium data, and expert taxonomists. The spelling and synonyms were standardized and verified by Flora do Brasil 2020 (Brazil Flora G., 2021) through the package 'flora' (Carvalho, 2020). All botanical material was deposited in the herbariums of Universidade Federal de Viçosa (VIC) and Universidade Federal do Espírito Santo (SAMES). The spelling of names, synonymy, and authors follow Flora do Brasil 2020 (Brazil Flora G., 2021) with APG IV (2016) circumscription for angiosperm families, and PPG I (2016) for monilophytes and lycophytes.

In each inselberg, 30 sampling units of 4 m² (2 x 2 m) were allocated randomly, distributed between small (≤ 4 m²) and larger patches (≥ 4 m²) with a minimum distance between patches of 5 m. The minimum size for the inclusion of a vegetation patch has been standardized at 0.5 m². On the larger patches, more than one sampling unit was sampled in order to represent the entire extent of the patch. In each sample, a survey of all species present was carried out, as well as the cover value of each species through its proportion in relation to the sample.

2.3. *Selection and measurements of traits*

The selection of species for the functional traits measurements was done through the Importance Value (IV) of each species in each community, considering as a minimum inclusion value of IV ≥ 1 to species selection. In the end, we collected and measured functional traits of 60 species, including poikilohydric mats, sclerophyllous shrubs, and rosettes and succulents species, selected across the eight inselbergs. Functional traits were collected in the rainy season (January to March of 2019 and 2020), considering the most favorable growth period. All measurements followed the standardized protocols described by Pérez-Harguindeguy et al. (2013). To quantify functional traits, two leaves per individual (totaling 10 individuals per species) of mature, fully expanded, and without signs of herbivory, pathogens, or malformation were collected in the field. The collected material was immediately saturated using a water spray and packed in moist paper bags and sealed in a plastic bag. The leaves were kept in a

refrigerator at 4ºC for a minimum of 12 h to achieve complete turgidity prior to measurements. Measurements of leaves (including the petiole) were taken until 48 h of collection.

We selected functional traits to reflect plant ecological strategies (Grime et al., 1997) and leaf economics spectrum in the harsh environmental conditions of inselbergs. We sampled five functional traits: mature plant height (H), leaf area (LA), leaf thickness (LT), leaf dry matter content (LDMC), and specific leaf area (SLA) (Pérez-Harguindeguy et al., 2013). Mature plant height was measured in the field with a graduated tape; leaf area was obtained using a desktop scanner and the software ImageJ (Schneider et al., 2012) calibrated by known area. Curved leaves were cut and positioned on the glass to complete contact with the scanner surface. Leaf fresh weight was obtained from turgid leaves (surfaces were dried with soft towel paper) and leaf dry weight was determined with an analytic scale (precision of 0.001 mg) after 96 h of drying in an oven at 60ºC. Leaf thickness was obtained with the use of a digital caliper (Digimess® 100.174BL, precision of 0,01mm). Final measurements of each trait include 20 leaves to generate an average value for each species.

2.4. *Measuring taxonomic and functional β-diversity*

Dissimilarity in species composition between a pair of communities is a classical assessment of biodiversity. One of the multiple meanings of taxonomic β-diversity can be represented by the percentage of dissimilarity in species composition between two communities: taxonomic β-diversity = (number of species not shared)/(total number of species) (Anderson et al., 2011; Baselga, 2012). However, taxonomic β-diversity could be close to its maximal value even if the two communities share some species, provided that one community has a much larger number of species than the other. Thus, taxonomic β-diversity is not only determined by species turnover among communities but also by the difference in species richness (Baselga, 2010; 2012). Some authors had suggested that taxonomic β-diversity is the sum of a turnover component (*i.e.* species replacement in the two communities) and a nestedness-resultant component (*i.e.* influenced by the difference in the number of species between the two communities) (Baselga, 2012; Villéger et al., 2013). This conceptualization can be expressed by:

$$\text{taxonomic } \beta\text{-diversity} = \frac{b+c}{a+b+c} = \frac{2 \times \min(b,c)}{a+2 \times \min(b,c)} + \frac{|b-c|}{a+b+c} \times \frac{a}{a+2 \times \min(b,c)} . \quad (1)$$

Thus, by analogy with taxonomic β-diversity, the functional β-diversity between two (C1 and C2) communities can be represented: functional β-diversity = (functional space not

shared)/(total functional space filled) (Villéger et al., 2011), where given the volume of the convex hulls of each of the two communities (V(C1) and V(C2)) and their intersection V(C1 ∩ C2), we can represent the functional β-diversity by:

$$\text{functional β-diversity} = \frac{V(C1)+V(2)-2 \text{ x } V(C1 \cap C2)}{V(C1)+V(2)-V(C1 \cap C2)}. \quad (2)$$

Following the framework proposed by Baselga (2012), the functional β-diversity can be decomposed into functional turnover and functional nestedness-resultant components, being functional β-diversity = functional turnover + functional nestedness-resultant, where:

$$\text{functional turnover} = \frac{2 \text{ x } \min(V(C1),V(2))-2 \text{ x } V(C1 \cap C2)}{2 \text{ x } \min(V(C1),V(2))-V(C1 \cap C2)} \quad (3)$$

and

$$\text{functional nestedness-resultant} = \frac{|V(C1)-V(2)|}{V(C1)+V(2)-V(C1 \cap C2)} \text{ x } \frac{V(C1 \cap C2)}{2 \text{ x } \min(V(C1),V(C2))-V(C1 \cap C2)}. \quad (4)$$

2.5. *Partition of taxonomic and functional β-diversity*

We partition the taxonomic and functional β-diversity into turnover and nestedness-resultant components among eight inselbergs assemblages (Villéger et al., 2013) totalizing 28 pairs of assemblages. All metrics were measured using Sørensen's dissimilarity index (Anderson et al., 2011; Baselga, 2012). The taxonomic β-diversity was measured following equation 1 (Villéger et al., 2013). The functional β-diversity, turnover, and nestedness-resultant components were computed following the equations 2, 3, and 4, respectively (Villéger et al., 2013).

2.6. *Data analyses*

2.6.1. *Changes in community composition, structure and α-diversity*

The quantification of biodiversity indices was calculated for each sampling area (inselberg) through species coverage (abundance). The α-diversity included: species richness, Shannon-Wiener, and Pielou evenness index (Magurran, 2004). Species richness refers to the total number of species recorded in each sampled area. The Shannon-Wiener index (*H'*) and Pielou evenness index (*J*) were calculated using the following equations: $H' = -\sum pi.\ln(pi)$ and $J = H'/H'max$, where *pi* is the absolute coverage of each species; *ln* is the natural logarithm; *H'max* is *ln* of *S* and *S* is the total number of species at a sampling area. All diversity indices were calculated using the 'vegan' package (Oksanen et al., 2020).

To compare the means of cover and α taxonomic diversity metrics, we verified the data normality and distribution by the Shapiro–Wilk test for normality and Q-Q graphs (Crawley, 2013). Differences between the metrics across inselbergs were analyzed by the Kruskal-Wallis test (for non-normally distributed data), followed by Dunn's multiple comparison test (Dinno, 2017). We analyze the differences in community composition among the inselberg through non-metric multidimensional scaling (NMDS) analysis (Clarke, 1993) using Bray-Curtis distance and considering the sum of coverage in each plot to standardize differences between plots. The NMDS was executed using the *metaMDS* function, and permutational multivariate analysis of variance (Permanova; Anderson, 2006) with 9999 permutations was performed to determine the differences in community composition among inselbergs, using the *adonis* function of the 'vegan' package (Oksanen et al., 2020).

To assess the changes in structure taxonomic data, we used the *betadisper* function in the 'vegan' package, based on the permutational analysis of multivariate dispersions (Permdisp; Anderson, 2006). We used the distance to group centroid as the method of assessing variability in community composition, based on Euclidean distances with 9999 permutations. In this analysis, greater dispersal of data points indicated greater heterogeneity of the groups. To compare the difference between communities we performed the one-way Anova test, followed by Tukey's post hoc test ($p < 0.05$).

2.6.2. *Estimating β-diversities and functional richness*

The taxonomic β-diversity and its components (functional turnover and functional nestedness-resultant) were calculated using the *beta.pair* function of the 'betapart' package (Baselga et al., 2021) with Sørensen index (Villéger et al., 2013). To quantify the functional dissimilarity between communities, we measure the convex hulls of each community with the Sørensen index (Villéger et al., 2008), and then were calculated the functional β-diversity and its components using the *functional.beta.pair* functions of the 'betapart' package (Baselga et al., 2021). The functional richness was measured through the *dbFD* function of the 'FD' package (Laliberté & Legendre, 2010). From functional richness and taxonomic richness, we generated a distance matrix through the *vegdist* function of the 'vegan' package (Oksanen et al., 2020) using Euclidean distance to functional richness and Jaccard distance to taxonomic richness.

2.6.3. *Testing the functional index in inselbergs assemblages*

We analyzed how taxonomic β-diversity and both components are related to its functional β-diversity. The correlations were tested by Mantel permutational (9999) tests with Pearson's correlations through the *mantel* function of the 'vegan' package (Oksanen et al., 2020). We also tested whether the functional richness of each inselberg differs from a random expectation given its taxonomic richness using Mantel permutational (9999) tests with Pearson's correlations through *mantel* function of 'vegan' package (Oksanen et al., 2019). All analyzes were carried out in the software R 4.0.3 (R Core Team, 2020). Finally, we used the package 'ggplot2' for graphical visualization (Wickham et al., 2020).

3. Results

3.1. *Floristic composition and structure*

We recorded a total of 242 species, being 140 species of vascular plants, including 2 lycophytes, 14 pteridophytes, and 124 angiosperms (three magnoliids, 49 monocots, and 72 eudicots). The richest family was Bromeliaceae with 14 species, followed by Asteraceae (13 spp.), Orchidaceae (10 spp.), Cyperaceae and Melastomataceae (eight spp. each), Cactaceae, Malvaceae and Polypodiaceae (6 spp. each), Apocynaceae, Euphorbiaceae, Gesneriaceae, Poaceae, Pteridaceae and Velloziaceae (five spp. each) and, Araceae, Clusiaceae and Rubiaceae with three species each family. The richest genus was *Pleroma* (Melastomataceae) with eight species, followed by *Alcantarea* (Bromeliaceae) and *Pseudobombax* (Malvaceae) with five species, *Bulbostylis* (Cyperaceae), *Doryopteris* (Pteridaceae), *Mandevilla* (Apocynaceae) with four species, and *Bradea* (Rubiaceae), *Clusia* (Clusiaceae), *Pitcairnia* (Bromeliaceae), *Serpocaulon* (Polypodiaceae), *Sinningia* (Gesneriaceae) and *Vellozia* (Velloziaceae) with three species each.

Regarding the North-South gradient, the southern areas were not richer than the northern areas, as well as the number of genera and families (Table 1). The percentage of unique genera found in sampled communities ranged between 81.8 – 100%, with the highest value being reached by Santa Terezinha inselberg; the families with only one species (unique family), the value ranged between 38.4 – 75%, with the highest percentage in Águia Branca and Pedra da Figueira inselbergs. The eight sites were organized in an oligarchic structure, where a few species dominant (average of 6 species) account for more than 60 % of the Importance Value (IV) (Tables S2 – S9 in Supplementary Material). We highlight the least value was in Santa

Terezinha with three species account for 66% and, the higher value was in Forno Grande with 10 dominant and codominant species account for 65% of IV.

3.2. *Changes in taxonomic α-diversities*, *communities composition and structure*

Concerning α-diversity measured by the cover value, species richness, Shannon-Wiener index (*H'*), and Pielou evenness index (*J*) the same pattern was observed regarding the North-South gradient, south areas were not the richer than the northern areas (Table 1). We observed significant differences in coverage (Kruskal-Wallis test: $Chi^2 = 104.39$, df = 7, $p < 2.2e\text{-}16$, Fig. 2a), species richness (Kruskal-Wallis test: $Chi^2 = 99.92$, df = 7, $p < 2.2e\text{-}16$, Fig. 2b), Shannon-Wiener index (Kruskal-Wallis test: $Chi^2 = 100.67$, df = 7, $p < 2.2e\text{-}16$, Fig. 2c) and Pielou evenness index (Kruskal-Wallis test: $Chi^2 = 46.84$, df = 7, $p < 5.99e\text{-}08$, Fig. 2d) among sites when we analysed them at the sampling unit scale.

The structure of inselbergs were significant different considering the NMDS analysis (Permanova: $r^2 = 0.49$; $p < 0.001$; Fig. 3a). It formed five groups with the first two NMDS axes explaining 32.66% of the variance in species data. We also observed significant differences in community composition between inselbergs (Permdisp: $p = 2.2e\text{-}16$; Fig. 3b; Fig. S1) with higher differences of species composition in Forno Grande, Pedra da Figueira and Pedra dos Pontões (Figure 3b).

Table 1 – Results of the community structure from eight inselbergs sampled in Espírito Santo State, southeastern Brazil.

	Águia Branca	Forno Grande	Pedra do Elefante	Pedra da Figueira	Pedra da Lajinha	Pedra de Pontões	Pedra do Submarino	Santa Terezinha
Nº of species	22	45	39	24	35	29	29	19
Nº of genera	20	37	29	22	27	25	24	19
Nº of families	16	22	22	16	21	15	13	14
Richest Families	Bromeliaceae (3) Cyperaceae (2) Velloziaceae (2)	Asteraceae (6) Bromeliaceae (4) Cyperaceae (4) Poaceae (4) Melastomataceae (3) Orchidaceae (3)	Asteraceae (4) Cyperaceae (3) Orchidaceae (3)	Bromeliaceae (4) Cyperaceae (3) Euphorbiaceae (3)	Asteraceae (5) Euphorbiaceae (3) Velloziaceae (3)	Orchidaceae (4) Velloziaceae (4) Cactaceae (3) Polypodiaceae (3)	Bromeliaceae (4) Orchidaceae (4) Velloziaceae (4) Asteraceae (3)	Bromeliaceae (2) Cactaceae (2) Orchidaceae (2) Pteridaceae (2)
Unique genera[1]	95 %	91.8 %	89.6 %	81.8 %	88.8 %	92 %	91.6 %	100 %
Unique family[2]	75 %	50 %	59 %	75 %	61.9 %	53.3 %	38.4 %	47.3 %
Shannon (*H'*)	1.62	3.37	2.11	2.55	3.18	1.82	2.48	1.32
Evenness (*J*)	0.52	0.88	0.57	0.80	0.89	0.54	0.73	0.44

[1]Unique genera: percentage of genera that present only one species.
[2]Unique family: percentage of family that present only one species.

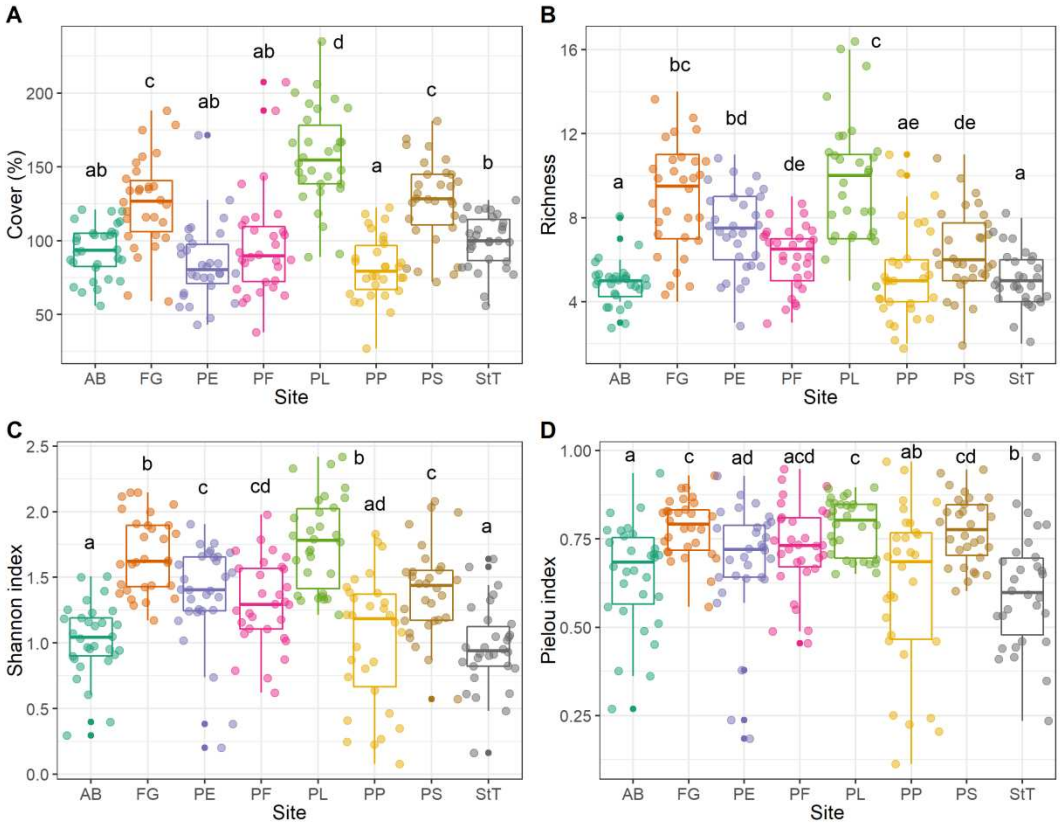

Figure 2 – Differences in diversity measure per plot in different sites: A - plant coverage, B - species richness, C - Shannon index and D - Pielou's evenness index along north-south gradient in Espírito Santo State, southeastern Brazil. Different letters indicate significant differences (*Dunn test*) among the inselbergs. AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra de Pontões, PS – Pedra do Submarino and StT – Santa Terezinha.

3.3. *Correlation and contribution of decomposed β-diversities*

Taxonomic β-diversity ranged from 0.5 to 0.92 with a mean value of 0.76 (± 0.09) (Table 2; Fig. 4a). In general, the turnover (0.73 ± 0.11) (Fig. 4b) was higher than the nestedness-resultant (0.029 ± 0.03) (Fig. 4c), with a difference of 0.70 (25 times higher than nestedness-resultant) (Table 2). The functional β-diversity showed a mean value higher than taxonomic, with a functional β-diversity mean value of 0.85 (± 0.13) and ranged from 0.51 to 1 (Table 2; Fig. 4d). On average, the turnover (0.73 ± 0.23) (Fig. 4e) was higher than the nestedness-resultant (0.12 ± 0.15) (Fig. 4f), with a value six times higher than the nestedness-resultant (Table 2).

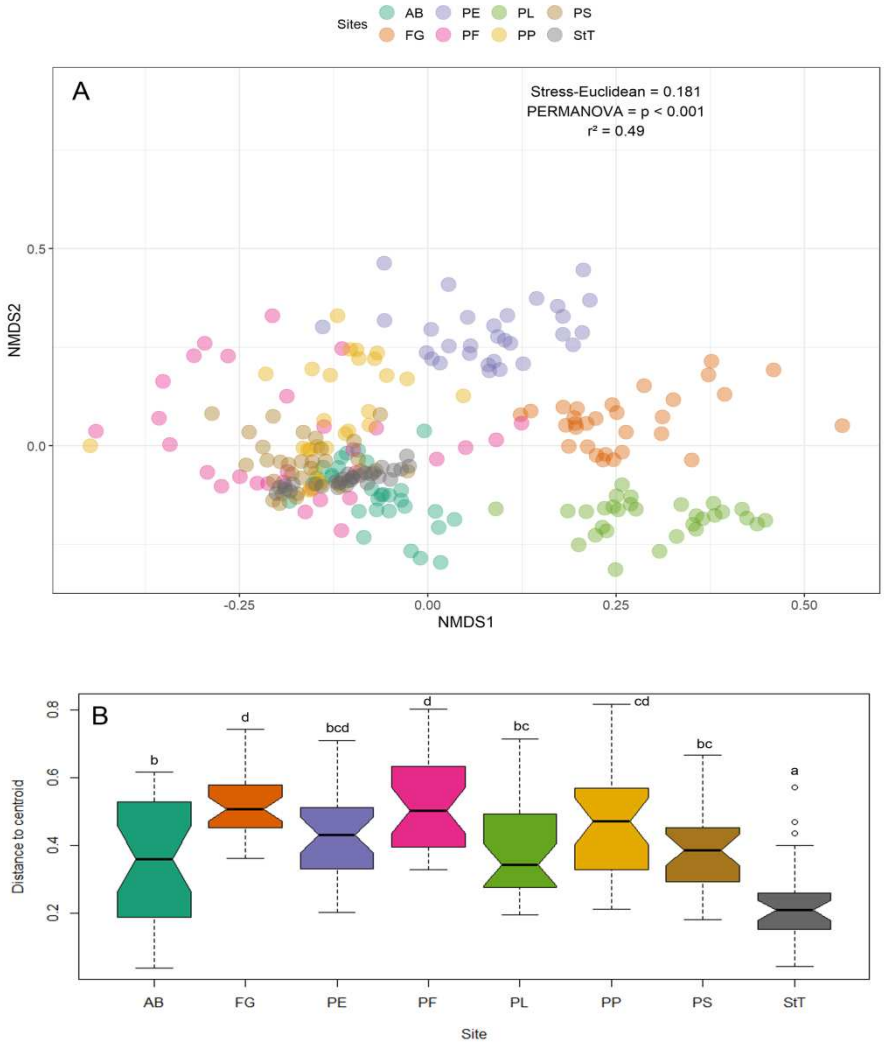

Figure 3 – Non metric multidimensional scaling (NMDS) based on species composition of eight inselbergs in Espírito Santo State, southeastern Brazil (A). Differences in community structure using multivariate analysis of dispersal (Permdisp) through distance of centroid (B). Groups: AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra de Pontões, PS – Pedra do Submarino and StT – Santa Terezinha.

The functional β-diversity was significantly correlated with taxonomic β-diversity (Mantel test, $r = 0.341$, $p = 0.04$; Fig. 5a) and presented higher average with a mean of 0.85 (± 0.13) (Table 2). Even as functional β-diversity, functional turnover was significantly correlated with taxonomic turnover (Mantel test, $r = 0.342$, $p = 0.04$; Fig. 5b) but showed a similar average value of 0.73 (± 0.23). In contrast, nestedness-resultant components of functional and taxonomic β-diversity were not significantly correlated (Mantel test, $r = -0.019$, $p = 0.476$; Fig. 5c), even not showing significant correlation functional nestedness-resultant presented higher average with a mean of 0.12 (± 0.15), value four times higher than the taxonomic nestedness-resultant.

Table 2 – Results of decomposition of taxonomic and functional β-diversity and theirs respective contributions to each β-diversity.

	Taxonomic	Functional
β-diversity	0.76 ± 0.09 (0.5 - 0.92)	0.85 ± 0.13 (0.51 - 1)
Turnover	0.73 ± 0.11 (0.33 - 0.92)	0.73 ± 0.23 (0.17 - 1)
Nestedness-resultant	0.029 ± 0.03 (0 - 0.16)	0.12 ± 0.15 (0 - 0.59)
Turnover contribution	96% (± 0.06)	85% (± 0.21)
Nestedness contribution	4% (± 0.06)	15% (± 0.21)

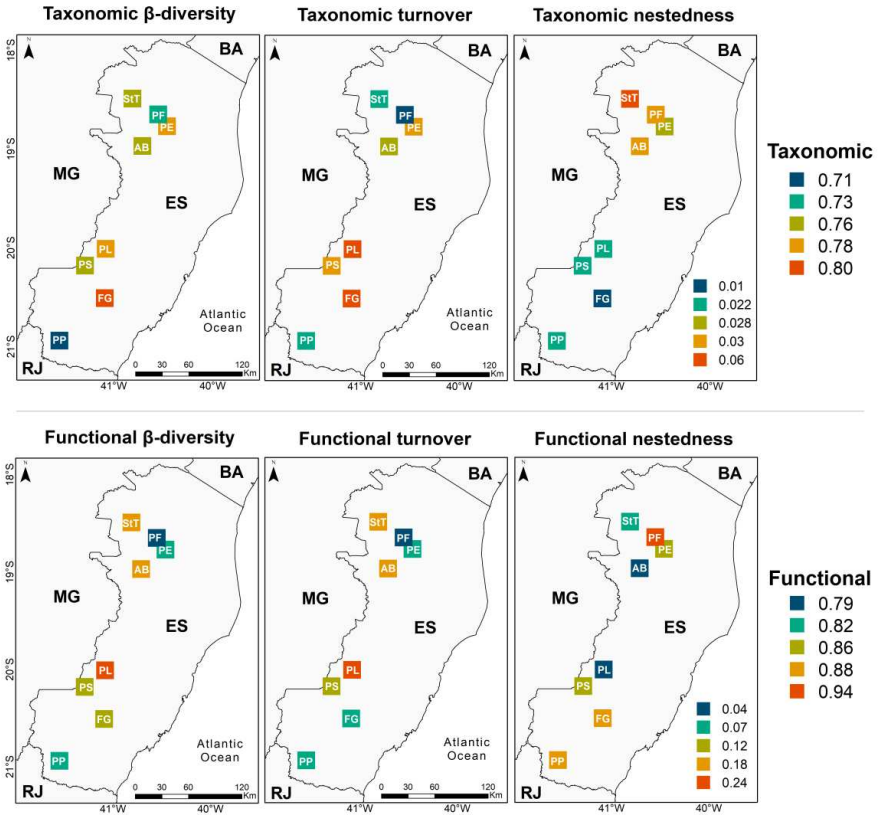

Figure 4 – Spatial patterns of taxonomic and functional β-diversity and their respective turnover and nestedness-resultant components for eight inselbergs in Espírito Santo State, southeastern Brazil. Index values for each inselberg correspond to the average of dissimilarity pairwise between inselbergs. AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra de Pontões, PS – Pedra do Submarino and StT – Santa Terezinha.

Taxonomic turnover contributed to 96% (± 0.06) of taxonomic β-diversity (Table 2), while the nestedness-resultant contributed with only 4% (± 0.06). The functional turnover contributed with 85% (± 0.21) of functional β-diversity (Table 2). The functional richness showed a ranged value between 0.75 – 5.47 with lower values in Forno Grande and higher in Pedra dos Pontões. Functional richness and taxonomic richness were not significantly correlated (Mantel test, r = -0.17, p = 0.83; Fig. 5d), presenting a negative relation and non-random species pool given the species richness.

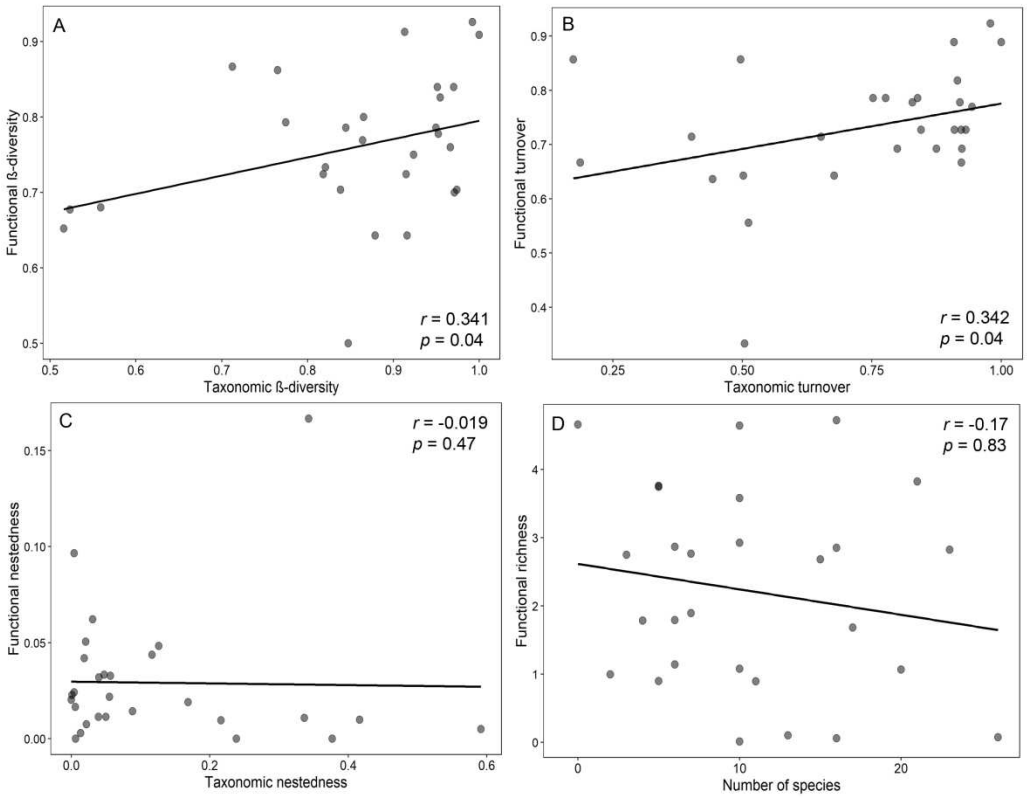

Figure 5 – Correlations of Mantel test among taxonomic and functional β-diversity (A), and their respective turnover (B) and nestedness-resultant components (C) for the 28 pairs of inselbergs communities in Espírito Santo State, southeastern Brazil. Taxonomic and functional richness (D) correlations obtained from the null model testing the relation between functional richness and taxonomic richness and the respective global pool of species.

4. Discussion

This study demonstrated the presence of a contrasting pattern in community structure, species richness, cover value, and α-diversity indexes among Neotropical Brazilian inselberg. Regarding the community structure, our results showed a higher number of rare species, characteristic that demonstrates the oligarchism present in the rupicolous communities (Scarano, 2002). When we compare with other studies focused on rocky outcrops (Meirelles, 1996; Conceição, 2003; Caiafa & Silva, 2007) our results demonstrated higher values of unique species, however showed similar values of unique species and families with other studies (Pinto-Junior et al., 2020a). The richest families, such as Bromeliaceae, Asteraceae, Orchidaceae, Melastomataceae, and Velloziaceae are important to inselberg communities due to the characteristic of mat-formers, which can promote the accumulation of sediments in depressions, contributing to a greater establishment of phanerophytes and consequently their plant habitats (mats and shrubs).

The adaptations to harsh conditions and high abundances of some families found in inselbergs are reported by some authors (Kluge & Brulfert, 2000; Conceição, 2003; Conceição

& Pirani, 2007), mainly to Velloziaceae family. One of the adaptations of this family is related to poikilohydric adaptation to water stress (Dinakar et al., 2012), during dry periods poikilohydric species tend to dehydrate, returning to a hydrated state with the rains, which is why they are also called "resurrection plants" (Porembski & Barthlott, 2000). Thus, this desiccation tolerance represents an important ecophysiological adaptation, what can influence the community structure and composition (Rietkerk & Koppel, 2008; Meloni et al., 2017), the abundance (Conceição & Pirani, 2007), diversity of species (Kluge & Brulfert, 2000) and plant phenology (Conceição, 2003).

Changes in species richness and composition, and consequently contrasting differences in species shared between inselbergs, can be explained by factors that are acting on communities at a local and fine-scale, such as soil properties and topography. Nonetheless, biogeographical drivers, as dispersal limitation, can act more powerfully in inselberg communities, which may explain the marked change in communities over relatively short distances (Schut et al., 2014). Island ecosystems such as inselbergs combine isolation with historical and environmental filtering and stochastic factors (Parmentier et al., 2005; Parmentier & Hardy, 2009). Therefore, the different degrees of antiquity, the co-occurrence in different biomes with a wide spectrum of sizes, can accentuate the effects of isolation (Porembski et al., 2000), as well as act as a shelter for xeric vegetation from other domains, such as the Cerrado and Caatinga (Ratter et al., 1997; Hmeljevski et al., 2017; Antonelli et al., 2010). Thus, like islands, inselbergs have an important phytogeographic contribution to landscape diversity and can help to better understand the biogeographic patterns and changes in Pleistocene climate cycles (Yates et al., 2019).

The partition of taxonomic and functional β-diversity presented the quantification of the respective contributions of turnover and nestedness-resultant component, and thus, reflects the taxonomic and functional space not shared by communities (turnover) and the influenced by the difference in the space filled by communities (nestedness-resultant) to the taxonomic and functional dissimilarity between communities (Villéger et al., 2013). Therefore, these metrics are influenced by the richness of the communities, even as the range of functional traits present in each community (Cornwell et al., 2006; Villéger et al., 2008; Mouchet et al., 2010). Thus, a pattern in functional space is evident, species with the most extreme trait combinations shaping the portion of all and opposites functional space filled by communities, while species with intermediate trait values shaping the intersection between convex hulls (overlap space) (Villéger et al., 2013).

The decomposed of β-diversities approach allows the functional β-diversity and its components to be measured, in an easy way, with similar taxonomic β-diversity and components, as proposed by Baselga (2012) and Villéger et al. (2013). Concerning the inselbergs communities, both functional and taxonomic β-diversity is higher, with higher functional β-diversity compared with taxonomic β-diversity (Table 2; Fig. 4), mainly due to a higher functional turnover, while nestedness-resultant of taxonomic and functional β-diversity were similarly low. The null model revealed that the functional richness was not significantly different from a random expectation given the regional pool of species and the species richness. The results above and showed by α-diversity can elucidate those inselberg communities are (in average) very dissimilar in terms of species composition and morphological traits. This pattern could result from a strong niche filtering process along an environmental gradient, which can induce a high level of taxonomic dissimilarity coupled to a high level of functional dissimilarity, due to varying of the functional strategies dominant along the gradient (Sokol et al., 2011; Stegen & Hurlbert, 2011).

Indeed, the high taxonomic and functional turnover could be explained by the natural fragmentation of this ecosystem as well as, historical events, such as quaternary climate shifts during the Last Glacial Maximum (LGM), which can afford diversification of several taxa and lineages during the recolonization process (Svenning et al., 2015), increasing the taxonomic turnover (and hence β-diversity) and speciation to fill all functional space (niche complimentary), increasing the functional turnover (Villéger et al., 2013). As inselbergs are naturally isolated, biogeographical barriers also can impose dispersal limitations to plant species, thus reflecting in a high taxonomic turnover, speciation, and isolated evolutionary lineages of the inselbergs flora.

Recent studies have demonstrated the effects of environmental filtering, mainly climatic factors, in inselbergs communities assembly (Hmeljevski et al., 2017; Sarthou et al., 2017; Henneron et al., 2019; Pinto-Junior et al., 2020b; de Paula et al., 2021). Climate buffered areas, such as inselbergs, have been drawing attention especially due to the theoretical approaches related to the climate stability areas (refugia) during Quaternary climatic fluctuations (Hmeljevski et al., 2017) and the OCBILs landscape (de Paula et al., 2021). Climate stability has an important role as environmental filtering driving the speciation and extinction of species (Morueta-Holme et al., 2013) and affects dispersal strategies and gene flow across plant (and animals) populations along the landscape (Thompson & Townsend, 2006; Morán-Ordóñez et al., 2015; Thiele et al., 2018; Oliveira et al., 2018).

The results showed here highlighting a combination of the patterns among taxonomic and functional diversity, a regional pool dominated by rare species, and the consistent presence of few abundant species (oligarchic structure). Furthermore, the abundant species are functionally distinct and at the same time dissimilar in most communities, increasing the alfa functional diversity. Thus, the inselberg communities do not have a dominant species, but several co-dominant species that replace each other in space and time, allowing the domain of certain species according to availability of resources and filled space. Since floristic dissimilarity between inselbergs is so high (high β-diversity), protect the inselbergs flora is a real challenge (de Paula et al., 2019). Effective conservation strategies will need to focus on protecting multiple inselbergs (Yates et al., 2019), rather than few or the richest inselbergs. Besides the ecological factors, the low genetic connectivity between isolated populations (*e.g. Encholirium horridum* – Bromeliaceae) (Hmeljevski et al., 2015; 2017), the current context of global change and human activities, such as species introductions and/or extinctions (taxonomic homogenization) (Qian & Ricklefs, 2006) in Espírito Santo State is already a strong indicator of need of a strategy of conserving multiple inselbergs.

5. Conclusion

Our study allows indicating differences in plant community structure and diversity among local and regional scale, as well as highlight the oligarchism present in the rupicolous communities, which enable the domain of certain species and co-existence with subordinate according to availability of resources and filled space. We reveal that higher taxonomic and functional β-diversity is driven by higher functional and taxonomic turnover in inselbergs of Espírito Santo State, Brazil. This pattern could result from a strong niche filtering process along an environmental gradient. Investigations on functional β-diversity are scarce compared with taxonomic β-diversity studies, although the two facets of biodiversity are complementary ecological indicators as illustrated by our study. Assessments of taxonomic and functional β-diversity and their components could help to prioritize conservation efforts at inselbergs and other ecosystems.

6. Acknowledgments

We acknowledge the Programa de Pós-Graduação em Botânica – UFV for supporting our research in Brazil and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing scholarships to the author. We are also grateful to Luis Fernando T. Menezes and Miriam C. A. Pereira for logistical support in Espírito Santo State. We would like to thank Thais Sperandio and Fernanda Favoreto for help in fieldwork. We thank Larissa A. C. Müller for their contributions in fieldwork, methodology, ideas, and suggestions, as well as all taxonomists who also kindly helped with plant identification. We thank to Instituto Estadual do Meio Ambiente e Recursos Hídricos do Espírito Santo (IEMA) for the research license and Neotropical Grassland Conservancy (NGC) for financial supporting.

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8. Supplementary Material

8.1. *Tables*

Table S1 – General descriptions of Neotropical inselbergs sampled in gradient north-south of Espírito Santo State, southeastern Brazil.

	Águia Branca	Forno Grande	Pedra do Elefante	Pedra da Figueira	Pedra da Lajinha	Pedra de Pontões	Pedra do Submarino	Santa Terezinha
Climate (Alvares et al., 2013)	Aw – Tropical zone with dry winter	Cwb – Humid subtropical zone with dry winter and temperate summer	Aw – Tropical zone with dry winter	Aw - Tropical zone with dry winter	Cwa - Humid subtropical zone with dry winter and hot summer	Cwb – Humid subtropical zone with dry winter and temperate summer	Cwa - Humid subtropical zone with dry winter and hot summer	Aw - Tropical zone with dry winter
Region	Northwest	South	Northwest	Northwest	South	South	South	Northwest
Mean annual temperature (Fick & Hijmans, 2017)	23.6°C	15.4ºC	22.8ºC	23.5ºC	19.8ºC	18.7ºC	18.3ºC	23.4ºC
Mean annual precipitation (Fick & Hijmans, 2017)	1,153 mm	1,392 mm	1,190 mm	1,169 mm	1,300 mm	1,279 mm	1,331 mm	1,136 mm
Forest matrix (Garbin et al., 2017)	Dense Ombrophylous Forest	Dense Ombrophylous Forest Montane	Dense Ombrophylous Forest	Dense Ombrophylous Forest	Dense Ombrophylous Forest	Seasonal Semideciduous Forest	Open Ombrophylous Forest	Dense Ombrophylous Forest
Elevation	260 m a.s.l.	1,480 m a.s.l.	675 m a.s.l.	123 m a.s.l.	789 m a.s.l.	980 m a.s.l.	1,150 m a.s.l.	410 m a.s.l.
Municipalities	Águia Branca	Castelo	Nova Venécia	Vila Pavão	Afonso Cláudio	Mimoso do Sul	Brejetuba	Ecoporanga
Geographic Coordenates	18°58'26.1" S 40°42'26.9" W	20°30'40.1" S 41°05'26.5" W	18°46'07.3" S 40°27'4.1" W	18°39'9.4" S 40°33'11.9" W	20°00'38.8" S 41°05'04.7" W	20°56'25.4" S 41°32'46.7" W	20°10'32.4" S 41°17'10.7" W	18°29'16.09" S 40°48'27.2" W
Status	Private	State Park	Environmental Protection Area	Private	Private	Private	Private	Private

Table S2 – Phytosociological parameters and species sampled in Águia Branca inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Vellozia plicata	Velloziaceae	44.12	30	1	20.27	0.368	39.42	29.84
Alcantarea nigripetala	Bromeliaceae	37.28	22	0.733	14.86	0.311	33.31	24.09
Trilepis lhotzkiana	Cyperaceae	12.10	28	0.933	18.92	0.101	10.81	14.87
Coleocephalocereus pluricostatus	Cactaceae	3.80	18	0.6	12.16	0.032	3.40	7.78
Mandevilla fistulosa	Apocynaceae	1.84	10	0.333	6.76	0.015	1.64	4.20
Pseudobombax aff. *longiflorum*	Malvaceae	3.08	6	0.2	4.05	0.026	2.75	3.40
Cnidoscolus hamosus	Euphorbiaceae	1.62	5	0.166	3.38	0.014	1.45	2.41
Vellozia candida	Velloziaceae	1.48	5	0.166	3.38	0.012	1.32	2.35
Doryopteris collina	Pteridaceae	0.09	6	0.2	4.05	0.001	0.08	2.07
Cololobus argenteus	Asteraceae	1.08	2	0.066	1.35	0.009	0.96	1.16
Selaginella convoluta	Selaginellaceae	0.22	3	0.1	2.03	0.002	0.20	1.11
Pleroma cucullatum	Melastomataceae	1.60	1	0.033	0.68	0.013	1.43	1.05
Paliavana prasinata	Gesneriaceae	0.48	2	0.066	1.35	0.004	0.43	0.89
Indeterminate	Indeterminate	0.80	1	0.033	0.68	0.007	0.71	0.70
Pitcairnia barbatostigma	Bromeliaceae	0.80	1	0.033	0.68	0.007	0.71	0.70
Cheilanthes geraniifolia	Pteridaceae	0.00	2	0.066	1.35	0.000	0.00	0.68
Oxossia rubrobracteata	Turneraceae	0.60	1	0.033	0.68	0.005	0.54	0.61
Encholirium horridum	Bromeliaceae	0.40	1	0.033	0.68	0.003	0.36	0.52
Scleria sp.	Cyperaceae	0.40	1	0.033	0.68	0.003	0.36	0.52
Philodendron edmundoi	Araceae	0.08	1	0.033	0.68	0.001	0.07	0.37
Pseudolaelia vellozicola	Orchidaceae	0.04	1	0.033	0.68	0.000	0.04	0.36
Aristolochia gracilipedunculata	Aristolochiaceae	0.02	1	0.033	0.68	0.000	0.02	0.35
Total		111.93		4.933	100	0.933	100	100

Table S3 – Phytosociological parameters and species sampled in Forno Grande inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Alcantarea extensa	Bromeliaceae	30.28	29	0.966	10.55	0.252	19.87	15.21
Pleroma castellense	Melastomataceae	23.08	11	0.366	4.00	0.192	15.15	9.57
Barbacenia pabstiana	Velloziaceae	17.38	16	0.533	5.82	0.145	11.41	8.61
Cyperus pohlii	Cyperaceae	7.76	22	0.733	8.00	0.065	5.09	6.55
Coleocephalocereus pluricostatus	Cactaceae	5.80	18	0.6	6.55	0.048	3.81	5.18
Sinningia magnifica	Gesneriaceae	5.12	17	0.566	6.18	0.043	3.36	4.77
Epidendrum secundum	Orchidaceae	4.02	16	0.533	5.82	0.034	2.64	4.23
Bradea anomala	Rubiaceae	7.28	8	0.266	2.91	0.061	4.78	3.84
Pleroma heteromallum	Melastomataceae	6.88	8	0.266	2.91	0.057	4.51	3.71
Heterocondylus alatus	Asteraceae	4.94	9	0.3	3.27	0.041	3.24	3.26
Baccharis dentata	Asteraceae	4.88	6	0.2	2.18	0.041	3.20	2.69
Bulbostylis junciformis	Cyperaceae	3.02	9	0.3	3.27	0.025	1.98	2.63
Cololobus rupestris	Asteraceae	3.56	8	0.266	2.91	0.030	2.34	2.62
Doryopteris collina	Pteridaceae	0.82	11	0.366	4.00	0.007	0.54	2.27
Scleria sp.	Cyperaceae	3.44	6	0.2	2.18	0.029	2.26	2.22
Serpocaulon sp.	Polypodiaceae	1.80	8	0.266	2.91	0.015	1.18	2.05

Vellozia candida	Velloziaceae	3.28	4	0.133	1.45	0.027	2.15	1.80
Clusia criuva	Clusiaceae	3.48	3	0.1	1.09	0.029	2.28	1.69
Asplenium sp.	Aspleniaceae	1.04	6	0.2	2.18	0.009	0.68	1.43
Phyllanthus niruri	Phyllanthaceae	0.72	6	0.2	2.18	0.006	0.48	1.33
Cyrtocymura scorpioides	Asteraceae	1.28	3	0.1	1.09	0.011	0.84	0.97
Gaylussacia pallida	Ericaceae	1.28	3	0.1	1.09	0.011	0.84	0.97
Pleroma fornograndense	Melastomataceae	1.28	3	0.1	1.09	0.011	0.84	0.97
Trilepis lhotzkiana	Cyperaceae	0.68	4	0.133	1.45	0.006	0.45	0.95
Poaceae 4	Poaceae	0.66	4	0.133	1.45	0.006	0.43	0.94
Pleopeltis sp.	Polypodiaceae	0.54	4	0.133	1.45	0.005	0.35	0.90
Philodendron edmundoi	Araceae	1.36	2	0.066	0.73	0.011	0.89	0.81
Doryopteris varians	Pteridaceae	0.20	4	0.133	1.45	0.002	0.13	0.79
Anthurium fragae	Araceae	0.56	3	0.1	1.09	0.005	0.37	0.73
Hippeastrum aulicum	Amaryllidaceae	0.38	3	0.1	1.09	0.003	0.25	0.67
Lepidaploa helophila	Asteraceae	0.34	3	0.1	1.09	0.003	0.22	0.66
Poaceae 2	Poaceae	0.56	2	0.066	0.73	0.005	0.37	0.55
Pitcairnia decidua	Bromeliaceae	0.52	2	0.066	0.73	0.004	0.34	0.53
Zygopetalum maculatum	Orchidaceae	0.52	2	0.066	0.73	0.004	0.34	0.53
Peperomia galioides	Piperaceae	0.48	2	0.066	0.73	0.004	0.31	0.52
Utricularia longifolia	Lentibulariaceae	1.00	1	0.033	0.36	0.008	0.66	0.51
Poaceae 1	Poaceae	0.60	1	0.033	0.36	0.005	0.39	0.38
Ipomoea saopaulista	Convolvulaceae	0.40	1	0.033	0.36	0.003	0.26	0.31
Vriesea pseudoatra	Bromeliaceae	0.28	1	0.033	0.36	0.002	0.18	0.27
Achyrocline satureioides	Asteraceae	0.20	1	0.033	0.36	0.002	0.13	0.25
Poaceae 3	Poaceae	0.20	1	0.033	0.36	0.002	0.13	0.25
Rhipsalis clavata	Cactaceae	0.20	1	0.033	0.36	0.002	0.13	0.25
Pitcairnia flammea	Bromeliaceae	0.12	1	0.033	0.36	0.001	0.08	0.22
Gomesa ramosa	Orchidaceae	0.10	1	0.033	0.36	0.001	0.07	0.21
Chamaecrista nictitans	Fabaceae	0.06	1	0.033	0.36	0.001	0.04	0.20
Total		152.39		9.17	100	1.27	100	100

Table S4 – Phytosociological parameters and species sampled in Pedra do Elefante inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Alcantarea trepida	Bromeliaceae	34.88	28	0.933	11.97	0.291	34.28	23.12
Pleroma cucullatum	Melatomastaceae	15.36	22	0.733	9.40	0.128	15.09	12.25
Coleocephalocereus pluricostatus	Cactaceae	5.92	25	0.833	10.68	0.049	5.82	8.25
Vellozia candida	Velloziaceae	10.44	13	0.433	5.56	0.087	10.26	7.91
Pleroma venetiense	Melastomataceae	5.72	16	0.533	6.84	0.048	5.62	6.23
Trilepis lhotzkiana	Cyperaceae	5.90	14	0.466	5.98	0.049	5.80	5.89
Cyperus pohlii	Cyperaceae	3.00	11	0.366	4.70	0.025	2.95	3.82
Philodendron edmundoi	Araceae	4.90	6	0.2	2.56	0.041	4.82	3.69
Vellozia variegata	Velloziaceae	3.76	6	0.2	2.56	0.031	3.69	3.13
Begonia lossiae	Begoniaceae	0.52	11	0.366	4.70	0.004	0.51	2.61
Doryopteris collina	Pteridaceae	0.21	10	0.333	4.27	0.002	0.20	2.24
Sinningia aghensis	Gesneriaceae	1.62	6	0.2	2.56	0.014	1.59	2.08
Achetaria crenata	Plantaginaceae	1.36	6	0.2	2.56	0.011	1.34	1.95

Prescottia plantaginifolia	Orchidaceae	0.52	7	0.233	2.99	0.004	0.51	1.75
Aeschynomene mollicula	Fabaceae	1.08	5	0.166	2.14	0.009	1.06	1.60
Cheilanthes geraniifolia	Pteridaceae	0.26	6	0.2	2.56	0.002	0.26	1.41
Encholirium horridum	Bromeliaceae	1.52	3	0.1	1.28	0.013	1.49	1.39
Acianthera prolifera	Orchidaceae	0.60	4	0.133	1.71	0.005	0.59	1.15
Portulaca hirsutissima	Portulacaceae	0.10	5	0.166	2.14	0.001	0.10	1.12
Sinningia brasiliensis	Gesneriaceae	0.56	3	0.1	1.28	0.005	0.55	0.92
Serpocaulon catharinae	Polypodiaceae	0.08	4	0.133	1.71	0.001	0.08	0.90
Peperomia incana	Piperaceae	0.20	3	0.1	1.28	0.002	0.20	0.74
Bradea sp. nov.	Rubiaceae	1.00	1	0.033	0.43	0.008	0.98	0.71
Pseudobombax petropolitanum	Malvaceae	0.60	1	0.033	0.43	0.005	0.59	0.51
Pseudotrimezia juncifolia	Iridaceae	0.14	2	0.066	0.85	0.001	0.14	0.50
Mandevilla fistulosa	Apocynaceae	0.08	2	0.066	0.85	0.001	0.08	0.47
Cnidoscolus urens	Euphorbiaceae	0.02	2	0.066	0.85	0.000	0.02	0.44
Oxossia rubrobracteata	Turneraceae	0.40	1	0.033	0.43	0.003	0.39	0.41
Indeterminate 2	Indeterminate	0.20	1	0.033	0.43	0.002	0.20	0.31
Cyrtopodium glutiniferum	Orchidaceae	0.16	1	0.033	0.43	0.001	0.16	0.29
Indeterminate 3	Indeterminate	0.12	1	0.033	0.43	0.001	0.12	0.27
Lepidaploa cotoneaster	Asteraceae	0.12	1	0.033	0.43	0.001	0.12	0.27
Sida spinosa	Malvaceae	0.12	1	0.033	0.43	0.001	0.12	0.27
Indeterminate 1	Indeterminate	0.10	1	0.033	0.43	0.001	0.10	0.26
Asteraceae 1	Asteraceae	0.08	1	0.033	0.43	0.001	0.08	0.25
Asteraceae 2	Asteraceae	0.04	1	0.033	0.43	0.000	0.04	0.23
Asteraceae 3	Asteraceae	0.04	1	0.033	0.43	0.000	0.04	0.23
Bulbostylis truncata	Cyperaceae	0.02	1	0.033	0.43	0.000	0.02	0.22
Indeterminate 4	Indeterminate	0.00	1	0.033	0.43	0.000	0.00	0.21
Total		101.76		7.8	100	0.848	100	100

Table S5 – Phytosociological parameters and species sampled in Pedra da Figueira inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Vellozia plicata	Velloziaceae	27.92	24	0.8	12.97	0.233	23.91	18.44
Coleocephalocereus decumbens	Cactaceae	13.60	30	1	16.22	0.113	11.65	13.93
Cheilanthes geraniifolia	Pteridaceae	3.87	27	0.9	14.59	0.032	3.31	8.95
Euphorbia holochlorina	Euphorbiaceae	9.86	11	0.366	5.95	0.082	8.45	7.20
Encholirium horridum	Bromeliaceae	10.00	7	0.233	3.78	0.083	8.57	6.17
Encholirium gracile	Bromeliaceae	7.08	8	0.266	4.32	0.059	6.06	5.19
Alcantarea extensa	Bromeliaceae	5.60	9	0.3	4.86	0.047	4.80	4.83
Vellozia candida	Velloziaceae	6.28	7	0.233	3.78	0.052	5.38	4.58
Pseudobombax sp.	Malvaceae	3.54	8	0.266	4.32	0.030	3.03	3.68
Clusia organensis	Clusiaceae	7.00	2	0.066	1.08	0.058	6.00	3.54
Syagrus ruschiana	Arecaceae	4.60	5	0.166	2.70	0.038	3.94	3.32
Cyperus pohlianus	Cyperaceae	2.16	8	0.266	4.32	0.018	1.85	3.09
Stillingia argutedentata	Euphorbiaceae	3.32	5	0.166	2.70	0.028	2.84	2.77
Philodendron edmundoi	Araceae	3.28	4	0.133	2.16	0.027	2.81	2.49
Selaginella sellowii	Selaginellaceae	0.88	7	0.233	3.78	0.007	0.75	2.27
Trilepis lhotzkiana	Cyperaceae	2.08	4	0.133	2.16	0.017	1.78	1.97

Eugenia astringens	Myrtaceae	3.32	2	0.066	1.08	0.028	2.84	1.96
Portulaca hirsutissima	Portulacaceae	0.74	4	0.133	2.16	0.006	0.63	1.40
Mandevilla grazielae	Apocynaceae	0.20	4	0.133	2.16	0.002	0.17	1.17
Orthophytum compactum	Bromeliaceae	0.22	3	0.1	1.62	0.002	0.19	0.91
Achetaria crenata	Plantaginaceae	0.40	2	0.066	1.08	0.003	0.34	0.71
Bulbostylis cf. *lagoensis*	Cyperaceae	0.16	2	0.066	1.08	0.001	0.14	0.61
Cnidoscolus hamosus	Euphorbiaceae	0.60	1	0.033	0.54	0.005	0.51	0.53
Stigmaphyllon crenatum	Malpighiaceae	0.04	1	0.033	0.54	0.000	0.03	0.29
Total		116.75		6.17	100	0.97	100	100

Table S6 – Phytosociological parameters and species sampled in Pedra da Lajinha inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Barbacenia pabstiana	Velloziaceae	50.20	28	0.933	9.52	0.418	26.69	18.10
Alcantarea longibracteata	Bromeliaceae	26.44	28	0.933	9.52	0.220	14.05	11.79
Pleroma fissinervium	Melastomataceae	20.14	24	0.8	8.16	0.168	10.71	9.43
Cnidoscolus urens	Euphorbiaceae	21.06	22	0.733	7.48	0.176	11.19	9.34
Stillingia argutedentata	Euphorbiaceae	15.02	16	0.533	5.44	0.125	7.98	6.71
Selaginella convoluta	Selaginellaceae	9.04	15	0.5	5.10	0.075	4.81	4.95
Doryopteris collina	Pteridaceae	3.14	24	0.8	8.16	0.026	1.67	4.92
Cololobus rupestris	Asteraceae	8.06	15	0.5	5.10	0.067	4.28	4.69
Cyperus pohlii	Cyperaceae	5.00	19	0.633	6.46	0.042	2.66	4.56
Aeschynomene mollicula	Fabaceae	7.56	11	0.366	3.74	0.063	4.02	3.88
Portulaca hirsutissima	Portulacaceae	1.68	15	0.5	5.10	0.014	0.89	3.00
Manihot pohlii	Euphorbiaceae	3.46	12	0.4	4.08	0.029	1.84	2.96
Trilepis lhotzkiana	Cyperaceae	3.16	12	0.4	4.08	0.026	1.68	2.88
Serpocaulon sp.	Polypodiaceae	2.38	10	0.333	3.40	0.020	1.27	2.33
Bradea borrerioides	Rubiaceae	1.00	4	0.133	1.36	0.008	0.53	0.95
Sinningia brasiliensis	Gesneriaceae	1.20	3	0.1	1.02	0.010	0.64	0.83
Anemia sp.	Anemiaceae	0.50	4	0.133	1.36	0.004	0.27	0.81
Asteraceae 2	Asteraceae	0.30	4	0.133	1.36	0.003	0.16	0.76
Pseudobombax sp.	Malvaceae	1.32	2	0.066	0.68	0.011	0.70	0.69
Vellozia plicata	Velloziaceae	1.08	2	0.066	0.68	0.009	0.57	0.63
Paliavana prasinata	Gesneriaceae	0.84	2	0.066	0.68	0.007	0.45	0.56
Poaceae 1	Poaceae	0.80	2	0.066	0.68	0.007	0.43	0.55
Vellozia candida	Velloziaceae	0.52	2	0.066	0.68	0.004	0.28	0.48
Begonia lossiae	Begoniaceae	0.44	2	0.066	0.68	0.004	0.23	0.46
Cyrtocymura scorpioides	Asteraceae	0.44	2	0.066	0.68	0.004	0.23	0.46
Phyllanthus niruri	Phyllanthaceae	0.40	2	0.066	0.68	0.003	0.21	0.45
Melinis minutiflora	Poaceae	0.40	2	0.066	0.68	0.003	0.21	0.45
Asteraceae 1	Asteraceae	0.28	2	0.066	0.68	0.002	0.15	0.41
Peperomia incana	Piperaceae	0.24	2	0.066	0.68	0.002	0.13	0.40
Alcantarea extensa	Bromeliaceae	0.60	1	0.033	0.34	0.005	0.32	0.33
Indeterminate	Indeterminate	0.60	1	0.033	0.34	0.005	0.32	0.33
Zygopetalum maculatum	Orchidaceae	0.28	1	0.033	0.34	0.002	0.15	0.24
Mandevilla ibitubana	Apocynaceae	0.24	1	0.033	0.34	0.002	0.13	0.23
Asteraceae 3	Asteraceae	0.20	1	0.033	0.34	0.002	0.11	0.22
Pseudolaelia canaanensis	Orchidaceae	0.10	1	0.033	0.34	0.001	0.05	0.20

Total	188.12		9.80	100	1.57	100	100

Table S7 – Phytosociological parameters and species sampled in Pedra dos Pontões inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Vellozia plicata	Velloziaceae	32.28	25	0.833	15.53	0.269	32.95	24.24
Alcantarea patriae	Bromeliaceae	24.00	23	0.766	14.29	0.200	24.50	19.39
Vellozia candida	Velloziaceae	15.28	17	0.566	10.56	0.127	15.60	13.08
Epidendrum secundum	Orchidaceae	4.72	20	0.666	12.42	0.039	4.82	8.62
Trilepis lhotzkiana	Cyperaceae	2.98	13	0.433	8.07	0.025	3.04	5.56
Doryopteris rediviva	Pteridaceae	0.20	10	0.333	6.21	0.002	0.21	3.21
Vellozia variegata	Velloziaceae	4.04	3	0.1	1.86	0.034	4.12	2.99
Serpocaulon latipes	Polypodiaceae	0.42	8	0.266	4.97	0.004	0.43	2.70
Pleroma castellense	Melastomataceae	2.40	4	0.133	2.48	0.020	2.45	2.47
Coleocephalocereus pluricostatus	Cactaceae	1.08	6	0.2	3.73	0.009	1.10	2.41
Selaginella convoluta	Selaginellaceae	1.48	5	0.166	3.11	0.012	1.51	2.31
Barbacenia tomentosa	Velloziaceae	3.00	1	0.033	0.62	0.025	3.06	1.84
Pseudobombax grandiflorum	Malvaceae	1.32	2	0.066	1.24	0.011	1.35	1.29
Cololobus rupestris	Asteraceae	1.80	1	0.033	0.62	0.015	1.84	1.23
Cyperus pohlii	Cyperaceae	0.16	3	0.1	1.86	0.001	0.16	1.01
Telmatoblechnum serrulatum	Blechnaceae	0.04	3	0.1	1.86	0.000	0.04	0.95
Clusia mexiae	Clusiaceae	1.20	1	0.033	0.62	0.010	1.22	0.92
Indeterminate	Indeterminate	0.36	2	0.066	1.24	0.003	0.37	0.80
Cyrtopodium glutiniferum	Orchidaceae	0.34	2	0.066	1.24	0.003	0.35	0.79
Prescottia plantaginifolia	Orchidaceae	0.08	2	0.066	1.24	0.001	0.08	0.66
Microgramma squamulosa	Polypodiaceae	0.06	2	0.066	1.24	0.001	0.06	0.65
Pleroma heteromallum	Polypodiaceae	0.32	1	0.033	0.62	0.003	0.33	0.47
Eremanthus crotonoides	Asteraceae	0.08	1	0.033	0.62	0.001	0.08	0.35
Ripsalis sp.	Cactaceae	0.08	1	0.033	0.62	0.001	0.08	0.35
Anemia sp.	Anemiaceae	0.08	1	0.033	0.62	0.001	0.08	0.35
Paliavana prasinata	Gesneriaceae	0.06	1	0.033	0.62	0.001	0.06	0.34
Pitcairnia flammea	Bromeliaceae	0.04	1	0.033	0.62	0.000	0.04	0.33
Zygopetalum maculatum	Orchidaceae	0.04	1	0.033	0.62	0.000	0.04	0.33
Hatiora cylindrica	Cactaceae	0.02	1	0.033	0.62	0.000	0.02	0.32
Total		97.96		5.37	100	0.82	100	100

Table S8 – Phytosociological parameters and species sampled in Pedra do Submarino inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Vellozia plicata	Velloziaceae	62.80	30	1	15.87	0.523	41.39	28.63
Trilepis lhotzkiana	Cyperaceae	15.92	20	0.666	10.58	0.133	10.49	10.54
Vellozia variegata	Velloziaceae	12.24	16	0.533	8.47	0.102	8.07	8.27
Vriesea fosteriana	Bromeliaceae	12.30	14	0.466	7.41	0.103	8.11	7.76
Dyckia saxatilis	Bromeliaceae	9.32	16	0.533	8.47	0.078	6.14	7.30
Vellozia candida	Velloziaceae	7.20	13	0.433	6.88	0.060	4.74	5.81

Pseudolaelia vellozicola	Orchidaceae	4.56	16	0.533	8.47	0.038	3.01	5.74
Marsdenia loniceroides	Apocynaceae	2.52	11	0.366	5.82	0.021	1.66	3.74
Pleroma subsessile	Melastomataceae	3.72	9	0.3	4.76	0.031	2.45	3.61
Alcantarea extensa	Bromeliaceae	6.76	5	0.166	2.65	0.056	4.45	3.55
Mandevilla lucida	Apocynaceae	2.48	8	0.266	4.23	0.021	1.63	2.93
Clusia criuva	Clusiaceae	1.60	4	0.133	2.12	0.013	1.05	1.59
Scleria sp.	Cyperaceae	1.48	3	0.1	1.59	0.012	0.98	1.28
Anemia sp.	Anemiaceae	0.48	4	0.133	2.12	0.004	0.32	1.22
Barbacenia tomentosa	Velloziaceae	1.20	3	0.1	1.59	0.010	0.79	1.19
Cololobus rupestris	Asteraceae	0.88	2	0.066	1.06	0.007	0.58	0.82
Lepidaploa cotoneaster	Asteraceae	0.80	2	0.066	1.06	0.007	0.53	0.79
Vanhouttea calcarata	Gesneriaceae	1.40	1	0.033	0.53	0.012	0.92	0.73
Pseudobombax sp.	Malvaceae	1.00	1	0.033	0.53	0.008	0.66	0.59
Bulbostylis sp.	Cyperaceae	0.16	2	0.066	1.06	0.001	0.11	0.58
Pleroma sp.	Melastomataceae	0.80	1	0.033	0.53	0.007	0.53	0.53
Epidendrum secundum	Orchidaceae	0.48	1	0.033	0.53	0.004	0.32	0.42
Pitcairnia decidua	Bromeliaceae	0.48	1	0.033	0.53	0.004	0.32	0.42
Poaceae 1	Poaceae	0.28	1	0.033	0.53	0.002	0.18	0.36
Zygopetalum maculatum	Orchidaceae	0.28	1	0.033	0.53	0.002	0.18	0.36
Poaceae 2	Poaceae	0.20	1	0.033	0.53	0.002	0.13	0.33
Acianthera teres	Orchidaceae	0.16	1	0.033	0.53	0.001	0.11	0.32
Pterocaulon alopecuroides	Asteraceae	0.12	1	0.033	0.53	0.001	0.08	0.30
Melananthus fasciculatus	Solanaceae	0.12	1	0.033	0.53	0.001	0.08	0.30
Total		151.74		6.3	100	1.265	100	100

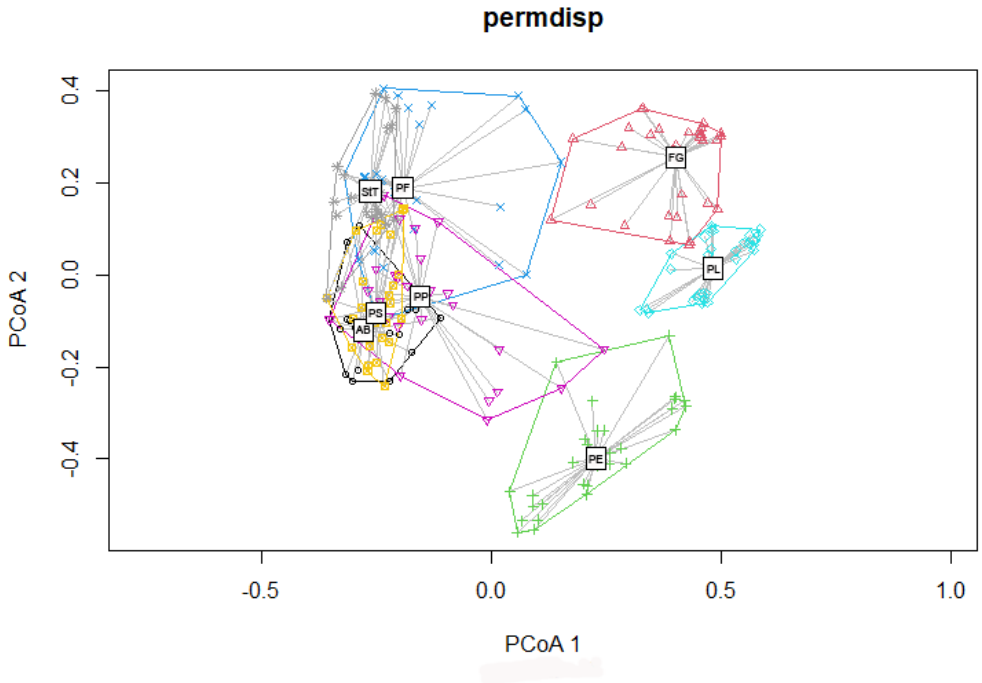
Table S9 – Phytosociological parameters and species sampled in Santa Terezinha inselberg. Parameters are organized in order decreasing of IV. Cov – Coverage (m²), K – Frequency, AF – Absolute Frequency, RF – Relative Frequency, ACo – Absolute Coverage, RCo – Relative Coverage, IV – Importance Value.

Species	Families	Cov	K	AF	RF	ACo	RCo	IV
Vellozia plicata	Velloziaceae	78.00	30	1	19.74	0.650	65.22	42.48
Alcantarea extensa	Bromeliaceae	17.32	22	0.733	14.47	0.144	14.48	14.48
Pseudolaelia vellozicola	Orchidaceae	5.32	22	0.733	14.47	0.044	4.45	9.46
Coleocephalocereus decumbens	Cactaceae	4.42	19	0.633	12.50	0.037	3.70	8.10
Trilepis lhotzkiana	Cyperaceae	5.48	16	0.533	10.53	0.046	4.58	7.55
Mandevilla grazielae	Apocynaceae	0.72	8	0.266	5.26	0.006	0.60	2.93
Cheilanthes geraniifolia	Pteridaceae	0.40	8	0.266	5.26	0.003	0.34	2.80
Encholirium horridum	Bromeliaceae	1.32	5	0.166	3.29	0.011	1.10	2.20
Doryopteris collina	Pteridaceae	0.26	5	0.166	3.29	0.002	0.22	1.75
Encyclia spiritusanctensis	Orchidaceae	0.84	4	0.133	2.63	0.007	0.70	1.67
Pseudobombax longiflorum	Malvaceae	2.40	2	0.066	1.32	0.020	2.01	1.66
Cereus fernambucensis subsp. *sericifer*	Cactaceae	1.24	3	0.1	1.97	0.010	1.04	1.51
Anthurium parasiticum	Araceae	0.42	2	0.066	1.32	0.004	0.35	0.83
Philodendron edmundoi	Araceae	0.52	1	0.033	0.66	0.004	0.43	0.55
Pleroma fissinervium	Melastomataceae	0.48	1	0.033	0.66	0.004	0.40	0.53
Dioscorea campestris	Dioscoreaceae	0.20	1	0.033	0.66	0.002	0.17	0.41
Sinningia brasiliensis	Gesneriaceae	0.20	1	0.033	0.66	0.002	0.17	0.41
Anemia sp.	Anemiaceae	0.04	1	0.033	0.66	0.000	0.03	0.35

Pecluma filicula	Polypodiaceae	0.02	1	0.033	0.66	0.000	0.02	0.34
Total		119.60		5.07	100	1.00	100	100

8.2. *Figures*

Figure S1 – Differences in community composition between inselbergs (β-diversity) using multivariate analysis of dispersal (Permidisp, $p = 2.2e\text{-}16$). Inselbergs: AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra de Pontões, PS – Pedra do Submarino and StT – Santa Terezinha.



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Chapter 2

Functional strategies and environment-trait effects in Neotropical inselbergs ecosystems

Abstract

Different factors can act in the selection of species, reflecting the response and the effect of communities on ecosystem properties. Leaf traits can be used to understanding how communities are shaped by environmental filtering and the factors that influence their dynamics. The use of functional strategies enables the assessment of the strategies in a standardized way, aiming to conclusions about the relationships between environmental fine-scale and plant species making it possible to understand how the balance between dominant and subordinate species may change in response to environmental disturbance. Due to harsh conditions we expect to find strategy related to both C- and S-corner, reflect the functional variability of species and the positive relationship between stable edaphic microhabitat variability and strategy specialization. We also expected species with more conservative traits at more limited environments, while at less limited conditions we expected to find species with more acquisitive traits. We used data from eight Neotropical inselbergs in Espírito Santo State, southeastern Brazil. Environmental drivers were characterized at each sampling unit. We used functional traits related with leaf economics spectrum and the strategies derived from CSR method of each plant species weighted by CWM. A contrasting pattern was observed in the coordinate's analysis between the species-functional traits, as well as at plot-environmental variables. Functional strategies showed a diversity of categories, with most species exhibits highly stress-tolerant and conservative strategies, representing the extremes of leaf economics and size spectra. Despite a strong edaphic filter selecting stress tolerance and conservative characteristic, fine-scale variability was capable of explaining the slight functional differences between species and their response to stable edaphic microhabitat variability in Neotropical inselbergs ecosystems.

Keywords: leaf economics spectrum; functional traits; environment drives; edaphic filters; CSR; rock outcrop; biodiversity conservation; Atlantic Forest

1. Introduction

The traits of a community can be the source for understanding how communities were set up and what factors influence the dynamics (Zakharova et al., 2019). Leaf traits can contribute in different ways to the construction of the functional characteristics of the community, through different processes (Dong et al., 2020). Different factors can act in the selection of species in a community through traits, consequently, the resulting functional structure represents both the response and the effect of communities on ecosystem properties (Lavorel & Garnier, 2002). Thus, different functional traits can demonstrate individual responses to different gradients, which means that important changes in diversity can occur with minimal change in richness, which can explain variations in the ecosystem (*e.g.* productivity and resilience) that richness cannot (Cadotte et al., 2011; Funk et al., 2017).

The relationship between environmental conditions and vegetation characteristics is a framework that allows us to understand the environmental filtering processes that governed the selection of species in the community (Lavorel & Garnier, 2002; Funk et al., 2017). The use of CSR strategies proposed by Pierce et al. (2017) makes it possible to assess the strategies in a standardized way with few foliar traits, even if the predictive power is reduced, it can contribute to investigating the response mechanisms of the communities (Pierce et al., 2017; Rosado & Mattos, 2017). The future application of CSR analysis in biogeographic and ecological contexts may allow general conclusions about the relationships between microsite factors and plant species and will make it possible to understand how the balance between dominant and subordinate species may change in response to environmental disturbance (Pierce et al., 2017).

Granite inselbergs have proven to be useful landscapes for pursuing studies of biogeographical patterns and processes (Porembski & Barthlott, 2000; Hopper et al., 2021), due to prominent features in the surrounding landscape (Porembski, 2007) and island-like outcrops of granite or gneissic rock (Hopper et al., 2021). They are characterized by extreme edaphic and microclimatic conditions, such as the scarcity of water and nutrients in the soil, few alternatives for fixing roots, seeds, and propagules, in addition to excessive exposure to wind, light, and abrupt daily thermal variation (Porembski, 2007). Typically, old, climatically buffered, infertile landscapes (OCBILs; Hopper, 2009) as inselbergs, are hypothesized to be rich in species and endemics, low dispersability and high clonality in many plants, as well as reduced extinction, marked palaeoendemism, small isolated populations, and adaptations to low-fertility soils (Hopper et al., 2021). The combination of all these attributes has been a challenge for the understanding of patterns of taxonomic, ecological, climate and

biogeographical, restoration and conservation biology studies (Pinto-Junior et al., 2020a; de Paula et al., 2021; Hopper et al., 2021).

Plant communities in inselbergs (*e.g*. ephemeral flush vegetation, monocotyledonous mats, and rock pools) are not randomly assembled, the composition of the community is differentiated from the surrounding matrix (Porembski et al., 2000). This feature is mainly due to the predominant ecological filters such as lack of soil, water, and high temperatures (Porembski & Barthlott, 2000; Porembski, 2007). These filters may also play an important role in structuring the different plant communities found in inselbergs (Porembski et al., 2000; Porembski, 2007), as well as help to predict and manage changes in ecosystem services and conservation and restoration strategies in the current scenario of global changes (de Bello et al., 2010; Drenovsky et al., 2012). Given the increasing destruction of natural systems and the extreme vulnerability of inselbergs to invasive species (Hopper et al., 2009), an approach based on functional traits can be a powerful way to understand the structure, dynamics, and the effect of the environment on the functional trait of inselberg plant communities (de Paula et al., 2015).

In the present study, we aimed to assess the relative importance of CSR-strategies to community assembly of different plant communities, as well as the effect of the environment at a fine-scale on functional traits (including CSR-strategies) in Neotropical inselbergs vegetation inserted on one regional gradient of Atlantic Forest. Thus, firstly we tested an initial hypothesis that a) a prevalence of stress tolerance strategies (S-strategy) is evident in the plant community, due to harsh conditions present in inselberg communities, furthering species with traits characteristic of a conservative stress resistance syndrome (Negreiros et al., 2014). Therefore, we expected b) despite the strong edaphic environmental filtering for stress tolerance, a strategy related to both C- and S-corner, reflect the functional variability of species and the positive relationship between stable edaphic microhabitat variability and strategy specialization. Regarding the effect of environment on the functional trait, we expected to c) find species with more conservative traits (small leaf area, high leaf dry matter content, and lower specific leaf area) at more limited environments (shallow soil, great slope), while at less limited conditions we expected to find species with more acquisitive traits, such as larger leaf area, lower leaf dry matter content and higher specific leaf area.

2. Materials and Methods

2.1. *Study area*

We studied eight inselbergs inserted in the Atlantic Forest matrix and distributed from north to south of Espírito Santo State, southeastern Brazil (Fig. 1). The rupicolous vegetation in inselbergs can be found between 0 and 1,480 m a.s.l., and is mainly associated with plant communities formed by monocotyledonous mats of Bromeliaceae, Cactaceae, Cyperaceae, and Velloziaceae distributed in patches and/or shrubs (Porembski, 2007; Pinto-Junior et al., 2020a) (more details in Table S1).

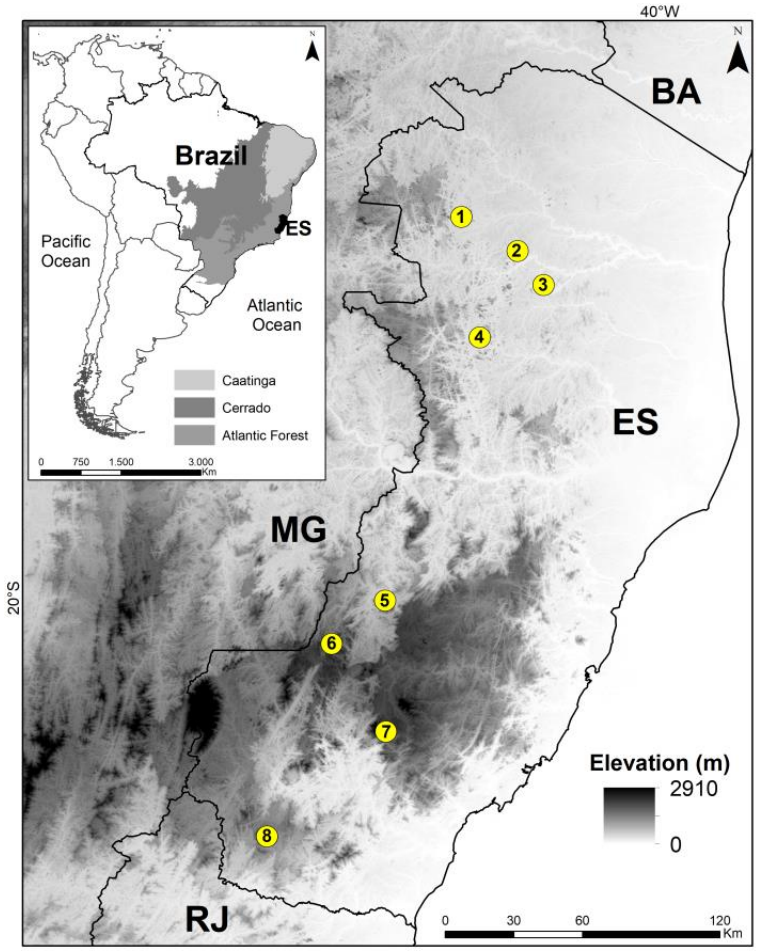

Figure 1 – Locations of inselbergs sampled in this study in relation to north-south gradient from Espírito Santo State, southeastern Brazil. Communities' number follows the sequence of one to eight: 1 - Santa Terezinha (Ecoporanga), 2 - Pedra da Figueira (Vila Pavão), 3 - Pedra do Elefante (Nova Venécia), 4 - Águia Branca (Águia Branca), 5 - Pedra da Lajinha (Afonso Cláudio), 6 - Pedra do Submarino (Brejetuba), 7 - Forno Grande (Castelo) and 8 - Pedra dos Pontões (Mimoso do Sul).

2.2. *Vegetation sampling*

In each inselberg, 30 sampling units of 4 m² (2 x 2 m) were allocated randomly, distributed between small (≤ 4 m²) and larger patches (≥ 4 m²) with a minimum distance between patches of 5 m. The minimum size for the inclusion of a vegetation patch has been standardized at 0.5 m². On the larger patches, more than one sampling unit was sampled to represent the entire extent of the patch. In each sample, a survey of all species present was carried out, as well as the cover value (percentage of specie per plot) of each species.

2.3. *Selection and measurements of traits*

The selection of species for the functional traits measurements was done through the Importance Value (IV) of each species in each community, considering as a minimum inclusion value of IV ≥ 1 to species selection. At the end we selected, collected, and measured functional traits of 107 species across the eight inselbergs. Functional traits were collected in the rainy season (January to March of 2019 and 2020), considering the most favorable growth period. All measurements followed the standardized protocols described by Pérez-Harguindeguy et al. (2013). To quantify functional traits, two leaves per individual (totaling 10 individuals per species) of mature, fully expanded, and without signs of herbivory, pathogens, or malformation were collected in the field. The collected material was immediately saturated using a water spray and packed in moist paper bags and sealed in a plastic bag. The leaves were kept in a refrigerator at 4ºC for a minimum of 12 h to achieve complete turgidity before measurements. Measurements of leaves (including the petiole) were taken until 48 h of collection.

We selected functional traits to reflect plant ecological strategies (Grime et al., 1997) and leaf economics spectrum in the harsh environmental conditions of inselbergs. We sampled five functional traits: mature plant height (H), leaf area (LA), leaf thickness (LT), leaf dry matter content (LDMC), and specific leaf area (SLA) (Pérez-Harguindeguy et al., 2013). Mature plant height was measured in the field with a graduated tape; leaf area was obtained using a desktop scanner and the software ImageJ (Schneider et al., 2012) calibrated by known area. Curved leaves were cut and positioned on the glass to complete contact with the scanner surface. Leaf fresh weight was obtained from turgid leaves (surfaces were dried with soft towel paper) and leaf dry weight was determined with an analytic scale (precision of 0.001 mg) after 96 h of drying in an oven at 60ºC. Leaf thickness was obtained with the use of a digital caliper (Digimess® 100.174BL, precision of 0,01mm). Final measurements of each trait include 20 leaves to generate an average value for each species.

2.4. *Environmental drivers*

We measured for each sample the following environmental drivers: soils depth, patch area, slope, chemical and physical soil properties. The soil depth down to the lithic contact was measured with a graduated ruler in five points of each plot. Patch area was determined measured the two axes of the patch and calculated as the ellipse area. Slope measurements were taken at the patch center using a clinometer. These drivers were chosen because they are already known for being key variables in structuring species diversity in plant communities arranged in vegetation patches (Ribeiro et al., 2007; de Paula et al., 2015; Campos et al., 2021). The soil's chemical and physical properties were determined for each plot. A composite sample of three surface soil subsamples (0–10 cm depth) was collected. Samples were air-dried and sifted through a 2 mm mesh sieve. The analyses included: granulometry (clay, silt, coarse and fine sand contents); active acidity (pH) in water; exchangeable potassium (K^{+}), sodium (Na^{+}), calcium (Ca^{2+}), magnesium (Mg^{2+}) and aluminium (Al^{3+}); potential acidity (H + Al); available phosphorus (P); remaining phosphorus (P-rem); sum of bases (BS); base saturation (V); aluminium saturation (m); effective cation exchange capacity (ECEC); total cation exchange capacity (CEC); micronutrients (Zn, Fe, Mn and Cu); and organic matter content (OM), according to international methods compiled by Embrapa (2017).

2.5. *CSR strategies*

Follow the protocol proposed by Pierce et al. (2017) we used three key foliar traits: SLA, LDMC, and LA, in the calculation of CSR strategies. To classification of CSR strategies, we access a Microsoft Excel spreadsheet 'StrateFy' (Pierce et al., 2017), where the value of the trait of each species was used to calculate the relative proportion (%) of Competitive, Stress-tolerance, and Ruderal selection (Grime, 2001). The representation of the CSR categories using colors was performed by converting the C, S, and R coordinates into red, green, and blue, respectively, as follows (Pierce et al., 2013; Pierce et al., 2017). Due to the share of species between inselbergs, we calculated the trait means among the shared species, reducing the number of species to 60 for calculating CSR strategies. To illustrate the most strategy dominant by inselberg and classified as competitive or stress-tolerant, we calculate the averages (between species) of foliar traits found in the community and using this information as a proxy to calculate the relative proportion of CSR strategies by inselberg. The representation of categories also was through converting the C, S, and R coordinates into red, green, and blue colors.

2.6. *Data analyses*

2.6.1. *Principal component analysis*

We performed a principal component analysis (PCA) at the species and at plot level to look for the main axes of variation and the relation between species × functional traits and, between plot × environmental variables, using the 'FactoMineR' package (Husson et al., 2017). Soil variables were standardized by logarithmic transformation (with exception of water pH because they are already expressed on a logarithmic scale) and summarized by using principal components analysis (PCA).

We used differential PCA's to extract the scores of the variability of chemical (PCA1c; Fig. S1) and physical soil properties (PCA1p; Fig. S2). To equalize their contributions on the axis and to reduce any strong correlations among soil attributes (Villa et al., 2018; Schmitz et al., 2020) we used the first axis as a proxy for soil fertility and texture in all models. The soil variables were correlated with each other (Pearson's correlation coefficient ($r > 0.7$); Fig. S3) and with PCA component scores to identify those factors most strongly associated with each PCA axes (Fig. S4; S5).

2.6.2. *Measuring community-weighted mean*

Following Garnier et al. (2004), the community-weighted mean trait (CWM-trait) values for each trait were calculated for every sample using species mean trait values and species relative cover: CWM = $\sum_{i=1}^{S} Pi \times \text{trait}_i$, where S is species richness, Pi is the proportional cover of species i, and trait_i is the trait value of species i. The traits used to calculate the CWM for each sample are H, LA, LT, LDMC, SLA, C, S, and R-strategies. We used the *dbFD* function of the 'FD' package (Laliberté et al., 2014) to calculate the CWM-traits.

2.6.3. *Testing the environmental effects*

Data normality and distribution were verified by the Shapiro–Wilk test for normality and Q-Q graphs (Crawley, 2013). The main effects of environmental variables on CWM-traits were tested using generalized linear mixed-effects models (GLMMs; Crawley, 2013) using as response variables the CWM-trait and as explanatory variables (fixed effects) the depth soil, patch area, slope, soil fertility, and texture. In all mixed models, the inselberg was included as a random factor. We used the Akaike information criterion (AIC) for the selection of the best models, with a correction for finite sample sizes (AICc) and AIC weights (Burnham & Anderson, 2002). The models with ΔAICc < 4 were considered equally parsimonious (Burnham

& Anderson, 2002). All models were calculated using the *glmer* function of the 'lme4' package (Bates et al., 2014) with Gaussian family. The significance of all models was calculated with type-II using the *Anova* function of the 'car' package (Fox & Weisberg, 2019). All analyzes were carried out in the software R 4.0.3 (R Core Team, 2020). Finally, we used the package 'ggplot2' for graphical visualization (Wickham et al., 2020).

3. Results

3.1. *Ordination of species and environmental variables*

A contrasting pattern of distribution was observed between the PCA species × functional traits among the 60 species sampled. The first two PCA axes of the overall functional trait space explained 58.5% of the total variation (Fig. 2a). The first axis (PCA1) explained 30% of the total variation in a functional trait, mainly the variability between stress-tolerant and ruderality species. The second axis (PCA2) explained 28.5% of the total variation in a functional trait and represents the variability of traits strategies associated with competitive species.

The PCA plot × environmental variables following the same contrasting pattern of distribution between the 240 plots. The first two PCA axes of the overall environmental space explained 60.9% of the total variation (Fig. 2b). The first axis (PCA1) explained 43.3% of the total variation in environmental variables, mostly by the variability among the soil fertility properties and the joint of soil textural properties, acidity, and topographic variables. The second axis (PCA2) explained 17.6% of the total variation in environmental variables by the effect of soil textural properties (mainly for the coarse sand) and the opposite effect of the joint of soil textural fine sand, silt, and micronutrient manganese. The physicochemical analysis of soils demonstrated a high acidity, with values ranging from 4.1 to 4.95 (Table S2). The entire samples showed low levels of calcium, magnesium, the sum of bases, and base saturation, revealing the oligotrophism present in the sampled soils of these inselbergs.

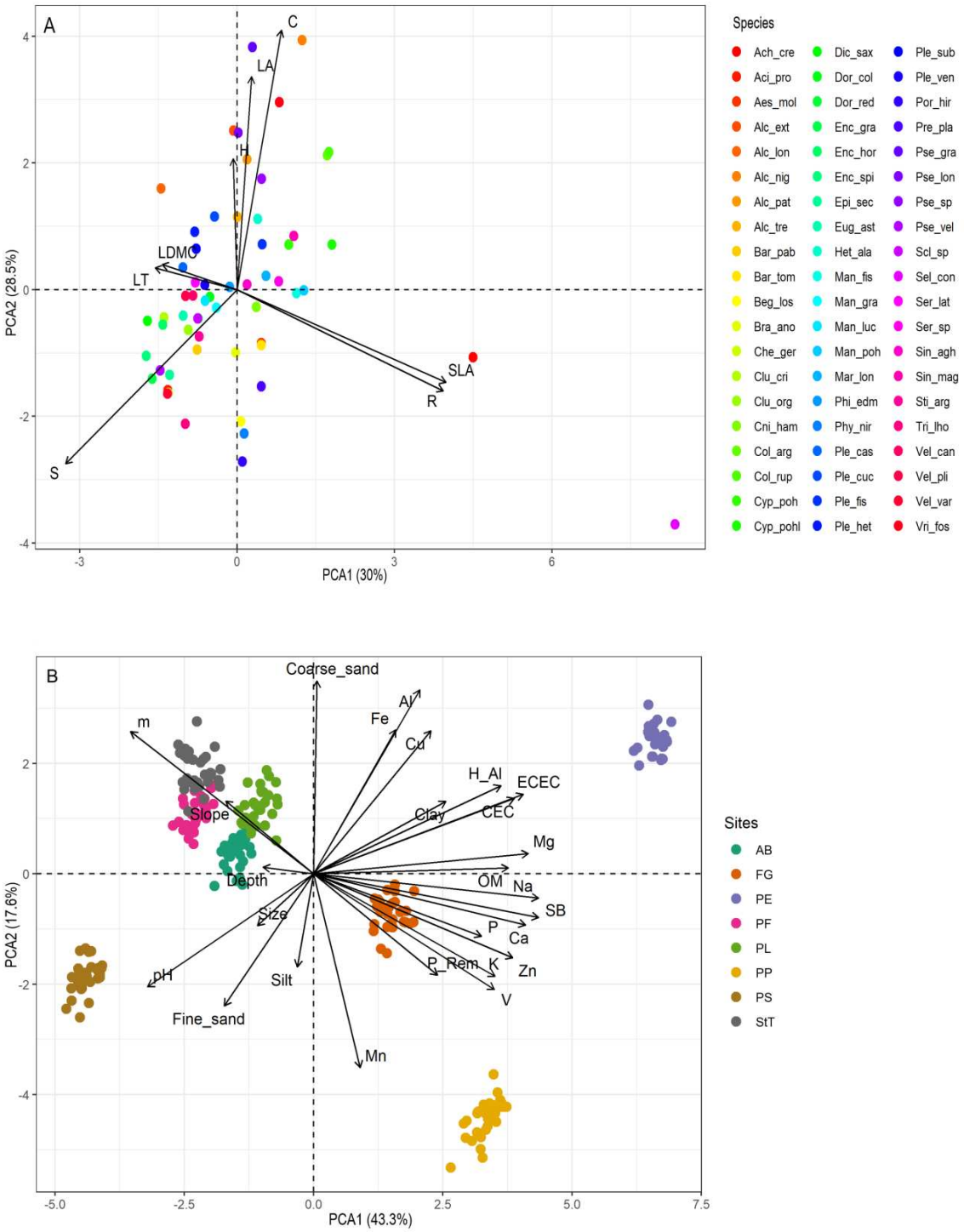

Figure 2 – Principal component analysis (PCA) between species and functional traits (A), and among sample units and environmental variables (B) of eight inselbergs from Espírito Santo State, southeastern Brazil. Species names follow Table 1. Sites: AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra dos Pontões, PS – Pedra do Submarino and StT – Santa Terezinha.

3.2. *Functional strategies*

The CSR strategies of the eight inselbergs species showed a diversity of categories, among 19 combinations (primary, secondary and tertiary types), 10 were found in our results. The species occupied mostly the region of the CSR triangle among C- and S-corner, with species, showed small leaves, high LDMC, and low SLA at the S-corner, while at the C-corner the species presented large leaves, low LDMC, and high SLA values (Fig. 3a; b). Only two species, *Achetaria crenata* (Ronse & Philcox) V.C.Souza and *Selaginella convoluta* (Arn.) Spring, showed ruderality strategy and occupied the R-corner (Fig. 3a; b). Sixty species belonging to 22 families were surveyed in this study (Table 1). The category most abundant were CS with 19 species (31.66%), follow by S/CS with 13 species (21.66%), C/CS with 9 (15%), S with 8 (13.33%), C and S/CSR with 3 (5% each category), CS/CSR with 2 (3.33%) and R, R/CR and S/SR with 1 species (1.66% each category) (Fig. 2a). Plant species showed similar patterns of range values, the competitive strategy showed values between 0% and 94%, stress-tolerant between 0% and 90%, and ruderality between 0% and 100%. The most competitive species was *Alcantarea nigripetala* Leme & L.Kollmann exhibiting a CSR signature of 94:6:0% (C:S:R), while the most stress-tolerant was *Portulaca hirsutissima* Cambess. and *Vellozia variegata* Goethart & Henrard exhibiting a CSR signature of 0:90:9% and 10:90:0% (C:S:R), respectively. Following the same pattern, the ruderality was represented by *S. convoluta* exhibiting a CSR signature of 0:0:100% (C:S:R).

When analyzed the CSR strategies among species in each inselberg we found a similar pattern found in the regional species scale, the category most representative in half of the sites (four of eight) was the CS category with an average of 35% of species in each inselberg, follow by S/CS category in three communities (37.5% of regional scale) with an average of 45% of species in each inselberg. Only one inselberg (12.5% of regional scale; Pedra do Elefante) showed S category as the most representative, with 31% of species exhibiting the stress-tolerance strategy (Fig. S6). The CSR strategies by inselbergs revealed a pattern similar to the regional species scale; with 62.5% (five of eight inselbergs) the C/CS category was the most representative, following by the S/CS category with 37.5% of inselbergs (Fig. 3c).

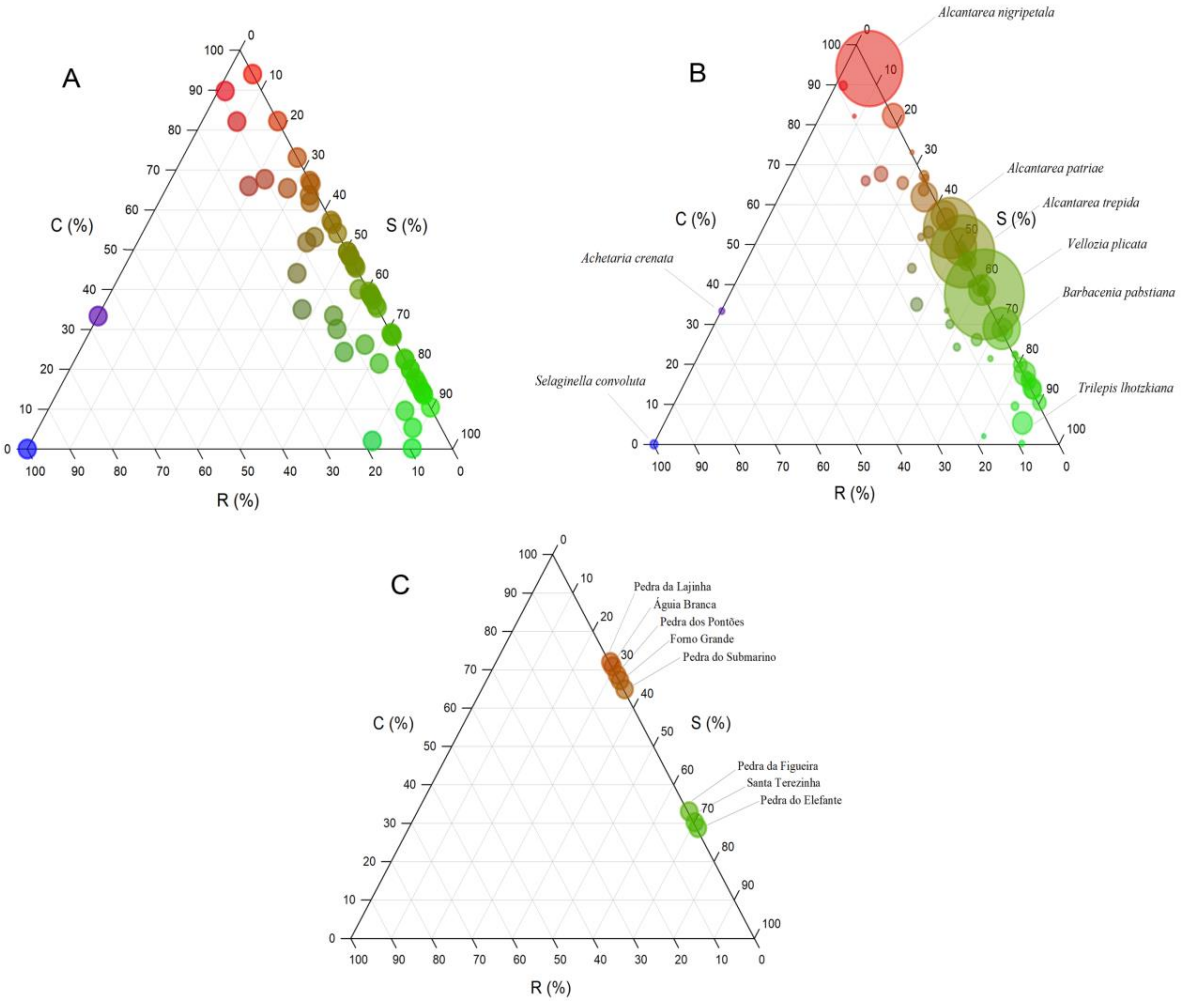

Figure 3 – CSR-strategies of 60 species sampled in inselberg communities from Espírito Santo State, southeastern Brazil. The strategies initials corresponded to C: competitiveness, S: stress tolerance, and R: ruderalism, generated through the StrateFy analytical tool available from Pierce et al. (2017). A – Species are represented without IV (Importance Value); B – Species represented by their proportion of IV and highlighted the most representative in each strategy. C – CSR-strategies of each inselbergs communities studied.

Table 1 – Functional strategies and respective functional strategies from eight inselbergs in Espírito Santo State, southeastern Brazil.

Species	Family	LA	LDMC	SLA	C:S:R	Strategy class
Acianthera prolifera (Herb. ex Lindl.) Pridgeon & M.W.Chase	Orchidaceae	1394	11.68	5.35	14:86:0	S
Aeschynomene mollicula Kunth	Fabaceae	1759	35.50	13.66	30:58:12	S/CSR
Alcantarea extensa (L.B.Sm.) J.R.Grant	Bromeliaceae	48818	23.12	5.44	57:43:0	CS
Alcantarea longibracteata Leme & Fraga	Bromeliaceae	29045	19.90	7.27	49:51:0	CS
Alcantarea nigripetala Leme & L.Kollmann	Bromeliaceae	46546	19.13	8.78	94:6:0	C
Alcantarea patriae Versieux & Wand.	Bromeliaceae	42582	19.38	8.24	54:46:0	CS
Alcantarea trepida Versieux & Wand.	Bromeliaceae	29472	16.15	8.30	48:52:0	CS
Barbacenia pabstiana L.B.Sm. & Ayensu	Velloziaceae	1009	33.55	8.2	29:71:0	S/CS
Barbacenia tomentosa Mart.	Velloziaceae	1511	30.31	12.6	33:55:11	S/CSR
Begonia lossiae L.Kollmann	Begoniaceae	822	7.40	13.97	10:84:6	S
Bradea anomala Brade	Rubiaceae	776	30.92	11.30	26:66:8	S/CS

Cheilanthes geraniifolia (Weath.) R.M.Tryon & A.F.Tryon	Pteridaceae	863	26.15	5.42	14:86:0	S
Clusia criuva Cambess.	Clusiaceae	2413	27.96	4.26	23:77:0	S/CS
Clusia organensis Planch. & Triana	Clusiaceae	1671	17.06	7.80	17:83:0	S/CS
Cnidoscolus hamosus Pohl	Euphorbiaceae	844	32.19	13.13	24:62:13	S/CSR
Cololobus argenteus M.Monge & Semir	Asteraceae	5612	17.86	11.73	82:8:10	C
Cololobus rupestres (Gardner) H.Rob.	Asteraceae	6893	16.82	11.53	90:2:9	C
Cyperus pohlianus (Nees) Kuntze	Cyperaceae	5778	20.67	14.01	66:19:15	C/CS
Cyperus pohlii (Nees) Steud.	Cyperaceae	4249	21.97	11.06	65:28:6	C/CS
Doryopteris collina (Raddi) J.Sm.	Pteridaceae	2976	31.44	6.88	45:55:0	CS
Doryopteris rediviva Fée	Pteridaceae	2488	35.94	7.23	38:62:0	CS
Dyckia saxatilis Mez	Bromeliaceae	4835	23.55	2.45	29:71:0	S/CS
Encholirium gracile L.B.Sm.	Bromeliaceae	1431	17.44	4.33	16:84:0	S
Encholirium horridum L.B.Sm.	Bromeliaceae	5473	17.78	3.53	28:72:0	S/CS
Encyclia spiritusanctensis L.C.Menezes	Orchidaceae	2058	22.68	1.67	20:80:0	S/CS
Epidendrum secundum Jacq.	Orchidaceae	1257	13.40	5.98	14:86:0	S
Eugenia astringens Cambess.	Myrtaceae	944	42.98	9.44	22:78:0	S/CS
Heterocondylus alatus (Vell.) R.M.King & H.Rob.	Asteraceae	1730	20.08	8.56	67:33:0	C/CS
Mandevilla fistulosa M.F.Sales et al.	Apocynaceae	1755	28.32	14.91	35:47:18	CS/CSR
Mandevilla grazielae M.F.Sales et al.	Apocynaceae	985	27.43	8.83	36:64:0	S/CS
Mandevilla lucida Woodson	Apocynaceae	2213	33.88	7.75	39:61:0	CS
Manihot pohlii Wawra	Euphorbiaceae	6320	35.14	16.99	44:41:15	CS/CSR
Marsdenia loniceroides (Hook.) E.Fourn.	Apocynaceae	3277	25.60	11.11	53:41:6	CS
Matourea crenata (Ronse & Philcox) Colletta & V.C.Souza	Plantaginaceae	393.5	13.76	19.07	33:0:67	R/CR
Philodendron edmundoi G.M.Barroso	Araceae	15967	10.76	6.85	38:62:0	CS
Phyllanthus niruri L.	Phyllanthaceae	41	30.10	12.87	2:80:18	S/SR
Pleroma castellense (Brade) P.J.F.Guim. & Michelang.	Melastomataceae	2305	34.55	5.42	39:61:0	CS
Pleroma cucullatum F.S.Mey., Fraga & R.Goldenb.	Melastomataceae	4268	27.35	6.14	57:43:0	CS
Pleroma fissinervium Schrank et Mart. ex DC.	Melastomataceae	5728	25.66	10.41	62:36:3	C/CS
Pleroma heteromallum (D.Don) D.Don	Melastomataceae	4957	34.07	5.10	49:51:0	CS
Pleroma subsessile F.S.Mey. & L.Kollmann	Melastomataceae	4781	34.66	5.09	48:52:0	CS
Pleroma venetiense F.S.Mey., L.Kollmann & R.Goldenb.	Melastomataceae	2325	28.69	5.60	46:54:0	CS
Portulaca hirsutissima Cambess.	Portulacaceae	29	8.89	15.67	0:90:9	S
Prescottia plantaginifolia Lindl. ex Hook.	Orchidaceae	4162	9.40	14.67	21:72:7	S/CS
Pseudobombax grandiflorum (Cav.) A.Robyns	Malvaceae	40356	35.94	7.26	73:27:0	C/CS
Pseudobombax longiflorum (Mart.) A.Robyns	Malvaceae	24174	37.28	6.69	67:33:0	C/CS
Pseudobombax sp.	Malvaceae	20364	36.87	10.67	64:34:2	C/CS
Pseudolaelia vellozicola (Hoehne) Porto & Brade	Orchidaceae	1322	30.34	3.67	18:82:0	S/CS
Scleria sp.	Cyperaceae	2553	40.17	8.37	35:65:0	S/CS
Selaginella convoluta (Arn.) Spring	Selaginellaceae	2.32	10	46.56	0:0:100	R
Serpocaulon latipes (Langsd. & Fisch.) A.R.Sm.	Polypodiaceae	5406	38.62	6.09	46:54:0	CS
Serpocaulon sp.	Polypodiaceae	7194	32.04	13.02	52:40:8	CS
Sinningia aghensis Chautems	Gesneriaceae	18013	13.25	11.27	40:58:2	CS
Sinningia magnifica (Otto & A.Dietr.) Wiehler	Gesneriaceae	3502	20.02	11.74	68:22:10	C/CS
Stillingia argutedentata Jabl.	Euphorbiaceae	2283	18.54	8.56	20:80:0	S/CS

Trilepis lhotzkiana Nees ex Arn.	Cyperaceae	138	53.16	11.82	5:88:7	S
Vellozia candida J.C.Mikan	Velloziaceae	3064	38	6.08	39:61:0	CS
Vellozia plicata Mart.	Velloziaceae	3255	41.75	6.31	38:62:0	CS
Vellozia variegata Goethart & Henrard	Velloziaceae	237	42.84	9.31	10:90:0	S
Vriesea fosteriana L.B.Sm.	Bromeliaceae	36352	25.53	8.55	82:18:0	C/CS

Abbreviations: C: competitiveness (%); S: stress tolerance (%); LA: leaf area (mm^2); SLA: specific leaf area ($mm^2\ mg^{-1}$); LDMC: leaf dry matter content (%). CSR category according to Hodgson et al. (1999).

3.3. *Effect of trait-environmental relationship*

According to GLMMs models, the effect of environmental variable on functional trait were explained by topography heterogeneity, such as soil depth and slope, and also the nutrients related to soil fertility (PCA1c) (Table 2). Among the twelve models with significant values ($p \leq 0.05$), nine models were explained by topographic variables, indicating the importance these variables to environmental-trait approach (Table 2). As stated by ours bests models, an increase in soil depth on inselberg patch increase the LDMC (GLMM, $p = 0.0002$, $r^2 = 0.978$; Fig. 4a) and S-strategy (GLMM, $p = 0.03$, $r^2 = 0.976$; Fig. 4b), however the increase in soil depth has a negative effect on the LA (GLMM, $p = 1.27e\text{-}08$, $r^2 = 0.152$; Fig. 4c) and C-strategy (GLMM, $p = 0.002$, $r^2 = 0.99$; Fig. 4d). In relation to slope, ours bests models showed a positive effect on LT (GLMM, $p = 0.03$, $r^2 = 0.05$; Fig. 4e) and SLA (GLMM, $p = 0.03$, $r^2 = 0.541$; Fig. 4f). Nonetheless, the increase in slope has a negative effect on the in R-strategy (GLMM, $p = 2.20e\text{-}16$, $r^2 = 0.834$; Fig. 4g). Finally, the best models related to soil fertility showed the positive effect of nutrient content on H (GLMM, $p = 0.03$, $r^2 = 0.018$; Fig. 4h) and R-strategy (GLMM, $p = 2.20e\text{-}16$, $r^2 = 0.811$; Fig. 4i).

Table 2 – Mixed effect models predicting the relationship between functional trait and environmental variable with Gaussian error distribution (generalized linear mixed effects model). Predictors: Depth, Slope, Size, PCA1c (variability of soil chemical properties) and PCA1p (variability of soil physical properties). Response variable: H – height, LA – leaf area, LT – leaf thickness, LDMC – leaf dry matter content, SLA – specific leaf area, C – competitive, S – stress-tolerance and R – ruderal strategies. *Significant model ($p \leq 0.05$).

Response variable	Models	d.f.	Log-likelihood	AICc	ΔAICc	AICcWt
H	~ PCA1c*	4	-1542.16	3096.8	0	0.629
	~ Slope	4	-1543.87	3100.2	3.4	0.113
	~ Size	4	-1543.94	3100.3	3.6	0.105
	~ PCA1p	4	-1544.23	3100.9	4.1	0.079
	~ Depth	4	-1544.32	3101.1	4.3	0.073
LA	~ Depth*	4	-2445.48	4903.4	0	1
	~ Slope*	4	-2461.59	4935.6	32.2	< 0.001
	~ PCA1c	4	-2462.21	4936.9	33.5	< 0.001
	~ Size	4	-2463.35	4939.1	35.7	< 0.001
	~ PCA1p	4	-2463.31	4939.1	35.7	< 0.001

LT	~ Slope*	4	-1.201	14.8	0	0.595
	~ Depth	4	-2.201	16.8	2	0.219
	~ Size	4	-3.384	19.2	4.4	0.067
	~ PCA1p	4	-3.499	19.4	4.6	0.06
	~ PCA1c	4	-3.51	19.5	4.6	0.059
LDMC	~ Depth*	4	-731.001	1474.4	0	0.9679
	~ PCA1c*	4	-734.753	1481.9	7.5	0.0227
	~ Slope	4	-736.163	1484.8	10.3	0.0055
	~ PCA1p	4	-737.124	1486.7	12.2	0.0021
	~ Size	4	-737.336	1487.1	12.7	0.0017
SLA	~ Slope*	4	-357.803	728.1	0	0.611
	~ Size	4	-359.222	730.9	2.8	0.148
	~ PCA1c	4	-359.55	731.5	3.5	0.107
	~ PCA1p	4	-359.971	732.4	4.3	0.07
	~ Depth	4	-360.053	732.6	4.5	0.064
C	~ Depth*	4	-868.618	1749.7	0	0.905
	~ Slope*	4	-871.286	1755	5.3	0.063
	~ Size	4	-872.959	1758.4	8.7	0.012
	~ PCA1c	4	-873.08	1758.6	8.9	0.01
	~ PCA1p	4	-873.099	1758.6	9	0.01
S	~ Depth*	4	-875.58	1763.6	0	0.588
	~ Slope	4	-876.855	1766.2	2.6	0.164
	~ PCA1p	4	-877.366	1767.2	3.6	0.098
	~ PCA1c	4	-877.651	1767.7	4.1	0.074
	~ Size	4	-877.63	1767.7	4.1	0.076
R	~ Slope*	4	-521.669	1055.8	0	0.539
	~ Size	4	-522.786	1058	2.2	0.176
	~ PCA1c*	4	-523.032	1058.5	2.7	0.138
	~ PCA1p	4	-523.462	1059.4	3.6	0.09
	~ Depth	4	-523.905	1060.3	4.5	0.058

Abbreviations: d.f. - model degrees of freedom; AICc - Akaike information criterion for small samples; ΔAICc - difference between the AICc of a given model and that of the best model; AICcWt - Akaike weights (based on AIC corrected for small sample sizes).

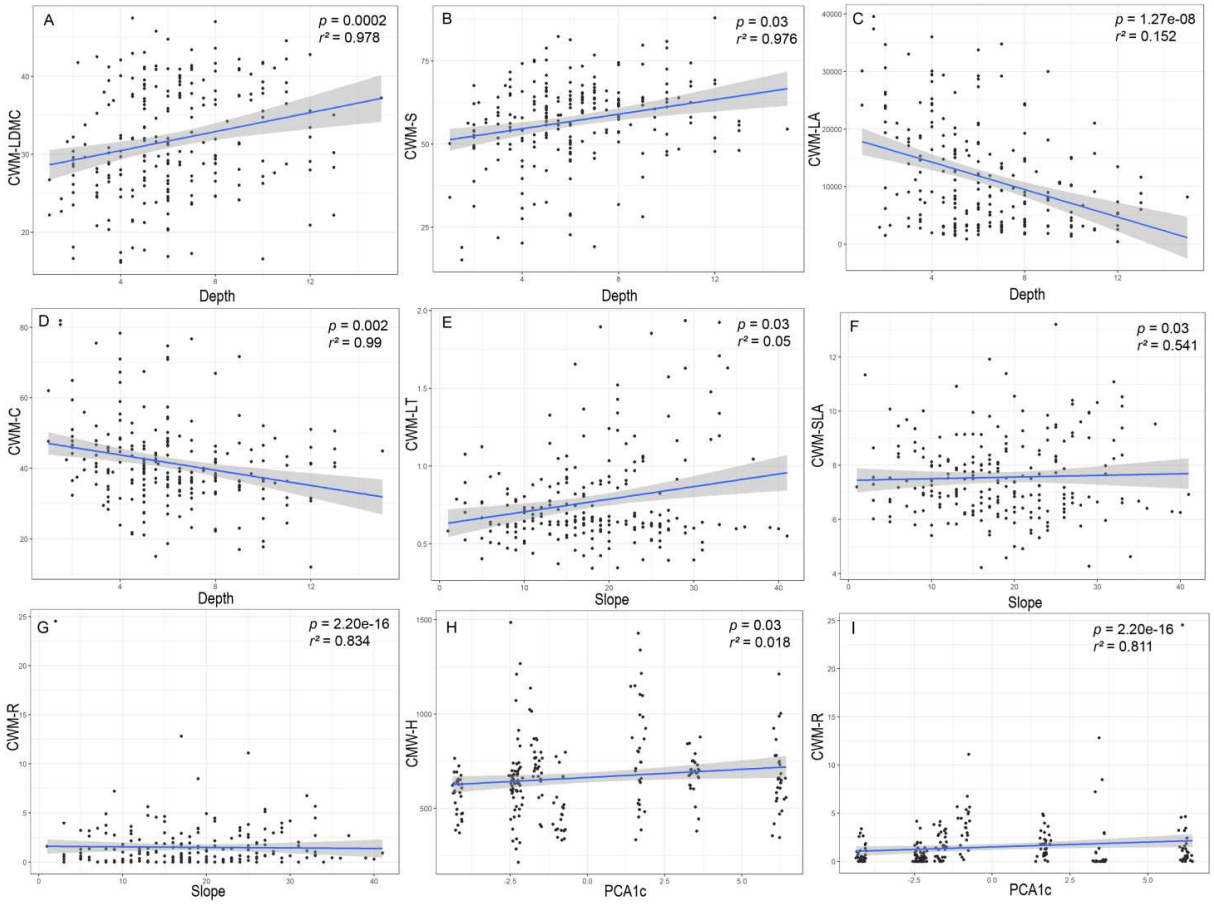

Fig. 4 – Generalized linear mixed-effects models (GLMMs) with significant effects on functional traits of inselbergs species, Espírito Santo State, southeastern Brazil. Predictors: Depth, Slope and PCA1c (variability of soil chemical properties). Abbreviations of the response variable: H – height, LA – leaf area, LT – leaf thickness, LDMC – leaf dry matter content, SLA – specific leaf area, C – competitive, S – stress-tolerance and R – ruderal strategies.

4. Discussion

Our results supported the hypothesis that despite an expected prevalence of stress tolerance strategies in inselbergs, a strategy related to both C- and S-corner would be more representative due to the positive relationship between stable edaphic microhabitat and strategy specialization inherent to inselberg vegetation. This evidence is in agreement with our first hypothesis that, even as an impoverished habitat, inselbergs can favor the coexistence of species with a conservative and acquisitive resource-use strategy. These results showing the role of environmental filters in the determination of plant functional diversity in inselberg habitats. Furthermore, the CSR-strategies and the functional traits related were explained mainly by topographic variables than soil properties, reflecting the importance of environmental heterogeneity to inselbergs community assembly. About CSR-strategies, our results showed that the majority of the inselberg community's present species with C- and S-strategy, being the

CS strategy found in most of the species followed by S/CS. Both strategies are predominating among the abundant species in each inselberg community. As expected, the functional traits of the species were associated with ecological strategies, such as competitiveness strategy associated with LA and stress-tolerant species with lower SLA, which reflected the opposite directions on the axis between S and R strategies (de Paula et al., 2015).

Although the strategies vary between the C- and S-corner of the triangle, the functional characteristics of the species were conservative resource-use syndrome with low SLA and high LDMC values (Negreiros et al., 2014; Díaz et al., 2016; Reich et al., 2014). These results were in agreement with other studies on rupicolous vegetation in environments with similar conditions such as granitic inselbergs (de Paula et al., 2015), ironstone grassland (Tameirão et al., 2021), and quartzitic rupestrian grassland (Negreiros et al., 2014). However, when compared to rupestrian grasslands (Negreiros et al., 2014; Tameirão et al., 2021), inselberg vegetation presents a greater variety of coexisting strategies. Only one species (*S. convoluta*) exhibiting a ruderality strategy, with the signature of 100% R-strategy. R-selected tropical species were evident and potentially occupy specific microsites at fine-scales, such as locally humid sites or with disturbance (Pierce et al., 2017). Another characteristic of ruderal species is the presence in the primary succession process, mainly annual therophytes, where the overall trajectory in this context is characterized by an initial shift from R- to S-strategy, with management increasing the range of strategies present and including a higher degree of C-selection relative to the other vegetation types (Pierce et al., 2017).

The impoverished soil and heterogeneity topographic of inselbergs may have acted as a major environmental filter to stress-tolerant strategy, confirming the idea that chronically unproductive environments can favor species with traits typical of stress-tolerance strategy (Grime et al., 1997; Negreiros et al., 2014; Pierce et al., 2017). On the other hand, a great number of conservative strategy species are apparently the result in the filtering of distinct functional traits promoted by slowly aggregation and turnover of nutrients in stable edaphic microhabitat. This process may reflect old disturbance events or current (and perhaps future) anthropogenic management, creating locally-rich patches and, consequently an edaphic heterogeneity selecting for a range of strategies, indicating a successional process (Pierce et al., 2017). In this sense, the contrasting CSR strategies between species have been invoked as a mechanism of coexistence and local biodiversity creation for granitic inselberg (de Paula et al., 2015; Pierce et al., 2017). Thus, the heterogeneity in ecological strategies has been related to microhabitat variability and niche partitioning, where different degrees of dominance (abundance or importance value) between CSR strategies are evident (Pierce et al., 2017).

A similar pattern has been related in xeric sand calcareous grasslands in Europe, with a mixture of stress-tolerance or competitive-ruderal herbs, the CSR strategies are markedly different between dominant and subordinate plants at the centimeter scale (Pierce et al., 2014). This pattern was also found in southeastern Brazil, quartzitic rupestrian grassland (Negreiros et al., 2014) and granitic inselberg (de Paula et al., 2015) showed opposite between competitiveness and stress-tolerance strategies, highlighting the importance of the role of fine-scale variability to rupestrian vegetation and their functional diversity. From rocky outcrops vegetation as inselberg, this functional diversity can be interpreted as the link between functional diversity and resource dynamics (Díaz & Cabido, 2001), where the differences between species found in each community can reflect the greater and complete resource use in spatially and isolated heterogeneous environment (Díaz & Cabido, 2001).

Regionally, the variation in strategies within inselbergs is likely to be influenced by the presence of contrasting growth forms or/and their importance value. Our results showed that shrubs and herbaceous species can exhibit abroad strategy diversity, since competitive until ruderalism, while generalists may exhibit strategy of R/CSR. Life forms as trees ranged from competitive to stress-tolerance, with a CS median strategy similar to the CS/CSR median strategies evident in tropical forests (Pierce et al., 2017). The presence or absence of particular strategies can be related to historical and/or phylogenetic constraints, with restriction of CSR strategies evident in some families but not others (Pierce et al., 2017). Concerning importance value, the weighting scheme reflects the idea that dominant species should have a greater influence on ecosystem processes (Díaz et al., 2007; Lavorel et al., 2011). Our results demonstrated that some genera and families had higher values of importance value, such as *Vellozia*, *Barbacenia*, and *Alcantarea*, and their respective families Velloziaceae and Bromeliaceae highlighted the great importance of these species to the functional diversity of inselbergs communities. Despite the CSR strategies by inselbergs showed a pattern similar to the regional species scale, a contrasting grouping among communities is evident (Fig. 3c). This pattern can be related to the LA of *Alcantarea* genus, which contributed to higher values of LA in competitiveness and lower values in stress-tolerance communities.

Our analyses have demonstrated that for traits related to soil chemical properties the effect of environment on functional traits following the same pattern of leaf economics spectrum, presenting a significant positive relationship with the availability of nutrient and functional traits, such as H and ruderality strategy. Nonetheless, the effect of environment on functional trait was not expected as the leaf economics spectrum (Wright et al., 2004), at more limited environments (shallow soil, great slope, and less fertility) hosts species exhibiting a strictly

conservative syndrome of resource use (stress-tolerant), such as low LA, high LDMC, and low SLA, what reflects in the contradictory pattern to respective strategies. This apparently contradictory association between high-stress tolerances with higher soil fertility was also reported to quartzitic rupestrian grassland and can be related to soil texture properties closely linked with water-retention capacity and fine soil availability (Negreiros et al., 2014). Another explanation is associated with the influence of climate variables on species composition of inselbergs communities (Pinto-Junior et al., 2020b; de Paula et al., 2021). These climate variables, mainly temperature and aridity, have been related to the prevalence of larger leaves (increase in LA) in warmer and/or stressed environments due to the lack of frost danger and effective transpirational cooling (Wright et al., 2017; Dong et al., 2020). Whereas for species that exhibiting an increase of LDMC in conservative sites, the reason for the discrepancy may be that low soil moisture can cause further reductions of stomatal conductance to prevent hydraulic conductivity loss (Martínez-Vilalta et al., 2014), and even, under very dry soil conditions, reductions in photosynthetic capacity (Zhou et al., 2013; Reich et al., 2018).

As well as the well-known positive relationship between LDMC and leaf longevity that maximizes the return on carbon invested in leaf construction (Kikuzawa et al., 2013). In the end, the increase of SLA and LT in extreme sites are related to a negative relationship between leaf trait and aridity, small leaves and consequently higher SLA and LT, allow leaves to avoid the transpiration and such overheating by remaining close to ambient air temperature, which would forbid the survival of large leaves (Dong et al., 2020). In this way, our results revealed strong contrasts among traits with the contribution on the community-mean trait, mainly to acclimation/adaptation within species vs species turnover, and reflect the processes in which plant communities achieve optimal function differ among functional traits (Dong et al., 2020). Thus, the relationship between community-mean trait and environmental variables is primarily a consequence of species turnover and requires changes in the competitive balance of coexisting species, which can enable the replacement of some or all species by others (Dong et al., 2020).

Old, climatically buffered, infertile landscapes (OCBILs; Hopper, 2009) as inselbergs are resilient to invasion by non-native exotic organisms if left undisturbed; otherwise this resilience leads to extreme vulnerability when disturbance regimes are changed (Hopper, 2009). From a functional point of view, low-resource environments are vulnerable to biological invasion (Funk et al., 2013). Some studies have reinforced the widespread impact that invaders are causing in inselberg communities (Porembski, 2000; Hopper, 2009; de Paula et al., 2015; Pinto-Junior et al., 2020a), mainly when the invasive species, as *Melinis minutiflora* P.Beauv., had high plant coverage in inselberg communities (Pinto-Junior et al., 2020a). In this way, in

impoverish habitats invasive grasses, as *M. minutiflora* and *M. repens* (Willd.) Zizka are also often restricted to disturbed and nutrient-enriched (Barbosa et al., 2010; Zenni & Ziller, 2011) or anthropized sites by so-called high altitude agriculture (Martinelli, 2007). The functional traits of invasive species can afford its persistence in more favorable micro-habitats, which can lead to exclusion or replacement of native, endemic, and/or threatened species, resulting in loss of functional and taxonomic diversity. Therefore, the biological invasion could alter the functional composition of the inselbergs, resulting in deep modifications in ecosystem processes, including water and nutrient dynamics and trophic transfers (Díaz & Cabido, 2001).

5. Conclusions

This study indicates that inselbergs exhibits highly stress-tolerant and conservative vegetation capable of dealing with the harsh conditions imposed by several environmental filtering. Our results indicating that the effect of environment on functional traits was capable of explaining the slight functional differences between species and their response to stable edaphic microhabitat variability. The CSR method provided is sufficiently sensitive to figure out the differences between plant strategies even sharing a majority of species in similar environmental conditions. We highlight the importance and support of our study to characterize the ecosystem of the inselberg through a functional approach, identifying the CSR strategies and functional traits. We also highlight that soil characteristics and functional traits need more studies to understand the rule of functional diversity in the inselberg ecosystem. Conservation actions aiming to preserve this ecosystem must take into account evident stable microhabitat specializations of the species.

6. Acknowledgments

We acknowledge the Programa de Pós-Graduação em Botânica – UFV for supporting our research in Brazil and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing scholarships to the author. We are also grateful to Luis Fernando T. Menezes and Miriam C. A. Pereira for logistical support in Espírito Santo State. We would like to thank Thais Sperandio and Fernanda Favoreto for help in fieldwork. We thank Larissa A. C. Müller for their contributions in fieldwork, methodology, ideas, and suggestions, as well as all taxonomists who also kindly helped with plant identification. We thank to Instituto Estadual do Meio Ambiente e Recursos Hídricos do Espírito Santo (IEMA) for the research license and Neotropical Grassland Conservancy (NGC) for financial supporting.

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8. Supplementary Material

8.1. *Tables*

Table S1. General descriptions of Neotropical inselbergs sampled in gradient north-south of Espírito Santo State, southeastern Brazil.

	Águia Branca	Forno Grande	Pedra do Elefante	Pedra da Figueira	Pedra da Lajinha	Pedra de Pontões	Pedra do Submarino	Santa Terezinha
Climate (Alvares et al., 2013)	Aw – Tropical zone with dry winter	Cwb – Humid subtropical zone with dry winter and temperate summer	Aw – Tropical zone with dry winter	Aw - Tropical zone with dry winter	Cwa - Humid subtropical zone with dry winter and hot summer	Cwb – Humid subtropical zone with dry winter and temperate summer	Cwa - Humid subtropical zone with dry winter and hot summer	Aw - Tropical zone with dry winter
Region	Northwest	South	Northwest	Northwest	South	South	South	Northwest
Mean annual temperature (Fick & Hijmans, 2017)	23.6°C	15.4ºC	22.8ºC	23.5ºC	19.8ºC	18.7ºC	18.3ºC	23.4ºC
Mean annual precipitation (Fick & Hijmans, 2017)	1,153 mm	1,392 mm	1,190 mm	1,169 mm	1,300 mm	1,279 mm	1,331 mm	1,136 mm
Forest matrix (Garbin et al., 2017)	Dense Ombrophylous Forest	Dense Ombrophylous Forest Montane	Dense Ombrophylous Forest	Dense Ombrophylous Forest	Dense Ombrophylous Forest	Seasonal Semideciduous Forest	Open Ombrophylous Forest	Dense Ombrophylous Forest
Elevation	260 m a.s.l.	1,480 m a.s.l.	675 m a.s.l.	123 m a.s.l.	789 m a.s.l.	980 m a.s.l.	1,150 m a.s.l.	410 m a.s.l.
Municipalities	Águia Branca	Castelo	Nova Venécia	Vila Pavão	Afonso Cláudio	Mimoso do Sul	Brejetuba	Ecoporanga
Geographic Coordenates	18°58'26.1" S 40°42'26.9" W	20°30'40.1" S 41°05'26.5" W	18°46'07.3" S 40°27'4.1" W	18°39'9.4" S 40°33'11.9" W	20°00'38.8" S 41°05'04.7" W	20°56'25.4" S 41°32'46.7" W	20°10'32.4" S 41°17'10.7" W	18°29'16.09" S 40°48'27.2" W
Status	Private	State Park	Environmental Protection Area	Private	Private	Private	Private	Private

Table S2 - Physicochemical parameters of soil samples from eight inselbergs in Espírito Santo State, southeastern Brazil.

	Values	**Min/Max**
pH (H_2O)	4.4 ± 0.24	4.1/4.97
P (mg/dm^3)	15.5 ± 4.49	8.5/21.7
K (mg/dm^3)	55.12 ± 18.5	35/82
Na(mg/dm^3)	1.33 ± 1.94	0/4.91
Ca^{2+} ($cmol_c/dm^3$)	0.47 ± 0.28	0.24/0.92
Mg^{2+} ($cmol_c/dm^3$)	0.13 ± 0.09	0.06/0.35
Al^{3+} ($cmol_c/dm^3$)	1.7 ± 0.37	1.18/2.17
H+Al ($cmol_c/dm^3$)	13.92 ± 2.99	8.9/18.2
SB ($cmol_c/dm^3$)	0.76 ± 0.40	0.42/1.47
ECEC ($cmol_c/dm^3$)	2.46 ± 0.63	1.61/3.64
CEC ($cmol_c/dm^3$)	14.68 ± 3.26	9.33/19.67
V (%)	5.06 ± 2.03	2.9/8.7
m (%)	70.25 ± 10.44	49.8/81.7
OM (dag/kg)	15.32 ± 4.12	9.78/21.52
P-Rem (mg/L)	35.35 ± 6.26	22.9/43.3
Cu (mg/dm^3)	0.32 ± 0.08	0.24/0.5
Mn (mg/dm^3)	5.55 ± 3.31	1.8/11.2
Fe (mg/dm^3)	103.16 ± 30.3	69.7/155.1
Zn (mg/dm^3)	2.25 ± 1.05	1.1/3.62
Coarse sand (kg/kg)	0.60 ± 0.05	0.51/0.67
Fine sand (kg/kg)	0.14 ± 0.05	0.07/0.23
Silt (kg/kg)	0.08 ± 0.05	0.004/0.15
Clay (kg/kg)	0.16 ± 0.03	0.13/0.24

± Standard deviation; cmolc - centimoles of charge; dag - decagram

8.2. *Figures*

Figure S1 – Principal Component Analysis (PCA) for the soil chemical properties of eight inselberg from Espírito Santo State, Brazil. Sites: AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra dos Pontões, PS – Pedra do Submarino and StT – Santa Terezinha. The chemical properties: pH – active acidity in water; K – exchangeable potassium, Na – sodium, Ca – calcium, Mg – magnesium, Al – aluminium, H + Al potential acidity, P – available phosphorus, P-rem – remaining phosphorus, BS – sum of bases, V – base saturation, m – aluminium saturation, ECEC – effective cation exchange capacity, CEC – total cation exchange capacity, Zn – zinc, Fe – irons, Mn – manganese, Cu – copper and OM – organic matter content.

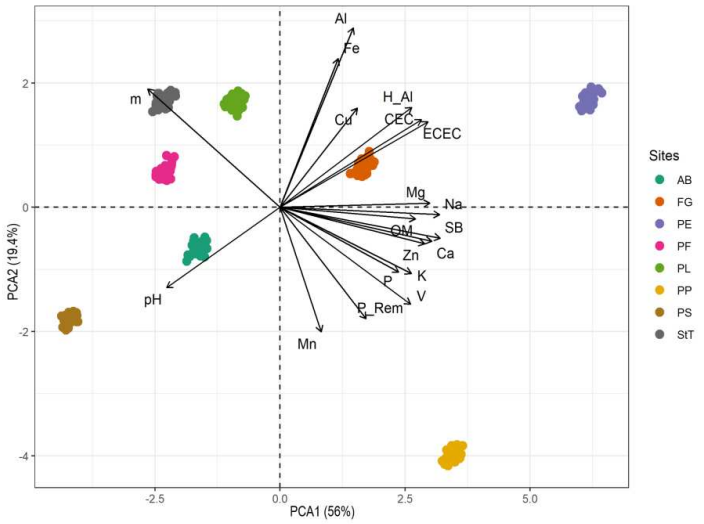


Figure S2 – Principal Component Analysis (PCA) for the soil physical properties of eight inselberg from Espírito Santo State, Brazil. Sites: AB – Águia Branca, FG – Forno Grande, PE – Pedra do Elefante, PF – Pedra da Figueira, PL – Pedra da Lajinha, PP – Pedra dos Pontões, PS – Pedra do Submarino and StT – Santa Terezinha. The physical properties: Fine_sand – fine sand, Coarse_sand – coarse sand, Clay – clay and Silt – silt.

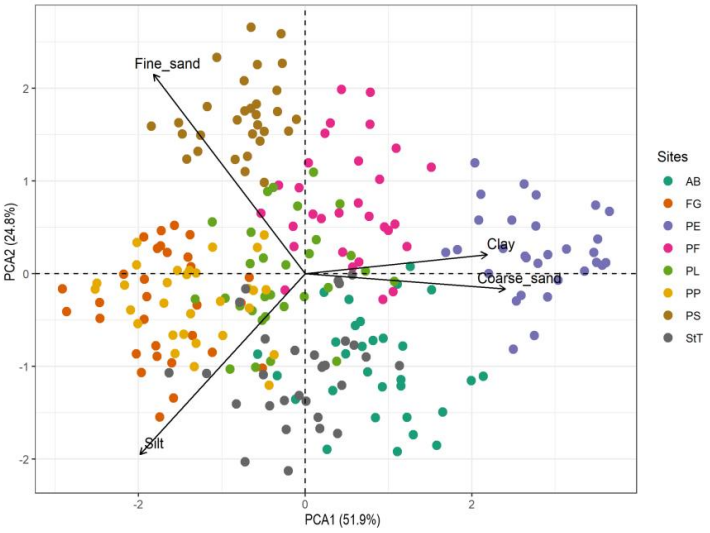


Figure S3 – Pearson correlation among all soil chemical and physical properties measured in 240 sampled units along eight inselbergs from Espírito Santo, Brazil. Scale correlation coefficients are provided. The predictors are: pH – active acidity in water; K – exchangeable potassium, Na – sodium, Ca – calcium, Mg – magnesium, Al – aluminium, H + Al potential acidity, P – available phosphorus, P-rem – remaining phosphorus, BS – sum of bases, V – base saturation, m – aluminium saturation, ECEC – effective cation exchange capacity, CEC – total cation exchange capacity, Zn – zinc, Fe – irons, Mn – manganese, Cu – copper, OM – organic matter content, Fine_sand – fine sand, Coarse_sand – coarse sand, Clay – clay and Silt – silt.

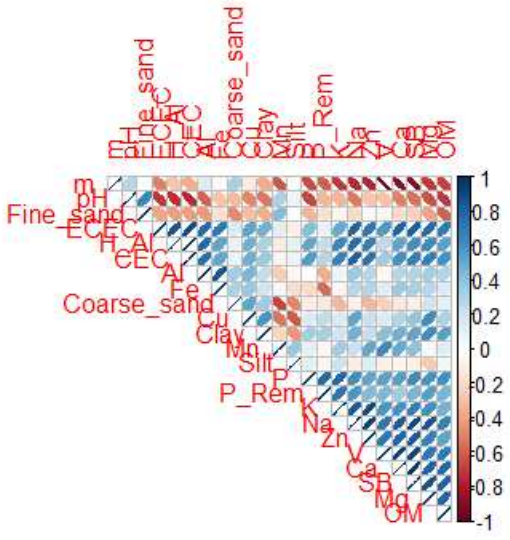


Figure S4 – Correlation between soil chemical properties and principal components of PCA from 240 sampled units plots along eight inselbergs from Espírito Santo, Brazil. Significance levels are based on Spearman coefficients. Scale correlation coefficients are provided. The predictors are: pH – active acidity in water; K – exchangeable potassium, Na – sodium, Ca – calcium, Mg – magnesium, Al – aluminium, H + Al potential acidity, P – available phosphorus, P-rem – remaining phosphorus, BS – sum of bases, V – base saturation, m – aluminium saturation, ECEC – effective cation exchange capacity, CEC – total cation exchange capacity, Zn – zinc, Fe – irons, Mn – manganese, Cu – copper and OM – organic matter content.

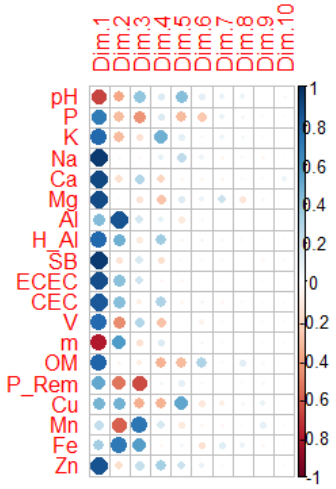


Figure S5 – Correlation between soil physical properties and principal components of PCA from 240 sampled units plots along eight inselbergs from Espírito Santo, Brazil. Significance levels are based on Spearman coefficients. Scale correlation coefficients are provided. The predictors are: Fine_sand – fine sand, Coarse_sand – coarse sand, Clay – clay and Silt – silt.

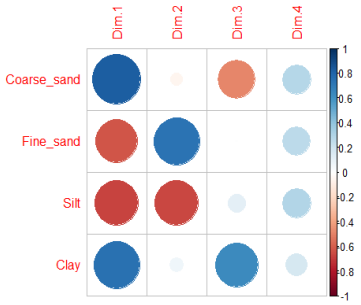
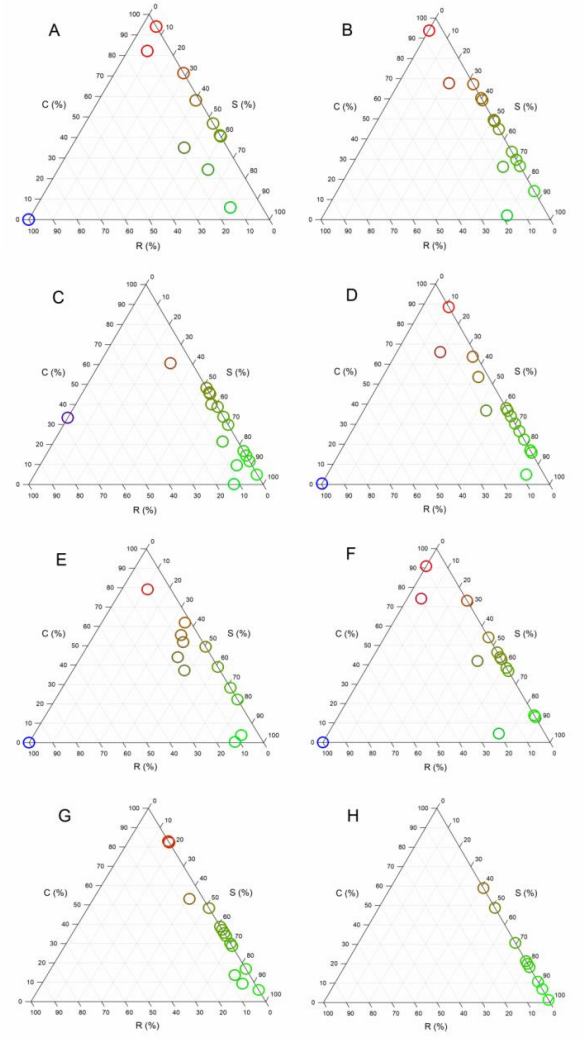


Figure S6 – CSR-strategies among species in each inselberg sampled from Espírito Santo State, Brazil. The strategies initials corresponded to C: competitiveness, S: stress tolerance and R: ruderalism, generated through the StrateFy analytical tool available from Pierce et al. (2017). A – Águia Branca, B – Forno Grande, C – Pedra do Elefante, D – Pedra da Figueira, E – Pedra da Lajinha, F – Pedra dos Pontões, G – Pedra do Submarino and H – Santa Terezinha.



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Chapter 3

Climate change enhances habitat losses in Neotropical inselbergs

Abstract

Despite being one of the most powerful drivers, little is known about how climate change can rearrange the variation of species range size. This information may be essential for identifying regions of high conservation importance and understanding the effects of climate changes on scenarios of biodiversity redistribution in Neotropical inselbergs. We applied ecological niche models to test the effects of climate change on general patterns of inselberg habitat and examine how the environmental filters drive this pattern. We used bioclimatic and topographic variables in conjunction to build the predictive habitat models to current, future and the changes of habitat suitability to protected areas. Our optimistic model detected a habitat loss of 40% in 2050 and 83% in 2070. The pessimistic model showed a habitat loss of 82.5% in 2050 and 86.7% in 2070. The habitat loss in the protected area showed losses in all models. Our models showed that inselbergs in both biomes will have severe losses in suitable area, even as protected areas whether efforts to reduce greenhouse gases are not adopted. We highlight that the conservation of mountain vegetation plays a fundamental role in the maintenance of ecosystem services provided by inselbergs of the Atlantic Forest and Caatinga.

Keywords: ecological niche model; geographical range size; rock outcrop; habitat area; loss suitability; biodiversity conservation; Atlantic Forest; Caatinga

1. Introduction

Multiple drivers regulate the species diversity and it has been a relevant theme in the ecology, mainly due to potential interactive effects and tradeoffs existing between drivers (Henneron et al., 2019). One of the strongest drivers that influence biodiversity is climate change, affecting species by altering the geographical distribution and species interactions (Walther et al., 2002). In response to climatic changes, species can rearrange their distributions rapidly along environmental gradients (Lenoir et al., 2020). Species' range may reflect a variety of factors, such as speciation, extinction and range transformations, being guided by two main mechanisms: habitat area and climatic stability (Morueta-Holme et al., 2013). Species distributions can differ in several orders of magnitude and distribution, which may be essential for identifying regions of high conservation importance (Guisan et al., 2013), as well as understanding the effects of climate changes on scenarios of biodiversity redistribution and its consequences on human well-being (Lenoir et al., 2020).

The restricted species distributions are associated with stable climate (Sandel et al., 2011) and small habitat area due to reduced dispersability (Hopper et al., 2016), high rare/endemics species (Porembski, 2007), strongly differentiated population systems (Hmeljevski et al., 2017) and high environmental filtering (Porembski, 2007). Comparing these areas with their landscape matrix, are expected to host more specific climate due to the determinant role of climate in range habitat (Morueta-Holme et al., 2013). It also expected more endemic species, reflecting the specialization and adaptability these species to severe environmental characteristics (Biedinger et al., 2000). Environment filtering reflects the strength of the climate gradients and associated habitat changes within an area, limiting the available habitat (*i.e.*, dispersion barriers) between similar environments, which can effectively restrict range size (Morueta-Holme et al., 2013).

Biodiversity of non-forest ecosystems, *e.g.* inselbergs, are comparable to forest ecosystems, being recognized worldwide for their importance (Overbeck et al., 2015) due to the provision of essential ecosystem services, such as water supply (Lima & Silva, 2008) and carbon storage (White et al., 2000). Currently, non-forest ecosystems represent 5.9% of the area of Brazil, 93% of which are made up of savannas and only 7% of rock outcrops (MapBiomas Project, 2020). The inselberg vegetation have restricted distribution and placed in a unique abiotic environment due to their isolation within a different surrounding landscape (Henneron et al., 2019; Pinto-Junior et al., 2020a, b). Despite this restricted distribution, inselbergs have rarely been considered in the context of the degradation of Earth's natural ecosystems

(Porembski et al., 2016), even having characteristics that can help in the development of hypotheses that explain ecology, evolution, and best conservation practices for OCBILs ecosystems (Hopper et al., 2016). Inselbergs build valuable landscape elements in Brazilian eastern, playing a role in the maintenance of biodiversity (Porembski et al., 2016), despite the few studies about the ecological and biogeographical features of the flora (Porembski, 2007) and the constant threats to this ecosystem (Pinto-Junior et al., 2020b).

Someway, the degree to which an ecosystem changes and its vegetation response to climate change depends on phenotypic plasticity and acclimatization, migration to suitable climatic conditions (Bussotti et al., 2015), and the intensity of exposure (Li et al., 2018). However, these changes and responses may be insufficient in harsh ecosystems such as inselbergs, with worrying consequences for the biodiversity maintenance, species interactions and ecosystem services (Porembski et al., 2016). In this way, ecological niche modelling (ENM) estimates species' habitat suitability by determining relationships between species' range and environmental predictors in space and time, forecasting how suitable areas may vary under different climate change scenarios (Araújo et al., 2019). ENMs represent a helpful tool in avoiding biodiversity decline, assessing the effectiveness and establishing of new protected areas, and restoring degraded habitats under climate change (Guisan et al., 2013). Then, understanding how climate changes and habitat area shapes the distribution of species (Morueta-Holme et al., 2013) and plant species diversity across environmental gradients (Lavergne et al., 2010) is one of the most crucial issues in plant ecology and conservation biodiversity.

In this study, we aimed to understand the geographical distributions of habitat suitability and the relative importance of environmental filtering (climate and topography) to Neotropical inselbergs ecosystems in the face of climate change. We used the location of 115 inselbergs throughout the Atlantic Forest and Caatinga biomes in Brazil. We applied ENMs to test the effects of climate change on general patterns of inselberg habitat area, and examine how the environmental filters drive this pattern, as well as the importance of these drivers to biodiversity. Finally, we assess the impact of our findings in light of conservation strategies.

2. Material and methods

2.1. *Inselbergs occurrence records*

Inselbergs are usually rocky granite outcrops that emerge abruptly from their surrounding ecosystems (Porembski et al., 2007), mainly in Atlantic Forest and Caatinga (Fig. 1). We opted to choose these biomes due to the greater and better expression of the inselbergs in Brazil. From field observations, high-spatial-resolution images (Google Earth) and published research, we compiled checklists with studies based on this ecosystem, totalizing 115 inselbergs in the southeastern and northeastern regions of Brazil. The geographical coordinates of each inselberg were used to indicate the habitats occupied by the species, thus relating "habitat" to "distribution area".

Figure 1 – Granitic inselbergs in Atlantic Forest (a, b) and Caatinga (c, d) and mat-forming species associate. (a) Granitic inselberg Cinco Pontões – Itaguaçu and Laranja da Terra (ES), (b) monocotyledonous mats formed by *Alcantarea trepida* (Bromeliaceae) localized at inselberg Pedra do Elefante – Nova Venécia (ES), (c) Granitic inselberg in Quixadá (CE) and (d) monocotyledonous mats formed by *Encholirium spectabile* (Bromeliaceae) localized at inselberg Serrote da Lagoa – Patos (PB).

2.2. *Environmental data and climate change scenarios*

We used two datasets (bioclimatic and topographic) in conjunction with the inselbergs selected to build the predictive habitat models. The majority of variables were from WorldClim 1.4 and WorldClim 2.1 (Hijmans et al., 2005; Fick & Hijmans, 2017) database; we also include models of other six bioclimatic and eight topographic variables (Table S1). All variables were obtained with a pixel resolution of 30' (~ 1 km²). We used the geology associated with inselbergs, such as granitic intrusions, migmatites and gneiss-migmatite complex; the relief (inselbergs, mountains and hill domains); slope (> 15º) and elevation (> 50 m a.s.l.), to building a binary variable (geology) that predominantly represent the areas associated with inselbergs. The shapefiles containing the geological information were obtained from the Brazilian Geological Survey (GeoSGB) and processed by ArcMap software (ESRI, 2015).

We eliminated the variables with strong biological correlation ($r > 0.9$) to inselbergs distributions remaining 16 bioclimatic and seven topographic variables (Table S1). Finally, we used the variables selected to build the current predictive habitat distribution. For future models, we used only 12 variables from WorldClim 1.4 with projections to 2050 and 2070 and seven topographic variables (Table S1); all based on the current model. The future models were based on two projections of representative concentration pathways (RCP 4.5 and 8.5) of two general circulation models (GCM) CCSM-4 and MIROC-ESM of Fifth Assessment Report of the Intergovernmental Panel on Climate Change (AR5 – IPCC).

2.3. *Predictive habitat distributions models*

The models of habitat distributions were made using MaxEnt v.3.4.1 (Phillips et al., 2017). We calculated the average of 10 replicates divided into 75% of training and 25% of random tests. We also used the jackknife procedure and permutation importance to estimate the relative influence of different predictor variables. The average threshold was calculated by the maximum training sensitivity and specificity of each GCM. To validate the models, we analyzed the specificity *vs* sensitivity by the value of area under the curve (AUC) of ROC (receiver operating characteristic). Values higher than 0.75 are considered useful, while values equal or close to unity indicate a good model (Phillips et al., 2006).

To measure the change between the current and future conditions, we summed the models (CCSM-4 and MIROC-ESM), then, we made the reclassification of the model generated by the sum of GCM in a binary model, based on the maximum sensitivity plus sensibility threshold (Liu et al., 2016). Finally, the values of gain, unchanged (presence in both models), and loss

were measured. All analysis was performed with ArcGIS software (ESRI, 2015). All values of suitability loss presented were considered the gain of the adequate area in the final result.

2.4. *Quantification of habitat suitability loss in biomes and protected area*

We overlapped the current with future models to quantify the gain, unchanged, and loss of habitat suitability to the entire range area (Atlantic Forest and Caatinga) and specific area of each biome. The protected areas' shapefiles with the current and future suitability areas were overlapped to measure how much area within protected areas will be affected by climate change. We assumed that the protected area would not change with time. The shapefiles of each biome were obtained from MapBiomas Project v.5.0 (MapBiomas Project, 2020) (base year 2019). The protected area shapefiles were obtained from the National Register of Conservation Units (CNUC) (in Portuguese, Cadastro Nacional de Unidades de Conservação - CNUC) (mapas.mma.gov.br/i3geo/datadownload) of the Ministry of Environment (MMA) (in Portuguese, Ministério do Meio Ambiente) containing data from federal, state and municipal protected areas.

3. Results

3.1. *Current and future projections*

The current range size of the inselberg habitat showed a habitat suitability area of 79,000 km² (Fig. 2), which corresponds to less than one percent (0.928%) of the Brazilian territory. In general, the datasets contributed to the good quality of the model; topographic variables had a better contribution in the training algorithm (72.9%), while climatic variables had more importance on the permutation of data (57.4%) (Table S2). We highlight some topographic variables (geology 48.2%, slope 14.9%, and roughness 7.4%) representing almost all percent of contribution (70.5%), however analyzing which variables had higher importance to permuted data, roughness (36.2%) was the most important variable, followed by temperature seasonality (20.2%) and isothermality (14.1%). The current model showed high accuracy with an AUC value of 0.976 and True Skill Statistic (TSS) of 0.883.

In our optimistic model (RCP 4.5), we identified a habitat loss of 31,665 km² (40%) in 2050 and 65,748 km² (83.2%) in 2070 (Fig. 3a, b). The pessimistic model (RCP 8.5) showed a higher habitat loss of 65,206 km² (82.5%) in 2050 and 68,500 km² (86.7%) in 2070 (Fig. 3c, d). The values of AUC and TSS of both models also indicated high accuracy (Table 1). Our results revealed suitability loss in important mountain ranges, such as *Serra do Mar*, *Serra da*

Mantiqueira, northern and northeastern parts of *Espinhaço* Range, *Planalto da Borborema* and *Planalto Sertanejo* of northeastern Brazil (Fig. 2).

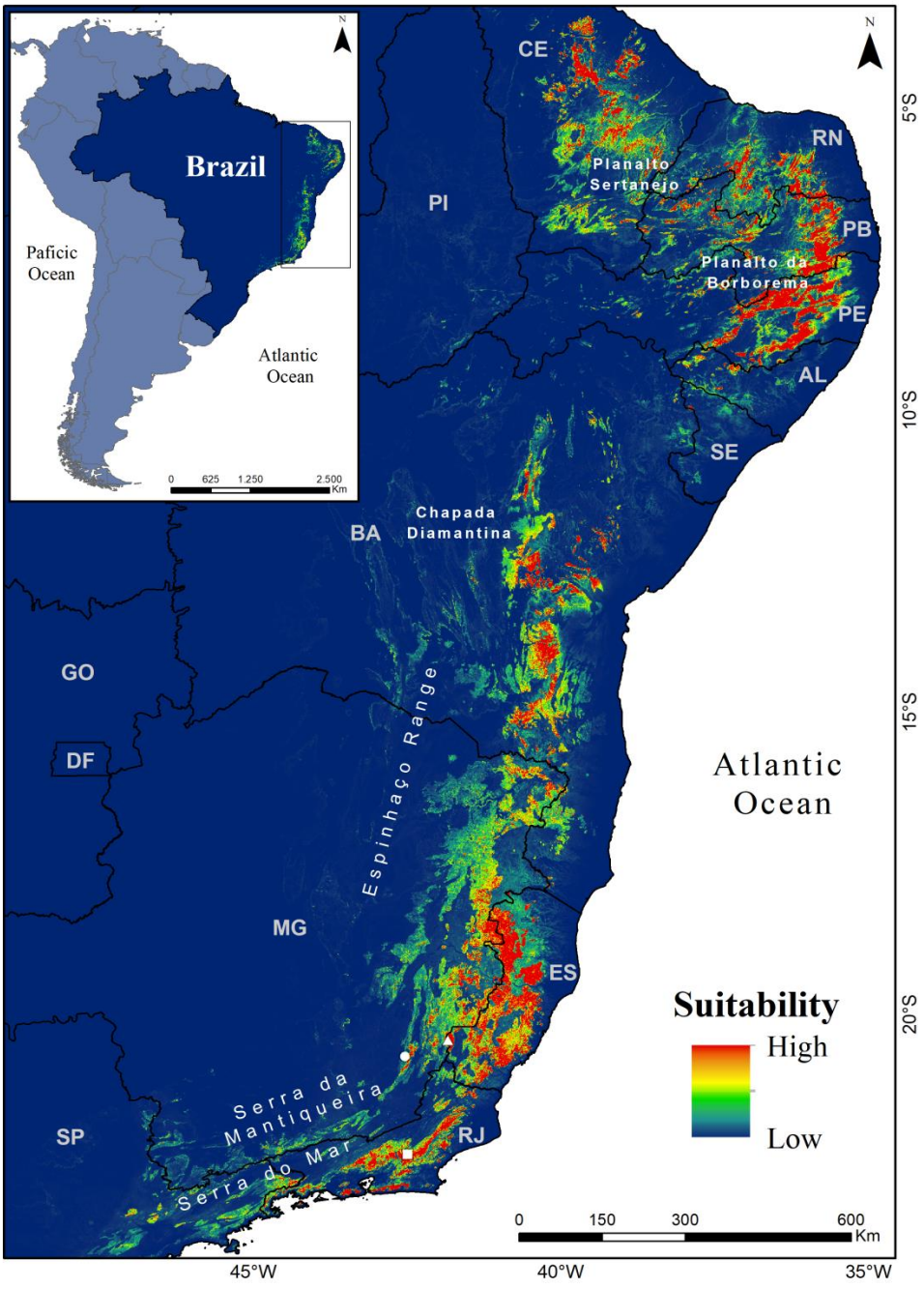

Figure 2 – Current model of habitat suitability to Neotropical inselbergs in Atlantic Forest and Caatinga. Predictions models were made by MaxEnt using two datasets (bioclimatic and topographic) in conjunction. Symbols: white triangle – Parque Nacional do Caparaó, white circle – Parque Estadual da Serra do Brigadeiro and white square – Parque Nacional da Serra dos Órgãos.

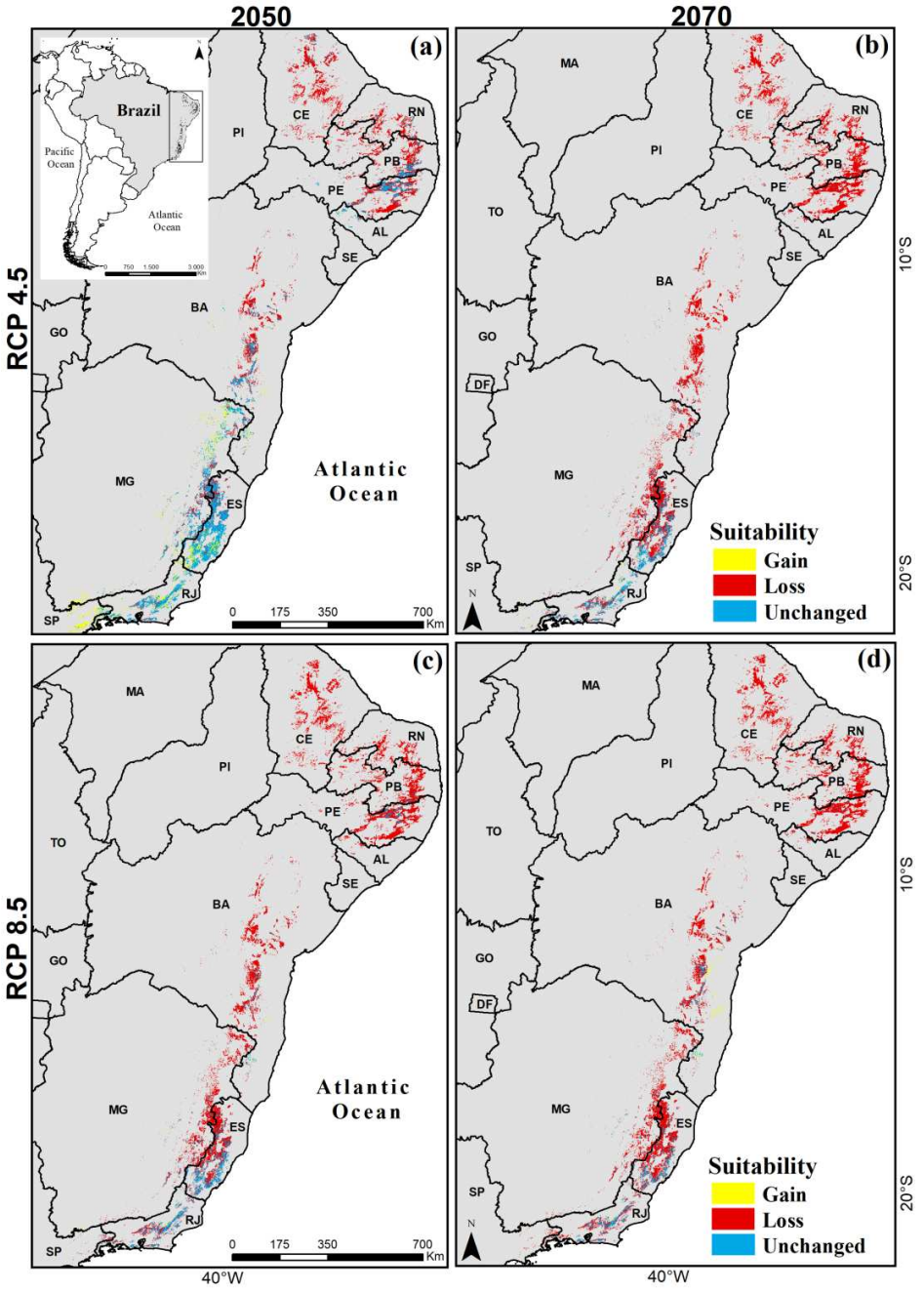

Figure 3 – Changes in future habitat suitability of Neotropical inselbergs in Atlantic Forest and Caatinga. (a) Optimistic model (RCP 4.5) to 2050, (b) optimistic model to 2070, (c) pessimistic model (RCP 8.5) to 2050, and (d) pessimistic model to 2070.

Table 1 – Values of Area Under the Curve (AUC) and True Skill Statistic (TSS) referent to the optimistic and pessimistic model generated by ecological niche models. Values closer to 1 indicate the high accuracy of the model.

Model (RCP – Year)	AUC	TSS
Optimistic (4.5 2050)	0. 972	0.866
Optimistic (4.5 2070)	0.969	0.852
Pessimistic (8.5 2050)	0.972	0.857
Pessimistic (8.5 2070)	0.975	0.883

3.2. *Habitat suitability for biome and protected area*

For each biome specific area, we estimated the habitat suitability of 41,293 km² (52%) for Atlantic Forest and 37,529 km² (47%) for Caatinga. Our optimistic model presented an expansion of 64% of habitat loss in the Atlantic Forest between 2050 and 2070. While the pessimistic model revealed a lower difference between the years (extension of 6.6%), it was still higher values of habitat loss (Table 2). The Caatinga presented similar patterns to Atlantic Forest, however with lower values of habitat loss (optimistic – 21% and pessimistic – 1.4% between 2050 and 2070) (Table 2).

According to the current model, only 3% (2,326.48 km²) of the total suitability area for inselbergs are under the protected area (Fig. 4a, d, g, j). In the optimistic model, the projections indicated a gain of 47.48 km² (2%) in the suitable area in 2050 (Fig. 4b, e), however in 2070, there would be a loss of 1,156.78 km² (50%) of habitat under protected area (Fig. 4h, k). In the pessimistic model, the extensions of habitat loss under protected area are higher, 48% (1,114.75 km²) and 63% (1,462.15 km²), for 2050 (Fig. 4c, f) and 2070 (Fig. 4i, l), respectively.

Table 2 – Values of habitat suitability loss to inselberg vegetation for Atlantic Forest and Caatinga biomes on two representative concentration pathways (RCP).

	RCP - Year	Suitability loss (km²)	Suitability loss[1] (%)	Suitability loss[2] (%)
Atlantic Forest	4.5 2050	2,340.8	3	5.6
	4.5 2070	28,683.05	36.3	69.4
	8.5 2050	29,332.74	37	71
	8.5 2070	32,052.33	40.5	77.6
Caatinga	4.5 2050	29,239.93	37	77.9
	4.5 2070	37,094.2	47	98.8
	8.5 2050	35,918.77	45.5	95.7
	8.5 2070	36,462.13	46	97.1

[1]Referring to the entire range area of the current model (79,000 km²).
[2]Referring to the specific area of biome (Atlantic Forest – 41,293.54 km² and Caatinga – 37,529.53 km²).

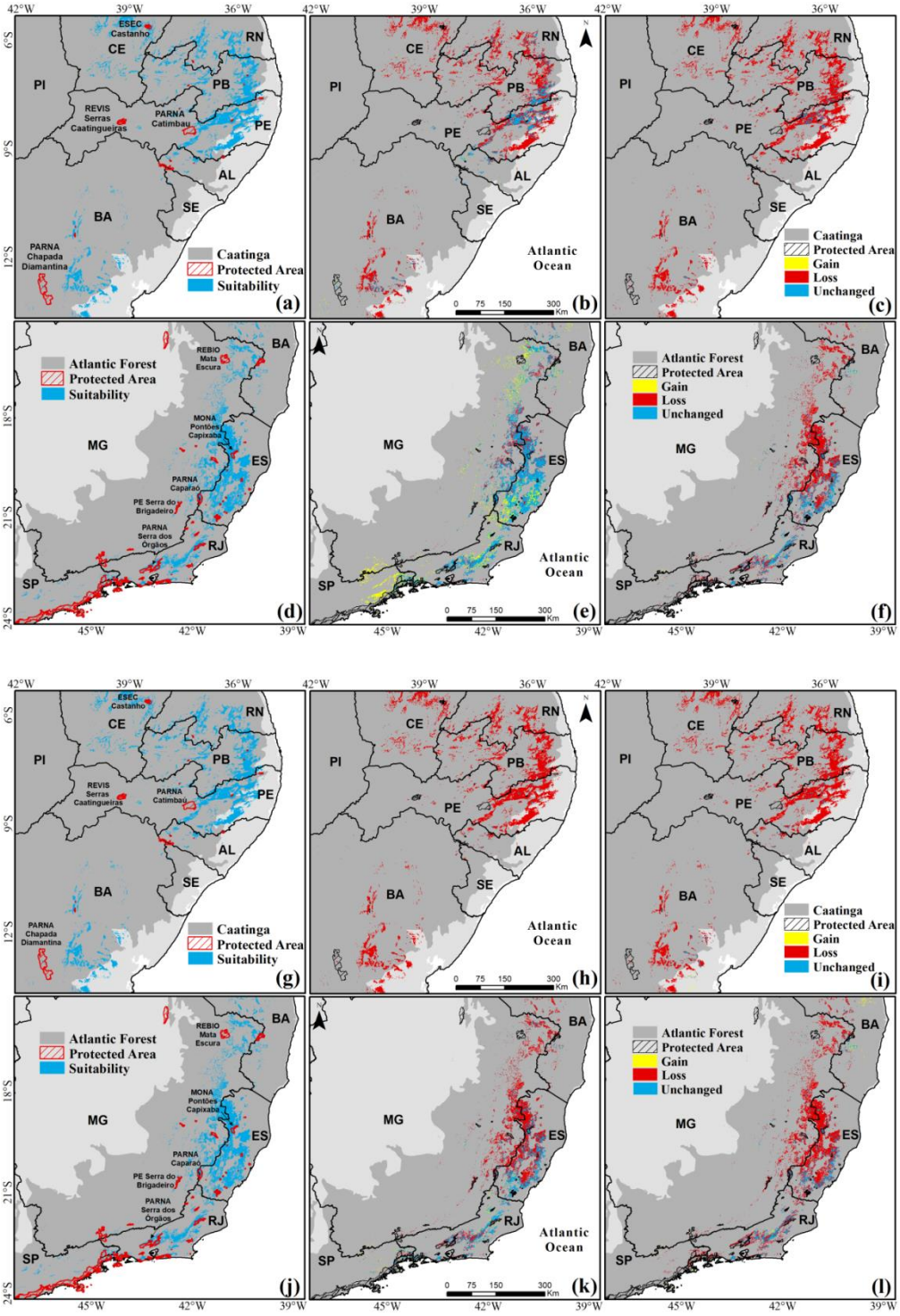

Figure 4 – Maps of the protected area affected by climate change in our predicted models. (a) Protected areas of Caatinga and suitability habitats, (b) changes in habitat suitability of Caatinga concerning the protected area of the optimistic model (RCP 4.5) to 2050, (c) pessimistic model (RCP 8.5) to 2050, (d) protected areas of Atlantic Forest and suitability habitats, (e) changes in habitat suitability of Atlantic Forest concerning the protected area of the optimistic model to 2050 and (f) pessimistic model to 2050. (g) Protected areas of Caatinga and suitability habitats, (h) changes in habitat suitability of Caatinga concerning the protected area of the optimistic model (RCP 4.5) to 2070, (i) pessimistic model (RCP 8.5) to 2070, (j) protected areas of Atlantic Forest and suitability habitats, (k) changes in habitat suitability of Atlantic Forest concerning the protected area of the optimistic model to 2070 and (l) pessimistic model to 2070. ESEC – Estação Ecológica, MONA – Monumento Natural, PARNA – Parque Nacional, PE – Parque Estadual, REBIO – Reserva Biológica and REVIS – Reserva da Vida Silvestre.

4. Discussion

As we expected, the distribution of suitable habitats to inselberg vegetation is influence by a combination of topographic and climatic drives, according to our models. The changes in climate factors will result in an extreme loss of suitable area, where all scenarios showed range contraction that can achieve losses up to 86.7% in the next 50 years. We also showed that Atlantic Forest and Caatinga and its protected area encompass in our models will have expressive losses in suitable areas, reaching losses up to 98% and 62%, respectively, in 2070. Nothing is more alarming than our findings to habitat suitability loss concerning the non-forest vegetation in Atlantic Forest and Caatinga inselbergs, reinforcing the requirement to increase the knowledge about species distributions models and environmental filtering, what is determinants to provide the conservation of neglected ecosystem as Neotropical inselbergs.

Considering the influence of abiotic factors on establishing and persistence of species (Walther et al., 2002; Lenoir et al., 2020), our current model reinforces the existence of a pattern in the role of environmental filters, driving habitat suitability. The roughness and climatic variables (temperature seasonality and isothermality) were the most relevant for the model construction. Other similar rupestrian grassland (*Campo Rupestre*) also has their distributions closely related to topographic and climatic variables (Fernandes et al., 2018). Thus, topography and climate variables have a noted influence on the geographic distribution of inselbergs habitats, and therefore, changes in some of these factors would influence their range size and conservation strategies.

During the 21st century, the projections of climate change point to the worsening of harsh conditions. The Caatinga biome will experience a rise in temperature from 1.5 to 2.5ºC and a decrease in rainfall between 25% and 35% (Souza et al., 2014). While, the Atlantic Forest will undergo a temperature rise (2 to 3ºC) and a decrease in rainfall (20 to 25%) on the northeast part, while the southeast portion will have an increase in temperature (1.5 to 2.5ºC) and rainfall (15 to 20%) (Souza et al., 2014). These predictions can potentially explain the variations of our future models of the inselberg suitability range.

First, the gain area (in the optimistic model) can be an outcome of the combination of increased temperature and variations in rainfall between the northeast and the southeast part of the Atlantic Forest (Pinto-Junior et al., 2020a) associated with peak and mountain ranges (Fig 3a). The rise of temperature and the decrease of rainfall will promote favourable conditions for autochorous species, while high temperatures with high precipitation will benefit anemochorous, zoochorous and hydrochorous species (Henneron et al., 2019). Lastly,

an expansion in the environmental filter can lead to the loss of a suitable area, since abiotic factors impact species richness and composition (Henneron et al., 2019; Pinto et al., 2020). The high altitude associate with high precipitation can disfavor autochorous species, while favoring anemochory species (Henneron et al., 2019). Therefore, the inselberg altitude combined with regional climate can impact species richness and composition (Pinto et al., 2020) and species functional traits (Sarthou et al., 2017).

Our projections point to a total reduction of 1.5% and 3.9% of non-forest vegetation in Atlantic Forest and Caatinga (MapBiomas Project, 2020) areas with threatened and exclusive species. This scenario indicates that the unique flora of inselberg ecosystems is threatened by the union of habitat loss, future climate changes and reduced dispersability of some species (Henneron et al., 2019). These dispersal limitations have been demonstrated by low gene flow (Barbará et al., 2007), strongly differentiated population systems (Hmeljevski et al., 2017) and reduced dispersability (Hopper et al., 2016) at the communities-level shown by inselbergs.

The granite inselberg flora at Atlantic Forest and Caatinga hold high plant richness, with a potential occurrence of at least 316 exclusively species, corresponding to approximately 53% of exclusive rupestrian species recorded in Brazil (Brazil Flora G., 2021). However, only 3% of the suitability area with the highest potential of rupestrian species existence is currently in a protected area. Our models point out that suitability loss can reach 63% of protected areas in 2070 whether efforts to reduce greenhouse gases are not adopted. Protected areas like Parque Nacional do Caparaó (ES/MG) and Serra dos Órgãos (RJ), Parque Estadual da Serra do Brigadeiro (MG) and Monumento Natural dos Pontões Capixabas (ES), located in the Atlantic Forest, will suffer severe habitat loss, being the protection areas most affected by climate change in our models. Most of the vegetation in these protected areas is identified as *Campos de Altitude* (Brazilian Páramos), showing the sharing of habitat and the close (sometimes confused) relationship of this two rupestrian vegetation (inselbergs and *Campos de Altitude*) in Atlantic Forest.

Our results also highlight that the Caatinga can be more sensitive to global warming (Seddon et al., 2016), which can be a consequence of the influence of the surrounding matrix on species traits and richness (Henneron et al., 2019; Sarthou et al., 2017). The projections of climate change indicate a modification in renewable surface and groundwater resources in most dry subtropical regions, increasing competition for water and increase of droughts frequency under RCP 8.5 (Souza et al., 2014). Consequently, another possible cause for the highest suitability loss of inselbergs in Caatinga (most in *Planalto da Borborema* and *Planalto Sertanejo* of northeastern Brazil) is related to the desertification process (Maestre et al., 2012).

The increase in aridity enhances the risk of extinction of the inselbergs biodiversity, mainly the rare and endemic plant species (Porembski et al., 2016). Therefore, our models highlight the need to create new protected areas, above all in the Caatinga, as well as the urgent need for more taxonomic, phytosociological and ecological studies that help in understanding the rupestrian vegetation present in Brazil, such as inselbergs, *Campos de Altitude*, *Campo Rupestre* and *Cangas*.

The creation of protected areas can be a tricky task because wrong decisions can result in biased protected areas, leading to the protection of the places less likely to suffer from direct human pressures (Joppa & Pfaf, 2009). Consequently, the conservation impact of a protected area tends to be small. Some studies have already predicted that climate change is likely to compromise the efficiency of the current protected area (Lemes & Loyola, 2013; Monteiro et al., 2020). Thus, our models demonstrate that a large part of the protected areas, mainly in the Atlantic Forest, can be considered efficient in the conservation of the beneficial environment of these habitats, both in the future and in the present. At least 40 new species were described to Brazilian inselbergs since 2015 (Table S3), in parts, this number can be associated to the efficiency of the protected area in maintain the biodiversity and the conservation impact.

On a large range of climatic and topographic variables like the vegetation gradient Caatinga-Atlantic Forest, the effects of habitat loss and climate changes will probably be heterogeneous. Studies demonstrated that a decrease in plant coverage might affect the sensitivity of dryland plant communities to environmental changes within the same vegetation type or within a given region (Vicente-Serrano et al., 2012). Thus, the vulnerability of inselberg species to climate change should consider a combination of specific adaptive traits (morphological, anatomical, physiological and functional attributes) (Biedinger et al., 2000), sensitivity and adaptability of each species, and level of exposure they face (Dawson et al., 2011). Aside from the intrinsic factors of each species, the protection of the flora on inselbergs is a real challenge due to the high degree of isolation, endemism, and species unique of each inselbergs (Pinto-Junior et al., 2020b).

We highlight the importance of these results for environmental managers and policymakers. Our models can assist in the identification of efficient areas for the creation of parks and reserves (mainly in Caatinga). Therefore, it avoids the creation of protected areas based on strategies with particular interests and overlooks the risks of land conversion and future uncertainty (*e.g.*, decisions solely on species richness or irreplaceability). Finally, we highlight the necessary of other critical conservation strategies (Pinto-Junior et al., 2020b), as well as the lack of studies on the impact of granite mining on the inselberg ecosystem, a threat

that may be as urgent as climate change. In this context, due to the combination of these drivers, the impact of climate changes should receive more attention to the conservation of granite inselberg habitat, even as other species of fauna and flora when we consider the scenarios of global warming.

5. Conclusions

Our study extremely demonstrated suitability loss for granite inselberg habitat using models that combine effects of climatic and topographic variables. Our models showed that inselbergs in Atlantic Forest and Caatinga will have severe losses in a suitable area of non-forest vegetation, as well as protected areas whether efforts to reduce greenhouse gases are not adopted. We highlight that the conservation of mountain vegetation plays a fundamental role in the maintenance of ecosystem services provided by inselbergs to plant, wildlife, and human of the whole biomes. We believe this study and conservation strategies can contribute to the development of international legislation for the conservation of inselberg flora, even as future experimental studies that would be needed to explore the integrated effect of environmental filtering on biotic interactions of inselbergs species.

6. Acknowledgements

We acknowledge the Programa de Pós-Graduação em Botânica – UFV for supporting our research in Brazil and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing scholarships to the author. We would like to thank Marcelo L. Bueno and Larissa A. C. Müller for contributions in methodology, ideas and suggestions in the final version of this manuscript. We are also grateful to Rérisson Máximo and Rafael F. Lopes-Silva for kindly helped with images of the Caatinga inselbergs. We thank to Instituto Estadual do Meio Ambiente e Recursos Hídricos do Espírito Santo (IEMA) for the research license, Neotropical Grassland Conservancy (NGC) for financial supporting and Deutscher Akademischer Austauschdienst (DAAD) for providing scholarships as visiting researcher in Institute of Landscape Ecology (ILÖK) University of Münster (WWU).

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8. Supplementary Material

8.1. *Tables*

Table S1 – Bioclimatic and topographic variables selected were after eliminating variables with strong biological correlation ($r > 0.9$).

Variable	Dataset	Status	References
Annual Mean Temperature (Bio 1)	Bioclimatic	Selected	Hijmans et al., 2005
Mean Diurnal Range (Bio 2)	Bioclimatic	Selected	Hijmans et al., 2005
Isothermality (Bio 3)	Bioclimatic	Selected	Hijmans et al., 2005
Temperature Seasonality (Bio 4)	Bioclimatic	Selected	Hijmans et al., 2005
Max Temperature of Warmest Month (Bio 5)	Bioclimatic	Selected	Hijmans et al., 2005
Min Temperature of Coldest Month (Bio 6)	Bioclimatic	Unselected	Hijmans et al., 2005
Temperature Annual Range (Bio 7)	Bioclimatic	Selected	Hijmans et al., 2005
Mean Temperature of Wettest Quarter (Bio 8)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temperature of Driest Quarter (Bio 9)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temperature of Warmest Quarter (Bio 10)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temperature of Coldest Quarter (Bio 11)	Bioclimatic	Unselected	Hijmans et al., 2005
Annual Precipitation (Bio 12)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Wettest Month (Bio 13)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Driest Month (Bio 14)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation Seasonality (Bio 15)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Wettest Quarter (Bio 16)	Bioclimatic	Unselected	Hijmans et al., 2005
Precipitation of Driest Quarter (Bio 17)	Bioclimatic	Unselected	Hijmans et al., 2005
Precipitation of Warmest Quarter (Bio 18)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Coldest Quarter (Bio 19)	Bioclimatic	Selected	Hijmans et al., 2005
Aspect-eastness	Topographic	Selected	Amatulli et al., 2018
Aspect-northness	Topographic	Selected	Amatulli et al., 2018
Cloud Cover	Bioclimatic	Selected	Wilson & Jetz, 2016
Elevation	Topographic	Selected	Amatulli et al., 2018
Geology	Topographic	Selected	Our study
Global Aridity Index	Bioclimatic	Unselected	Zomer et al., 2008
Global Potential Evapotranspiration (PET)	Bioclimatic	Selected	Zomer et al., 2007
Mean Annual Actual Evapotranspiration (AET)	Bioclimatic	Unselected	Trabucco & Zomer, 2019
Roughness	Topographic	Selected	Amatulli et al., 2018
Slope	Topographic	Selected	Amatulli et al., 2018
Solar Radiation	Bioclimatic	Selected	Fick & Hijmans, 2017
Terrain Ruggedness Index (TRI)	Topographic	Unselected	Amatulli et al., 2018
Topographic Position Index (TPI)	Topographic	Selected	Amatulli et al., 2018
Wind Speed	Bioclimatic	Selected	Fick & Hijmans, 2017

Table S2 – Percent of Contribution (PC) and Permutation Importance (PI) of bioclimatic and topographic variables used to building the current and future models. Representative concentration pathway (RCP) values refer to the average of both General Circulation Models (CCSM-4 and MIROC-ESM). Variables are organized by Permutation Importance of Current model.

	Models									
	Current		RCP 4.5 2050		RCP 4.5 2070		RCP 8.5 2050		RCP 8.5 2070	
Variables	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Roughness	7.4	36.2	5.7	37.9	7.1	42.7	6.6	42.4	5.7	43.7
Temperature Seasonality (Bio 4)	1.3	20.2	0.9	11.3	1	11	0.95	13.5	1.6	12.6
Isothermality (Bio 3)	1.1	14.1	1.4	8.8	1.4	10.8	1.45	9.3	1.5	11.1
Precipitation Wettest Month (Bio 13)	1.6	7.5	2.2	5.8	2.3	3.1	2	4.5	2.5	4.2
Precipitation Coldest Quarter (Bio 19)	5.6	6.4	6.1	8.9	5.4	6.1	5.6	5.6	5.3	5
Geology	48.2	3.8	49.9	5.4	51.2	6.1	50.3	5.6	52.5	6.5
Precipitation Warmest Quarter (Bio 18)	0.5	2.2	1.1	2.7	0.9	3	1	2.3	1.8	2.1
Precipitation Driest Month (Bio 14)	0.4	2.2	0.7	4.5	0.8	4.3	1	3.7	0.8	4.8
Global Potential Evapotranspiration (PET)	2.2	1.7	-	-	-	-	-	-	-	-
Aspect-eastness	0.3	1.5	0.1	0.9	0.2	1.4	0.25	1.1	0.2	1.6
Precipitation Seasonality (Bio 15)	2.4	1.4	3	1.9	2.7	2	2.6	1.7	2.7	1.7
Temperature Annual Range (Bio 7)	1.7	0.7	2.5	2.8	2.5	1.9	2.6	2.4	2.2	1
Elevation	1.1	0.6	0.8	1.2	1.2	1.9	1.3	1.5	1.2	1.4
Mean Diurnal Range (Bio 2)	1.2	0.4	2.1	1.8	2.1	1.3	1.9	1.9	2.2	0.55
Topographic Position Index (TPI)	0.9	0.4	0.9	0.5	0.8	0.4	0.7	0.4	1.3	0.5
Annual Precipitation (Bio 12)	2.8	0.2	2.2	0	2.5	0.15	2.9	0.25	1.6	0
Cloud Cover	1.2	0.2	-	-	-	-	-	-	-	-
Aspect-northness	0.1	0.2	0.05	0.4	0.05	0.8	0.1	0.4	0.05	0.6
Slope	14.9	0.1	17.5	1.8	14.6	0.3	15.6	0.3	13.8	0.2
Annual Mean Temperature (Bio 1)	1.5	0.1	2.2	2.4	2.3	1.9	2.6	2.3	2	1.3
Max Temp. Warmest Month (Bio 5)	0.2	0.1	0.3	0.4	0.6	0.7	0.4	0.5	0.55	0.75
Solar Radiation	2.5	0	-	-	-	-	-	-	-	-
Wind Speed	0.8	0	-	-	-	-	-	-	-	-

Table S3 – Plant species recently described in Neotropical Brazilian inselbergs between 2015 and 2020.

Species	Family	Year	References
Anchietea ballardii	Violaceae	2016	Paula-Souza, J.; Pirani, J.R. Novelties in Brazilian *Anchietea* A.St.-Hil. (Violaceae): A new species from inselbergs in the Atlantic rainforest and an update on the conservation status of *Anchietea ferrucciae* Paula-Souza & Zmarzty. Phytotaxa 280: 63–69, 2016.
Anthurium mucuri	Araceae	2016	Gonçalves, E.G.; de Paula, L.F.A. A new species of *Anthurium* (Araceae) from Minas Gerais State, Southeastern Brazil. Phytotaxa 247: 281–286, 2016.
Behuria mestrealvarensis	Melastomataceae	2016	Iglesias, D.T.; Dutra, V.F.; Goldenberg, R. *Behuria mestrealvarensis* (Melastomataceae): a

			new species on an inselberg in Espírito Santo, Brazil. Phytotaxa 255: 281–286, 2016.
Bradea borrerioides	Rubiaceae	2016	Oliveira, J.A.; Sobrado, S.V. *Bradea borrerioides* (Rubiaceae), a new species from Brazilian inselbergs. Phytotaxa 243: 83–90, 2016.
Catimbaua pendula	Linderniaceae	2019	Almeida, E.M.; Wanderley, A.M.; Santos, A.S. et al. Two new genera and species of Linderniaceae (Lamiales) from inselbergs in northeastern Brazil: morphological and karyological evidence. Phytotaxa 400: 215–226, 2019.
Cololobus argenteus	Asteraceae	2018	Monge, M.; Volet, D.P.; Semir, J. Five new species of Vernonieae (Asteraceae) from Espírito Santo, Brazil. Rodriguésia 69: 595–610, 2018.
Critoniopsis canaliculata	Asteraceae	2019	Monge, M.; Volet, D.P.; Semir, J. Two new species of Vernonieae (Asteraceae) from Espírito Santo, Southeastern Brazil. Systematic Botany 44: 439–445, 2019.
Dichorisandra saxatilis	Commelinaceae	2016	Aona, L.Y.S.; Faden R.B.; Bittrich, V.; Amaral, M.C.E. Four new species of *Dichorisandra* (Commelinaceae) endemic from Bahia State, Brazil. Brittonia 68: 61–73, 2016.
Dichorisandra striatula	Commelinaceae	2019	Moraes, Q.S.; Pellegrini, M.O.O.; Alves-Araújo, A. A New Species of *Dichorisandra* (Commelinaceae) with Speckled Leaves from Brazil. Systematic Botany 44: 783–789, 2019.
Eugenia gracilifolia	Myrtaceae	2020	Faria, J.E.Q.; Fernandes, T. A new species of *Eugenia* sect. *Pilothecium* (Myrtaceae) from the Atlantic Forest inselbergs of Southeastern Brazil. Phytotaxa 470: 249–255, 2020.
Euphorbia tetrangularis	Euphorbiaceae	2018	Hurbath, F.; Leal, B.S.S.; Silva, O.L.M. et al. A new species and molecular phylogeny of Brazilian succulent *Euphorbia* sect. *Brasilienses*. Systematics and Biodiversity 16: 658–667, 2018.
Gomesa caatingana	Orchidaceae	2018	Cordeiro, J.M.P.; Nollet, F.; Buril, M.T. A new species of *Gomesa* (Oncidiinae, Orchidaceae) from inselbergs in Brazilian caatinga: morphological and karyological evidence. Phytotaxa 374: 147–154, 2018.
Griffinia meerowiana	Amaryllidaceae	2018	Campos-Rocha, A.; Semir, J.; Peixoto, M. *Griffinia meerowiana*, a remarkable new species of Amaryllidaceae from Espírito Santo state, Brazil. Phytotaxa 344: 228–238, 2018.
Isabelcristinia aromatica	Linderniaceae	2019	Almeida, E.M.; Wanderley, A.M.; Santos, A.S. et al. Two new genera and species of Linderniaceae (Lamiales) from inselbergs in northeastern Brazil: morphological and karyological evidence. Phytotaxa 400: 215–226, 2019.
Kielmeyera cataractae	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.

Kielmeyera colibri	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.
Kielmeyera doceana	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.
Kielmeyera inopinata	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.
Kielmeyera oreophila	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.
Kielmeyera stevensii	Calophyllaceae	2020	Trad, R.J.; Bittrich, V.; Amaral, M.C.E. Hardly a Surprise: Six New *Kielmeyera* Species (Calophyllaceae) from Brazilian Southeast Atlantic Forest. Systematic Botany 45: 102–121, 2020.
Lepidaploa congesta	Asteraceae	2019	Monge, M.; Volet, D.P.; Semir, J. Two new species of Vernonieae (Asteraceae) from Espírito Santo, Southeastern Brazil. Systematic Botany 44: 439–445, 2019.
Lessingianthus squamosus	Asteraceae	2018	Monge, M.; Volet, D.P.; Semir, J. Five new species of Vernonieae (Asteraceae) from Espírito Santo, Brazil. Rodriguésia 69: 595–610, 2018.
Lippia diversifolia	Verbenaceae	2019	Cardoso, P.H.; Menini Neto, L.; Salimena, F.R.G. A new species of *Lippia* (Verbenaceae) from the inselbergs of Brazilian Atlantic Forest. Phytotaxa 406: 243–249, 2019.
Mandevilla alata	Apocynaceae	2019	Morales, J.F.; Kollmann, L.J.C. Increasing the known floristic diversity of Brazilian inselbergs: two new species of *Mandevilla* (Apocynaceae) from Espírito Santo. Acta Botanica Brasilica 34: 107–116, 2020.
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Pleroma cucullatum	Melastomataceae	2018	Meyer, F.S.; Kollmann, L.J.C.; Fraga, C.N.; Goldenberg, R. Four new rupicolous species of

			Pleroma (Melastomataceae) endemic to Espírito Santo, Brazil. Phytotaxa 348: 235–253, 2018.
Pleroma fontanae	Melastomataceae	2018	Meyer, F.S.; Kollmann, L.J.C.; Fraga, C.N.; Goldenberg, R. Four new rupicolous species of *Pleroma* (Melastomataceae) endemic to Espírito Santo, Brazil. Phytotaxa 348: 235–253, 2018.
Pleroma fornograndense	Melastomataceae	2018	Meyer, F.S.; Kollmann, L.J.C.; Fraga, C.N.; Goldenberg, R. Four new rupicolous species of *Pleroma* (Melastomataceae) endemic to Espírito Santo, Brazil. Phytotaxa 348: 235–253, 2018.
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Pleroma kollmanniana	Melastomataceae	2016	Meyer, F.S.; Goldenberg, R.; Kollmann, L.J.C. Three new species of *Pleroma* (Melastomataceae) from Inselbergs of Espírito Santo, Brazil. Phytotaxa 282: 197–210, 2016.
Pleroma leopoldinensis	Melastomataceae	2016	Goldenberg, R.; Kollmann, L.J.C. Two new species of *Pleroma* (Melastomataceae) from Espírito Santo, Brazil. Brittonia 68: 37–45, 2016.
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Chapter 4

Biogeographic isolation and climate shape the evolutionary heritage of Neotropical inselbergs

Abstract

Climate shifts in Quaternary may be the main determinants of current diversity gradients, what might have resulted in higher species richness and diversity of several lineages at climatically buffered areas. Old, climatically buffered, infertile landscapes (OCBILs) as inselbergs can be useful landscapes for pursuing studies of biogeographical patterns and processes mainly due to isolated nature of inselberg that allows the investigate the underlying landscape connectivity patterns in the past and current scenarios. This is a matter of major concern to planning conservation strategies owing to current fast global climate and land-use change scenario. Thus, the combination of phylogenetic approaches and temporal landscape connectivity, allows one for disentangling the mechanisms involved in the origin of the disjunct distribution for a Neotropical plant species and the evolutionary heritage of Neotropical inselbergs. We used a compiled dataset of 42 inselbergs communities across the Atlantic Forest and Caatinga biome to describe the structure and phylogenetic diversity, map the resistance between inselbergs and testing the effects of resistance distance on phylobetadiversity and, finally, identify the effectiveness of protected areas, as well as assess the conservation gaps for conservation of plant species in inselbergs ecosystems. We found evidence of dispersal limitations in inselbergs communities and the existence of a latitudinal gradient in species richness and sesPD of plants species, across the Neotropical inselberg landscape, with greater isolation between the northeastern and southeastern core areas. Our findings indicate that high mountain ranges can lead to a high phylobetadiversity, thus imposing isolation to the evolutionary lineages of the inselbergs' flora. Furthermore, our findings suggest that they can be explained by the Pleistocene Arc Hypothesis (PAH), which contributing to greater isolation of inselberg species. Our results provide a valuable baseline to promote conservation strategies capable of safeguarding the inselberg biodiversity and mitigating threats in these iconic landscapes.

Keywords: resistance distance; connectivity; phylogenetic diversity; rock outcrops; conservation strategies; Atlantic Forest; Caatinga

1. Introduction

Quaternary climate shifts have been hypothesized as main determinants of current diversity gradients in several taxa (Svenning et al., 2015), resulting in higher species richness at climatically stable areas and sheltering substantial diversify of several lineages, as suggested by Pleistocene refugia hypothesis (Svenning et al., 2015). Furthermore, expansions of semiarid lineages by routes from drier surrounding environments have also been hypothesized as an outcome of the Pleistocene Arc Hypothesis (PAH) (Prado, 2000) of refugia during the Last Glacial Maximum (LGM). Among the main consequences, climate of the highlands during the LGM became cold and dry (Behling & Lichte, 1997; Salgado-Labouriau et al., 1998), with grassland-type vegetation dominating most of southern and central Brazil (Behling, 1998; Ledru et al., 1998). In such scenario, inselbergs, isolated rocky outcrops mainly of granite or gneiss, are remnants of the Tertiary and Quaternary ages throughout Brazil, testifying to the importance of different past semiarid climate in currently humid forested landscapes as Atlantic Forest (Safford, 2000) and dry forest landscapes as Caatinga (Arango et al., 2020).

Inselbergs are important centers of plant diversity and endemism and are among the main "old, climatically buffered, infertile ecosystems" in the world (OCBILs, Hopper et al., 2016; Silveira et al., 2020). The inselbergs ecosystem constitutes isolated rocky granite or gneiss outcrops, as terrestrial habitats islands, that emerge abruptly from their surrounding ecosystems, such as savannah and forests (Porembski et al., 2000). Inselbergs are home for at least 316 species of plants, which corresponds to approximately 53% of exclusive rupestrian species recorded in Brazil (Brazil Flora G., 2021). Nevertheless, in spite of its importance in biodiversity, this is one of the more neglected and threatened ecosystems, which raises the urgency for conservation priority plans (Porembski et al., 2016). The isolated nature of inselberg is interesting for studies of the plant evolutionary processes analyzing long-term climatic shifts (*e.g.* paleoclimatic models) (Svenning et al., 2015), while investigating the underlying landscape connectivity patterns in the past and current scenarios. Understanding such connectivity among inselbergs and populations is vital, since it represents a critical factor determining a wide range of ecological phenomena, *e.g.* meta-population dynamics and maintenance of biodiversity (McRae et al., 2008), and this is a matter of major concern in the current fast global climate and land-use change scenario (Saura et al., 2014).

The combination of phylogenetic approaches and temporal landscape connectivity, allows one for disentangling the mechanisms involved in the origin of the disjunct distribution for a Neotropical plant species (Hmeljevski et al., 2017) and effects of Quaternary climatic

dynamics on several aspects of biodiversity patterns (Fordham et al., 2018). Among the promising approaches measuring isolation among habitats is to estimate resistance distance among areas. It measures the inverse of connectivity among areas, which can be interpreted ecologically as the successful dispersal of a plant species to reach an available and suitable habitat while crossing the landscape (Heringer et al., 2020; Oliveira-Junior et al., 2020). In short, we can assume resistance distance measures the isolation among areas, whereas its inverse measures the effective conductance (*i.e*., connectivity). Resistance distance is based on circuit theory and measures the isolation considering both multiple connections and variable suitability of land-cover for dispersal (McRae, 2006). Therefore, resistance distance and connectivity offers an intuitive and flexible approach to more thoroughly integrate spatial heterogeneity into studies of natural populations like population demography, migration rates, gene flow and phylogenetic diversification (McRae, 2006; McRae et al., 2008), and can stress the major drivers of species richness, phylogenetic diversity and species turnover (Leibold et al., 2004). The isolation among ancient inselbergs due to reduced dispersability (Hopper et al., 2016) led to a high number of local rare/endemics species (Porembski, 2007), with strongly differentiated population systems (Hmeljevski et al., 2017).

Phylogeographic studies of inselberg have provided insights into evolutionary processes leading to diversification of lineages and species, strong phylogeographic structure and, extensive genetic diversity levels (Palma-Silva et al., 2011; Barbosa et al., 2012; Hmeljevski et al., 2017). These results support the view that the inselbergs acted as refugia for xerophytic or cold-adapted species during glacial/interglacial cycles (Speziale & Ezcurra, 2012). This illustrates how phylogeographic studies of multiple co-occurring species may be particularly useful for understanding the role of stochasticity, as well as deterministic (*e.g.* current climate) factors in the present and the evolution of these naturally fragmented landscapes (Porembski et al., 1998). Moreover, over the last decade, an increasingly number of studies on the multiple drivers assembling plant community in tropical inselbergs came out, mainly the ones assessing the effects of local scale environmental factors on the taxonomic diversity (*i.e.* de Paula et al., 2017; Villa et al., 2018a; 2018b; Pinto-Junior et al., 2020a; 2020b). Nevertheless, such approach has limitations when disentangling processes on plant community assembly (Rezende et al., 2020). Thus raising the need of employment for more suitable and efficient alpha and beta phylogenetic metrics (*e.g.* evolutionary distinctiveness – ED and phylobetadiversity indices) capable to properly catch the turnover of these plant communities, since they carry backbone information of biogeographical processes underlying the evolutionary history of species (Rezende et al., 2020; Segovia et al., 2020). Such phylogenetic information can be incorporated

into regionalization schemes, which provide new insights into the spatial structure of biodiversity and reveal evolutionary affinities between vegetation types and regions (Rezende et al., 2020; Segovia et al., 2020).

Since plant community phylodiversity and phylobetadiversity are driven by several deterministic ecological processes (*e.g.* landscape connectivity, environmental filtering and interactions) at multiple spatial scales. The resultant intra-community phylodiversity will also depend significantly on the strength of the dispersal abilities of the species and their ability to overcome environmental harshness (Eiserhardt et al., 2013; Qian et al., 2020). Thus, the isolation between inselbergs and strong environmental filtering are expected to sort functional and phylogenetic close species (Götzenberger et al., 2012; Lebrija-trejos et al., 2015). At broad temporal and spatial scales, different macroecological processes, such as macroclimate factors, landscape-related habitats factors (*i.e.* connectivity and resistance), and filtering species from a larger pool (Eiserhardt et al., 2013; Qian et al., 2013; 2020; Rezende et al., 2019; 2020) are expected to drive phylogenetic random communities (Cavender-Bares et al., 2009).

In this study, we use a promissory approach by assessing environmental barriers that might rule community assembly level by estimating effects of landscape connectivity on phylogenetic diversity. For that, we used the greatest compiled dataset with the taxonomic composition of 42 inselbergs communities across the Atlantic Forest and Caatinga biome to 1) describe the phylogenetic diversity (alpha and beta) and structure of inselbergs communities; 2) map the resistance between inselbergs of Atlantic Forest and Caatinga and testing the effects of resistance distance on phylobetadiversity and 3) identify the effectiveness of protected areas and assess the conservation gaps for conservation of these centers of plant diversity and endemism (OCBILs habitat). First, 1a) we expected clustered phylogenetic structure at community assemblage scale due to climate refugia (Qian et al., 2014; Webb, 2000) and isolation among inselbergs; as well as 1b) we expected a random phylogenetic substitution at biome and landscape scale owing to dispersal limitations. Assuming isolation acts as a strong barrier to plant species, 2a) we expected an increase of phylogenetic turnover with the increase of isolation; furthermore 2b) we predict significant phylogenetic substitution of species (high turnover) in Atlantic Forest inselbergs supporting the *in situ* diversification and later migrations. Finally, in relation to protected area, 3a) we expect to find weak effectiveness of protected areas due to their reduced numbers in relation to hotspots areas, where conservation strategies are necessary to maintenance of phylogenetic connectivity in neglected climate refugia landscape.

2. Materials and Methods

2.1. *Study area*

The inselbergs studied here are distributed from northeastern to southeastern of Brazil, through the Caatinga and Atlantic Forest biomes (Fig. 1). They are on average 8.12 km distant from each other and cover the entire geographical range where the inselbergs occur in Brazil. The rupicolous vegetation in inselbergs can be found between 0 and 1,480 m a.s.l., is mainly associated with plant communities formed by monocotyledonous mats of Bromeliaceae, Cactaceae, Cyperaceae, and Velloziaceae distributed in patches and/or shrubs (more details in Table S1). We searched in the web of science for terms related to inselberg and plant to compile checklists of plant communities in inselbergs with taxonomic data. At the end of the search, we found 21 studies and 34 inselbergs with the complete checklist. We additionally conducted fieldworks in order to increase our sample size and the spatial distribution of the sampled inselbergs, totalizing 42 inselbergs with plant community data.

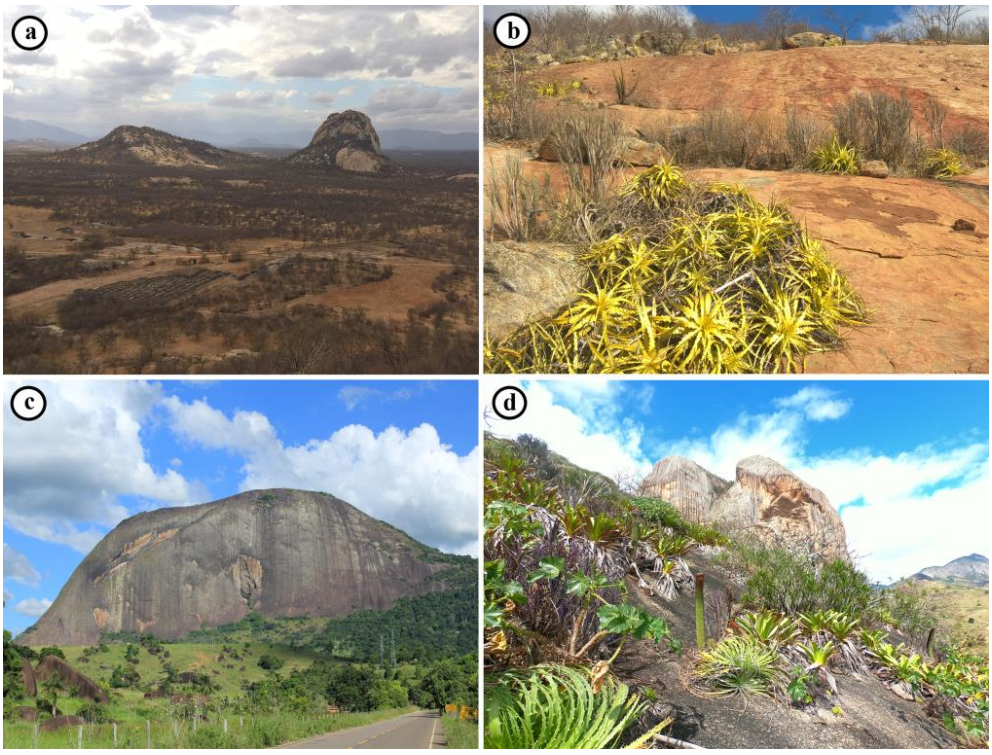

Figure 1 – Examples of inselbergs distributed from northeastern to southeastern of Brazil, through the Caatinga and Atlantic Forest biomes. a) Landscape of inselbergs from Caatinga in municipality of Patos – PB, b) monocotyledonous mats formed by *Encholirium spectabile* (Bromeliaceae) and *Vellozia plicata* (Velloziaceae) localized at inselberg Serrote da Lagoa – Patos (PB), c) Landscape of inselberg from Atlantic Forest in municipality of Nova Venécia – ES and d) monocotyledonous mats formed by *Encholirium horridum* (Bromeliaceae), *Alcantarea* sp. (Bromeliaceae), *Cnidoscolus urens* (Euphorbiaceae), *Coleocephalocereus* sp. (Cactaceae) and *Vellozia plicata* (Velloziaceae) situated at inselberg Pedra Bonita – Rubim (MG).

2.2. *Taxonomic data set*

The taxonomic information (spelling and synonyms) of inselbergs checklists was standardized and verified by Flora do Brasil 2020 (Brazil Flora G., 2021) through package 'flora' (Carvalho, 2020) and Taxonomic Name Resolution Service (TNRS) (Boyle et al., 2021), with APG IV (2016) circumscription for angiosperm families. As a result, a total of 1530 species and 602 genera distributed in 130 families, were recorded for this study.

2.3. *Phylogenetic reconstruction and metrics*

We pruned the megatree GBOTB.extended to all species found within this study using the *phylo.maker* function from the 'V.PhyloMaker' package (Jin & Qian, 2019) in R version 4.0.3 (R Core Team, 2020). Then, we extracted the largest cluster's root and basal node at the genus or family-level of angiosperms by using the function *build.nodes.1*, which in combination with the evolutionary hypothesis of scenario 3 generated our phylogenetic tree (Jin & Qian, 2019). The resultant phylogenetic tree generated with scenario 3 binds the tip for a new genus to the midway point of the family branch (Qian & Jin, 2016; Diniz et al., 2021).

The aforementioned reconstructed phylogenetic tree contained 1530 tips and 1045 internal nodes, which encompasses 68.3% of resolved taxa and 31.7% of unresolved taxa. Unresolved taxa, *i.e.* polytomies, can affect the phylogenetic diversity and dispersion pattern (clustering and overdispersion) causing underestimation or overestimation of results (Swenson, 2009). Thus, in order to avoid substantial biases promoted by the presence of polytomies, we broken them by randomly generating 10,000 fully bifurcated phylogenies into a series of dichotomies using the algorithm *bifurcatr* in 'PDcalc' package (Nipperess & Wilson, 2020).

From the fully resolved phylogeny, we calculated alpha- and beta-community phylogenetic metrics that represent the phylogenetic diversity and structure of inselbergs sampled. The alpha-communities metrics were PD, MPD, MNTD, sesPD, sesMPD and sesMNTD. The phylogenetic diversity (PD) (Faith, 1992) represents the sum of the branch lengths of a phylogenetic tree of each community (*e.g.* inselberg); the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD) represent, respectively, mean pairwise distance separating all pairs of co-occurring taxa in a community and the average distance separating each taxa or individual in the community from its closest heterospecific relative (Webb, 2000; Webb et al., 2002). These metrics are complementary, since MPD is more sensitive to phylogeny-wide (*i.e.* older clades and nodes) patterns of phylogenetic dispersion

(clustering and overdispersion), whereas MNTD is more sensitive to the patterns closer to the tips of the phylogeny (*i.e.* evolutionarily recent and shallower clades) (Webb et al., 2002).

In order to demonstrate the patterns of phylogenetic dispersion (clustering and overdispersion), we computed the standardized effect size (ses) of PD, MPD and MNTD using, respectively, the functions *ses.pd*, *ses.mpd* and *ses.mntd* of the 'picante' package (Kembel et al., 2010). Significant positive values of sesMPD and sesMNTD indicate phylogenetic overdispersion, *i.e.* community with most species more phylogenetically distant than the expected by chance; negative values indicate phylogenetic clustering, *i.e.* most of the species are more phylogenetically close than the expected by chance. For sesPD, significant positive and negative values indicate, respectively, more and less phylogenetic diversity than the expected by chance. The calculation of sesPD, sesMPD and sesMNTD was computed using 10,000 randomizations under the null model phylogeny pool (*i.e.* unconstrained null model), which randomizes the community data matrix by drawing species from pool of species occurring in the distance matrix (phylogeny pool) with equal probability to be included in the random communities (Kembel & Hubbell, 2006; Kembel et al., 2010).

We analyzed the phylobetadiversity (beta-community) by calculating the phylogenetic turnover between all pairs of inselbergs' communities. For that, we computed the indices βMPD (β mean pairwise distance) and βMNTD (β mean nearest taxon distance) through the functions *comdist* and *comdistnt*, respectively, in the package 'picante' (Kembel et al., 2010). The calculation of these indices allows one to evaluate the degree of phylogenetic turnover, while avoiding bias caused by differences in species richness among different sample communities. Then, we computed the standardized effect size (ses) of βMNTD and βMPD to demonstrate the degree (low or high) of phylogenetic turnover between the pairs of inselbergs using, respectively, the functions *ses.comdist* and *ses.comdistnt* of the package 'MicEco' (Russel, 2020). We computed sesβMNTD and sesβMPD by using 10,000 randomizations under the null model phylogeny pool (*i.e.* unconstrained null model) (Kembel & Hubbell, 2006). Significant positive values of sesβMNTD and sesβMPD indicate a pair of communities having higher phylogenetic turnover than the expected by chance, while significant negative values imply low phylogenetic turnover (Kembel et al., 2010; Swenson, 2014). We considered the significance of sesβMNTD and sesβMPD between a pair of inselbergs as values greater than 1.96 (significant high phylogenetic turnover) and values lower than -1.96 (significant low turnover) (Gotelli & Entsminger, 2003).

Additionally, we performed regression between all metrics (sesPD, sesMPD, sesMNTD, sesβMPD and sesβMNTD) from the unresolved phylogeny and, the same metrics

from the resolved (fully bifurcated) phylogeny in order to ensure a clear diagnostic on how much the aforementioned proportion of lack of phylogenetic resolution (*i.e.* presence of polytomies) influence their outcomes (Swenson, 2009). Coefficient of correlation (r^2) and slope equal to 1 indicate that lack of phylogenetic resolution does not affect the phylogenetic diversity or dispersion (clustering or overdispersion) measures. Conversely, slopes different from one can over- or underestimate the phylogenetic dispersion and indicate a substantial influence of the lack of phylogenetic resolution (Swenson, 2009; Diniz et al., 2021).

Finally, we extracted evolutionary distinctiveness scores (ED) from the phylogenies to describe species uniqueness (Isaac et al., 2007; Pontara et al., 2018), using the *evol.distinct* function in 'picante' package (Kembel et al., 2010), which allowed us to evaluate the evolutionary heritage of the inselbergs in a biogeographic context. This metric shows the degree of evolutionary isolation at the species level and how much the species contributed to a phylogenetic tree, *i.e.* the evolutionary history of communities. Thus, species most evolutionarily isolated have higher values of ED, which imply greater functional and genetic importance at communities than their occurrence (Cadotte et al., 2008; 2010). Therefore, ED enabled us to disentangle inselberg communities with distinct levels of evolutionary uniqueness, thus prioritizing them according to the level phylogenetic isolation of their species.

2.4. *Land use data*

We download the land use classification data provided by MapBiomas Project v.5.0 (MapBiomas Project, 2020) to Atlantic Forest and Caatinga biomes and clipped the land use map using a buffer zone with 100 km of radius around the inselbergs selected that delimit our study area. Later, we extracted the coverage and land use information, resampling to a pixel resolution of ~ 1 km² and used the following classes: rock outcrops, native forest, savannah, grasslands and water + anthropogenic activity. Anthropogenic activity includes all land use classes generated by human activities assigned by MapBiomas Project, such as agricultural, forest plantations, mining, and urban areas.

2.5. *Ecological niche modeling*

Ecological niche models (ENM) of the current climate scenario were built from the 42 inselbergs selected for this study, more 73 inselbergs identified through field observations, high-spatial-resolution images (Google Earth) and published research, totalizing 115 inselbergs in the southeastern and northeastern regions of Brazil. The geographical coordinates of each inselbergs were used to indicate the habitats occupied by the species, thus relating "habitat" to

"distribution area". The predictive climate models were built using two datasets (bioclimatic and topographic) in conjunction. The bioclimatic variables were obtained from WorldClim 2.1 (Fick & Hijmans, 2017) database; we also include models of others six bioclimatic and eight topographic variables (Table S2). All variables were obtained with a pixel of 30' (~ 1 km²). We eliminated the variables with strong biological correlation ($r > 0.9$) (Bueno et al., 2017) to inselbergs distributions, remaining 16 bioclimatic and seven topographic variables (Tab. S1). Finally, we used the variables selected (Tab. S1) to build the current predictive habitat distribution.

The current model was made using MaxEnt v.3.4.1 (Phillips et al., 2017) using two general circulation models (GCM), CCSM-4 and MIROC-ESM of Fifth Assessment Report of the Intergovernmental Panel on Climate Change (AR5 – IPCC). We calculated the average of 10 replicates (subsamples) divided in 75% of training and 25% of random tests. We also used the jackknife procedure and permutation importance to estimate the relative influence of different predictor variables. The average threshold of the models was calculated by the maximum training sensitivity (true positive rate) and specificity (false positive rate) of each global climatic model. To validate the models created, we analyzed the specificity *vs* sensitivity of the model by the value of area under the curve (AUC) of ROC (receiver operating characteristic) (Phillips et al., 2006). Finally, we converted the output map to binary rasters with presence and absence of suitable areas of inselberg distribution generated by climate models. All the climatic variables were extracted and processed by ArcMap software (ESRI, 2015).

2.6. *Landscape analysis*

Based on circuit theory (McRae et al., 2008), we used the land use classification and binary raster of suitable areas to build six hypothetical resistance surface maps by assigning each element in the land use map and the suitable climate areas with different resistance values (Table 1). The values assigned vary from 1 to 100 (minimum and maximum resistance, respectively). Hence, land use classified as inselberg and suitable climate areas were assigned with lower values, whereas the other land use classes were assigned with higher values of resistance. These resistance surface maps were used as input ground in the Linkage Mapper plugin from ArcGIS software (McRae et al., 2014; 2016) to calculate the resistance distance between each inselberg and generated therefore six hypothetical resistance distance surface maps. They represent six models of resistance exerted by the landscape to the plant dispersal among inselbergs. Therefore, the cost of moving through the cells is affected by the value of resistance attributed to pixel (Oliveira-Junior et al., 2020). The values of hypothetical models

were generated by Jaccard dissimilarity through species shared between inselbergs and others land use classes (native forest, savannah, grasslands and water + anthropogenic activity) (Fig. 2a). To model the connections between Atlantic Forest and Caatinga, and the 42 studies areas, we used the six models of resistance as an input in Linkage Mapper Tool (McRae et al., 2014; 2016).

Table 1 – Hypothetical model of resistance constructed to represent the landscape connectivity between sampled areas and Atlantic Forest and Caatinga biomes.

Landcover	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Inselberg + Suitable climate	1	1	-	-	-	-
Inselberg	5	5	1	-	-	1
Suitable Climate	5	-	-	1	1	-
Native Forest	40	100	100	100	40	40
Savannah	60	100	100	100	60	60
Grasslands	70	100	100	100	70	70
Water + Anthropogenic activity	100	100	100	100	100	100

2.7. *Data analysis*

To select the best hypothetical resistance distance model to be used in further analysis, we generated six beta regressions models through the *betareg* function in 'betareg' package (Cribari-Neto & Zeileis, 2010) to test the effect of pairwise resistance distance among inselbergs from each of the six models of Jaccard dissimilarity (Thiele et al., 2018; Heringer et al., 2020; Oliveira-Junior et al., 2020). As Jaccard dissimilarity measures how much species are not shared between pairs of inselbergs, we assume as greater the resistance distance between areas greater the isolation and greater the Jaccard dissimilarity (Oliveira-Junior et al., 2020) (Fig. S1). Then, we selected the best model by using Akaike Information Criterion (AIC) assessed with *model.sel* function in 'MuMIn' package (Bartón, 2020), where models with $\Delta AIC < 2$ were considered well fitted and equally plausible to be selected (Burnham et al., 2010). To calculate the Jaccard dissimilarity between inselbergs we use the *vegdist* function in 'vegan' package (Oksanen, 2020). After selected the best model and validate how well-fitted it is our resistance model, we rerun the model of connections between Atlantic Forest and Caatinga, and all 115 inselbergs used in ecological niche models, to up-scale our resistance model from a regional to a biogeographic model.

We used the best model of resistance distance selected by AIC to test the relationship of phylobetadiversity (βMPD, sesβMPD, βMNTD and sesβMNTD) on isolation effect. These relationships were tested using generalized linear models (GLM) with *glm* function in 'stats'

package (R Core Team, 2020) and test the normality of residuals were checked using Q-Q plots and *shapiro.test* function in the 'stats' package (R Core Team, 2020). The significance of the relationships of all regression models was calculated with type-II using the *Anova* function of 'car' package (Fox & Weisberg, 2019). We used the 'ggplot2' package (Wickham et al., 2020) for graphical visualization. All analysis was carried out with R software version 4.0.3 (R Core Team, 2020). We carried out complementary tests with Wilcoxon rank sum test in R to evaluate whether the phylogenetic diversity (sesPD) of inselbergs belonging to Caatinga biome differs significantly from the ones belonging to Atlantic Forest.

2.8. *Linking landscape-diversity connectivity with conservation*

In order to identify areas that indicate high effects of resistance distance (*e.g.* isolation) and high taxonomic and phylogenetic diversity we produced maps of 10 km^2 grid cells of six metrics: species richness, resistance distance average, PD, sesPD, ED average and proportion of top 10% high-ED. The proportion of 10% high-ED was measured by dividing the number of species with the 10% high-ED values by the total number of species (Pontara et al., 2018). We marked the grid cell as a hotspot if the value of this grid was higher than 20% of the highest value of a certain index. We produced maps of the overlapping between the hotspots that showed more than four metrics in grid cells in order to illustrate the multi-metric hotspots. Finally, we overlapped the hotspots map with the coverage of protected areas across the Atlantic Forest and Caatinga and measured how much protected area is under protection. The protected area shapefiles were obtained from the National Register of Conservation Units (in Portuguese, Cadastro Nacional de Unidades de Conservação - CNUC) (mapas.mma.gov.br/i3geo/datadownload) containing data from federal, state, and municipal protected areas of Brazil.

3. Results

3.1. *Phylogenetic relationships*

The phylogenetic diversity demonstrated by sesPD evidenced that among the 42 inselbergs, 19 (45.2%) of them had significantly lower diversity than expected by chance, *i.e.*, inselbergs with most of the phylodiversity represented by close relatives. Interestingly, among these 19 inselbergs with significant sesPD, 13 (or 31% of the total 42 inselbergs) are from the Atlantic Forest biome. This is congruent with significantly greater ($W = 135$, $p = 0.034$) phylogenetic diversity of inselbergs from Caatinga than the ones from Atlantic Forest.

Overall, the results of sesMPD showed that among the 42 inselbergs, 17 (or 40.4%) presented significant phylogenetic clustering, which includes basal clades and old nodes in the phylogeny. Among these 17 inselbergs with significant clustering, 11 (26.2% of the total of 42 inselbergs) are from the Caatinga. Following the same trends, sesMNTD showed 19 inselbergs (45.2% of the total of 42 inselbergs) with significant phylogenetic dispersion, all evidencing phylogenetic significant clustering between taxa from recently evolved clades and shallower nodes in the phylogeny. At biome level, among the 19 inselbergs with significant clustering, 14 (33.3% of the total of 42 inselbergs) are from the Atlantic Forest. From these results, we can highlight that Atlantic Forest shelters a higher percentage of phylogenetic clustered species when considering the most recently evolved clades demonstrated by sesMNTD.

3.2. *Phylogenetic turnover*

In relation to phylogenetic turnover between pairs of inselbergs' communities, the results considering the entire phylogeny (*i.e.* including basal nodes and old clades) demonstrated by sesβMPD showed that among the 861 pairwise phylogenetic distances between inselbergs, 511 (59.3%) had a non-significant phylogenetic turnover, *i.e.* phylogenetic replacement of species between the communities does not differ from the expected by chance. Furthermore, the amount of significant pairwise scores of sesβMPD regarding high (178 – 50.8%) and low (172 – 49.2%) turnover does not differ statistically. Concerning to phylogenetic relationships between clades of more recent evolutionary history demonstrated by sesβMNTD, we observed that among the 861 inselberg pairwise phylogenetic turnover, 461 (or 53.6%) were not significant, while 400 (or 46.4%) had significant phylogenetic turnover patterns. Besides that, we also found that sesβMNTD presented significantly more pairwise higher phylogenetic turnover (237 – 59.2%) than low/phylogenetic turnover (163 – 40.8%).

We did not find substantial influence of lack of phylogenetic resolution in the outcomes of the beta phylogenetic indices we computed, since the regression analysis between these metrics derived from the unresolved phylogeny and from the fully resolved phylogeny showed high coefficients ($r^2 \geq 0.99$) and, slope values ranging from 0.99 to 1 (Table S3). Thus, we can assume our outcomes of phylobetadiversity as non-biased.

3.3. *Landscape resistance analysis*

Among the six resistance distance models, three were selected under $\Delta AIC > 2$ and considered as having the best fit and equally parsimonious: model 4 (p = 2e-16, r^2 = 0.277, $\Delta AIC = 0.00$), model 2 (p = 2e-16, r^2 = 0.275, $\Delta AIC = 1.70$) and model 3 (p = 2e-16, r^2 = 0.275,

ΔAIC = 1.87). All selected models presented highest resistance to landscape connection and can be considered equally explanatory, which agree that landscapes weakly connected are a barrier to plant dispersal among inselbergs communities. Although the three models selected are acceptable, we used the model 4 in the following steps of our study to represent the inselbergs' evolutionary biogeography history.

Despite the extremely disjunct distribution of inselbergs, the relative lower resistance corridors showed the existence of weak habitat corridors among the inselbergs of the Atlantic Forest and Caatinga (Fig. 2b). The least-cost paths among the sampled inselbergs indicate the existence of core areas with relatively low resistance distance to dispersal and, consequently less isolated set of inselbergs, in 12 points: eight in Caatinga (Ceará (CE), Central and South of Rio Grande do Norte (RN), East and West of Paraíba (PB), Pernambuco (PE), North and Central of Bahia (BA)) and four in Atlantic Forest (two in North of Minas Gerais (MG), Central-Axis Espírito Santo/Minas Gerais (ES/MG) and Rio de Janeiro (RJ)) (Fig. 2c). When considering intermediate and low resistance distance (0.85 – 2.52), we get three major core areas: northeastern, Bahia and southeastern. In contrast, we can consider two areas with high distance and great cost to movement or dispersal: the Central core of Bahia and the isolated inselberg in Bahia (Fig. 2c).

All phylobetadiversity metrics showed a positive relationship with resistance distance effect: βMPD (GLM: p = 2e-16, r^2 = 0.330, Fig. 3a), sesβMPD (GLM: p = 2e-16, r^2 = 0.339, Fig. 3b), βMNTD (GLM: p = 2e-16, r^2 = 0.263, Fig. 3c) and sesβMNTD (GLM: p = 2e-16, r^2 = 0.246, Fig. 3d), which confirms that the increase in resistance distance among communities represent dispersal barriers, leading to high phylogenetic turnover between inselbergs.

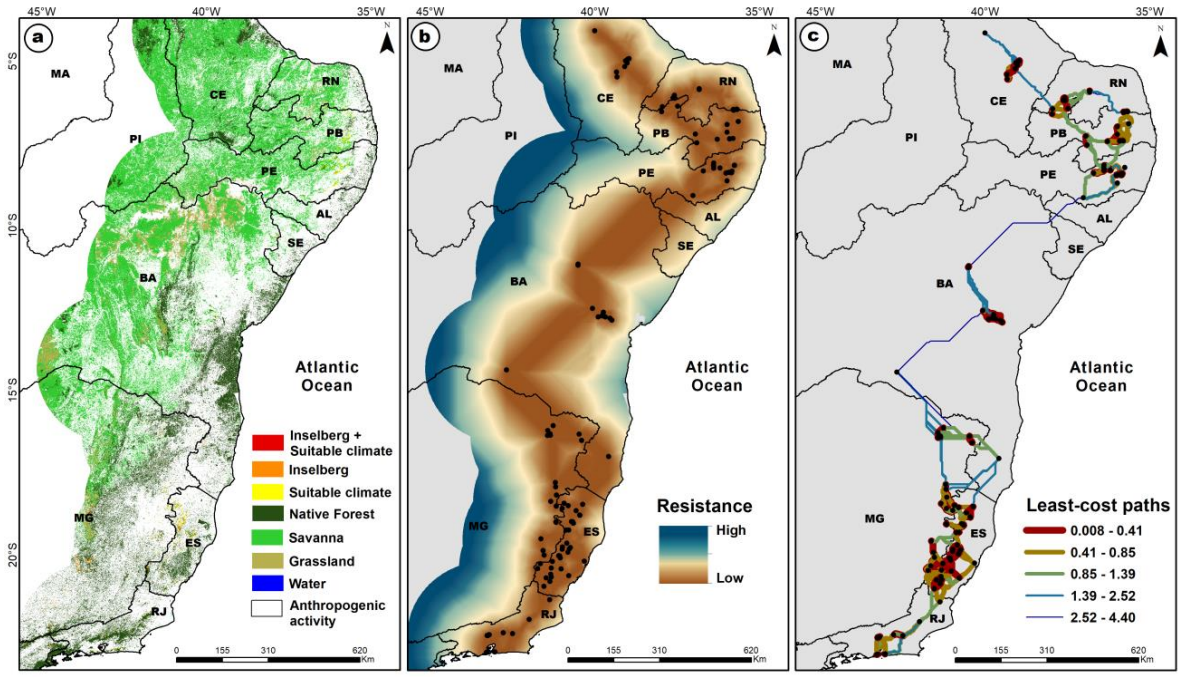

Figure 2 – Map of landcover classification, lower cost corridors and least-cost paths (LCP) generated across Atlantic Forest and Caatinga inselbergs at Brazilian eastern. a) Landcover classification and predictive climate distributions used to build the hypothetical resistance surface models, b) lower cost corridors map of model 4 (most explanatory model) illustrating the resistance of landscape connectivity, and c) least-cost paths map. Black circles are the sample sites. Geographic coordinate system datum: WGS-84.

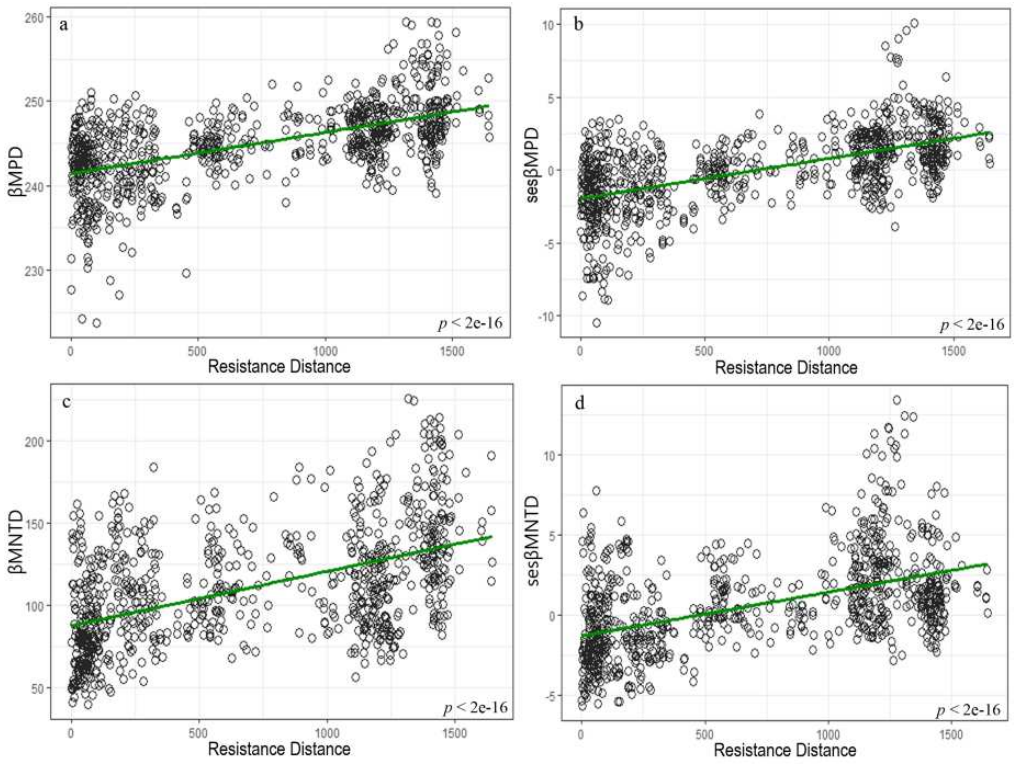

Figure 3 – Relationship between phylobetadiversity metrics and resistance distance: a) β mean pairwise distance, b) standardized effect size (ses) β mean pairwise distance, c) β mean nearest taxon distance and d) ses β mean nearest taxon distance.

3.4. *Conservation strategies*

The overlaps of all metrics showed greater values of hotspots in Caatinga, nevertheless we highlight that the higher values which account for all six metrics are present only in Atlantic Forest (Fig. 4a). When analyzing metric-by-metric, a latitudinal gradient was observed to taxonomic and phylogenetic metrics (Fig. S2). Species richness, PD, ED average and proportion of top 10% high-ED had similar patterns of distribution along the latitudinal gradient (Fig. S2a, c, e, f) with greater values in northeastern and decreasing to southeastern. Though, Atlantic Forest presents higher values for sesPD (Fig. S2d). Isolation by resistance (Fig. S2b) showed similar distribution trends between the biomes compared. Analyzing the areas identified as hotspots, again, a latitudinal gradient was observed to taxonomic and phylogenetic metrics (Fig. S3). Caatinga showed greater values to species richness and sesPD (Fig. S3a, d), while Atlantic Forest showed higher values to PD (Fig. S3c). Interestingly, all grid plots showed greater values for ED average (Fig. S3e); meanwhile for isolation by resistance Atlantic Forest showed higher values, although Caatinga showed higher values for 10% high-ED (Fig. S3b, f). The hotspots area and the protected area showed low overlap (Fig. 4b), since only nine protected areas were found inside the hotspots area. In relation to the 83 species with top 10% high-ED, only 54.2% were found inside at least one protected area.

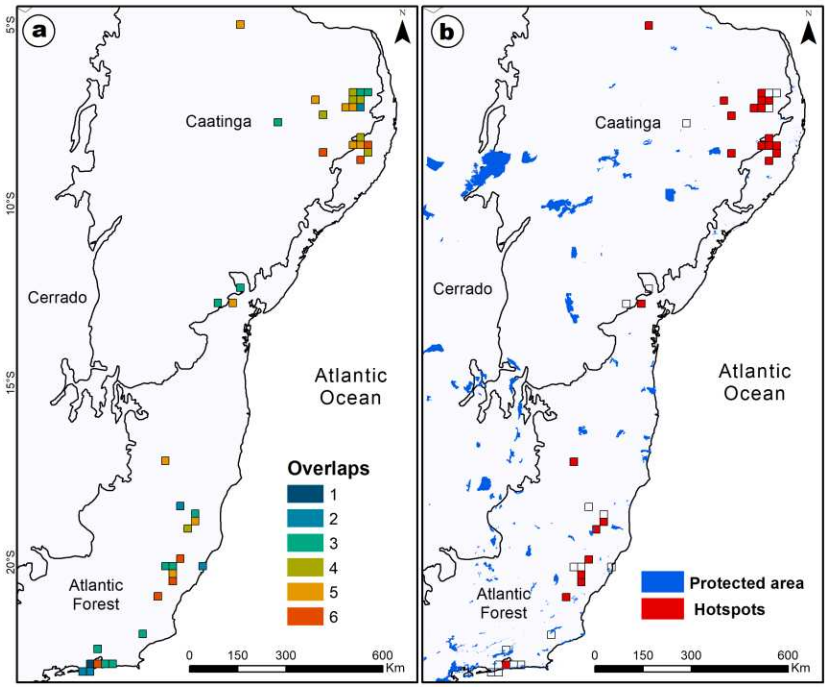

Figure 4 – Geographic distribution and the overlapping of all conservation metrics and between protected areas across Atlantic Forest and Caatinga inselbergs in Brazilian eastern. The grid cells represent a buffer area of 10 km². a) Overlap of all conservation metrics and b) overlap the hotspots areas and protected area (municipality, state and federal). Grid cells with ≥ 4 conservations metrics overlapped were indicated as hotspots.

4. Discussion

To our knowledge, this is the first study to use circuit theory to model landscape isolation and investigate its influence on phylogenetic metrics at community level. Our focus has been on inselbergs ecosystems, across high mountain ranges between Atlantic Forest and Caatinga biomes, which are naturally isolated in the landscape (Fig. 1). We found evidence for some dispersal limitations in inselbergs communities indicating that high mountain ranges can lead to a high phylobetadiversity, thus imposing isolation to the evolutionary lineages of the inselbergs' flora. Furthermore, we found evidence supporting the existence of a latitudinal gradient in species richness and sesPD of plants species, across the Neotropical inselberg landscape, and greater isolation between the northeastern and southeastern core areas. Thus, our findings suggest that they can be explained by the Pleistocene Arc Hypothesis - PAH, which reached its maximum extension during the Last Glacial Maximum (LGM) (Prado, 2000), contributing to greater isolation of inselberg species. Given the widespread and fast current climate changes occurring in the Atlantic Forest and Caatinga, our results provide a valuable baseline to promote conservation strategies capable of safeguarding biodiversity and mitigating threats in these iconic landscapes.

Our results of phylogenetic diversity and structure showed significant differences between inselbergs communities from the two biomes, where Caatinga inselbergs had higher phylogenetic diversity (sesPD) and more phylogenetically clustered communities regarding the entire phylogeny (*i.e.* including old clades and basal nodes measured by sesMPD). Atlantic Forest inselbergs showed more phylogenetically clustered communities regarding closer taxa sharing more recent evolutionary history (sesMNTD). Phylogenetic diversity (sesPD) of inselbergs assemblages showed similar latitudinal gradient with species richness, despite not showing the same pattern within biome. This evidence suggests that in regional scale, dispersal limitations could rule sesPD across inselbergs assemblages, influencing differently richness across the Brazilian inselbergs assemblages. Arango et al. (2020) presented a similar interpretation regarding the Caatinga tree assemblage of SDTFs, but an inverse latitudinal gradient. The Caatinga inselbergs assemblage with high sesPD coincide with the proposed refugia nuclei by Pleistocene Arc Hypothesis to SDTFs in Brazilian northeastern (Prado, 2000). The phylogenetically clustered species for Caatinga inselbergs (demonstrated by sesPD and sesMPD) indicated similar pattern as SDTFs. The lineages accumulated over time from either local speciation and/or low extinction of early diverged clades, with some derived lineages later expanding their distribution to south (Cortes et al., 2015; Arango et al., 2020). This southern

expansion formed assemblages of low sesPD, such as Atlantic Forest inselbergs, composed by both closely and distantly related species.

The proportions of high phylogenetic turnover among inselbergs suggest effects of strong environmental filtering derived from extreme edaphic conditions furthering evolutionary distinct lineages with convergent attributes (Cavender-Bares et al., 2009; Kissling et al., 2012; Arango et al., 2020). Despite we observed significant higher and lower phylogenetic turnover for sesβMPD and sesβMNTD, over half pairs of communities had a non-significant turnover, which suggests the phylogenetic replacement of species as an outcome influenced by stochastic factors balancing the phylobetadiversity among the inselbergs. This indicates the replacement (*i.e.* turnover) of phylogenetic lineages among these inselbergs' communities does not differ from what is randomly expected. Such a majority of random phylogenetic turnover may be an outcome of the inselbergs sharing a higher proportion of lineages within a regional pool of species than between biomes, thus suggesting influence of dispersal limitations across regions as the most important driver of their phylogenetic relationships and exchanges. Furthermore, proportions of significant low phylogenetic turnover between inselbergs indicate the presence of closely related lineages that diversified in situ due to isolation effects, agreeing with phylogenetic diversity and structure outcomes and with PAH (Prado, 2000).

The resistance distance models exemplify the potential of assessments of isolation and dispersal events for models of regional population and meta-community dynamics. This observed scenario with all models presenting highest resistance value for all landcover resistances lead us to draw the assumption that differences between landcover resistance values do not affect the landscape connectivity. This might be expected for extremely fragmented habitats like the inselbergs. Thus, the scenarios such as the inselbergs are inserted comprising different types of habitats and might vary in the resistances to dispersal (or migration) within and among communities and at regional scale (Thiele et al., 2018). This is congruent with our best resistance model, *i.e.* based in climate habitat, like the most explanatory of the inselbergs connectivity. According to our finding, the LCP indicated the existence of core areas with relatively low path cost within-biome and great cost between-biome and isolated areas. Thus, an existence of significant isolation among opposite phylogenetic patterns, suggests that isolation is the main driver of turnover phylogenetic between inselbergs assemblages.

Several genetic studies have indicated an association between low gene flow and high isolation among populations (Palma-Silva et al., 2011; Hmeljevski et al., 2017). This is congruent with our outcomes of the connectivity model, suggesting the existence of ancient connections between the northeastern and southeastern core areas, confirming the

contemporary connections within-region, given to inselbergs climate stability areas (refugia) of PAH since the LGM. For instance, distributions and dispersal corridors of *Encholirium horridum* L.B.Sm. (Bromeliaceae), an endangered rupiculous species of inselbergs has demonstrated dispersal routes across Quaternary period (Hmeljevski et al., 2017). As well as the species of genus *Hoffmannseggella* (Orchidaceae) presented rapid radiation around the Middle/Late Miocene (11–14 Mya) from southern Minas Gerais via corridors to northern Minas Gerais, Espírito Santo, Rio de Janeiro and, Bahia (Antonelli et al., 2010).

Due to edaphic-climatic characteristics, climatic factors as drivers in explaining the inselbergs community assembly has been increasingly assumed (Hmeljevski et al., 2017; Pinto-Junior et al., 2020; de Paula et al., 2021). Especially due the theoretical approaches related to the climate stability areas (refugia) during Quaternary climatic fluctuations (Hmeljevski et al., 2017) and the OCBILs landscape (de Paula et al., 2021). Thus, the phylogenetic structure of assemblages also reveals deep-evolutionary and biogeographic processes (Kissling et al., 2012), what is congruent with paleoclimatology evidences that point to their origin to the climatic shifts at Cenozoic, beginning with the onset of extreme aridity in the Late Paleogene (Safford & Martinelli, 2000). Recent studies have demonstrated the effects of environmental filtering in inselbergs communities (Sarthou et al., 2017; Henneron et al., 2019; Pinto-Junior et al., 2020a; de Paula et al., 2021), nevertheless never been demonstrated the effects of environmental filtering from past climate conditions. We can highlight the Atlantic Forest inselbergs, due to the positive relationship between temperature-related variables and species richness (Pinto-Junior et al., 2020a). This may have afforded more suitable habitat to the establishment and diversification of more recent lineages, as showed by higher percentage of phylogenetically clustered inselbergs regarding the clades with the most recent evolution history (sesMNTD).

The climate stability has an important role as an environmental filtering driving the speciation and extinction of species, as well as the size of their geographical range of isolation (Morueta-Holme et al., 2013). This consequently affects dispersal strategies and gene flow across plant (and animals) populations along the landscape. Strong effects of isolation on short and long-distance dispersed species have been found in plants (Morán-Ordóñez et al., 2015; Thiele et al., 2018) and animals (Thompson & Townsend, 2006; Oliveira et al., 2018). Another study found that altitude and rainfall exerted contrasting effects on plant diversity depending on species dispersal modes, short dispersal (autochorous) are disfavoured by steeper slopes of taller inselbergs and higher intensity of water runoff, sweeping recently fallen seeds. On the other hand, large dispersal (anemochorous and zoochorous) could be benefited by increase in atmospheric turbulence and presence of seed-dispersing animals (Henneron et al., 2019).

Isolation seems also plays a role in the evolutionary distinctiveness (ED) among inselbergs, since our findings pointed to greater values of high-ED in the inselbergs in Caatinga and low proportion in Atlantic Forest. This pattern leads us to assume of higher ED in the inselbergs of Caatinga shelter more relict species phylogenetically specialized than those that radiated recently (Pontara et al., 2018) to the inselbergs in Atlantic Forest. Regions holding with ED are considered "cradles" and "museums" of biodiversity (Jetz et al., 2014), which shelter high concentrations of species restricted to mountainous niches, such as inselbergs. Such type of mountainous niche is generally assumed as refugia keeping long-term climatic stability, where we might expect to see ancient/relictual lineages (Sandel et al., 2011; Pontara et al., 2018). Further, we also highlight the importance of inselbergs with high-ED from Atlantic Forest due to the high number of endemic species, according to Flora do Brasil (Brazil Flora G., 2021). One example illustrating this is the fact that Atlantic Forest inselbergs had at least five times more rupicolous species described as endemic than Caatinga inselbergs.

The total of hotspots overlapped by protected areas (less than one percent of Brazilian protected area) is not surprising to inselberg ecosystems. Among 153 species included in ED, 45.8% of high-ED was found in any protected area. In other words, we can lose a significant part of evolutionary history of climate refugia since LGM due to lack of efforts in environmental policies by Brazilian policymakers, mainly in face of the current Brazilian federal environmental legislation. As protected areas are one of the most effective strategies to preserve biodiversity and threatened species (Oliveira et al., 2017; Heringer et al., 2020), it is notorious that inselbergs plant communities are currently dangerously unprotected. Actually, non-forest ecosystems, such as inselbergs, represent 5.9% of the area of Brazil, 93% of which are made up of savannas and only 7% of rock outcrops (MapBiomas Project, 2020). Despite this disjunct distribution, inselbergs have rarely been considered in the context of the degradation of Earth's natural ecosystems (Porembski et al., 2016). Moreover, inselbergs have characteristics that can help in the development of hypotheses that explain ecology and evolution, thus generating information that assist for better conservation practices for OCBILs landscapes (Hopper et al., 2016).

We would like to highlight the importance of these results (*e.g.* hotspots areas) for environmental managers and policymakers, since our models can assist in the identification of efficient areas for the creation of parks and reserves, mainly in Caatinga. These type of information is important to avoid the creation of protected areas based on arbitrary criteria, *e.g.*, decisions solely on species richness, irreplaceability or complementarity (myopic scenario in Drechsler (2005)), that ignores the risk of land cover loss and future uncertainty on ecosystem

services. Due this reason, we highlighting the strategies pointed by Pinto-Junior et al. (2020b) and also effective conservation strategies that can drive the efforts to inselbergs conservations: 1) focus on protecting mainly isolated inselbergs, as well as multiple groups of each core areas and 2) implementation of effective restoration strategies that minimize the effect of isolation among core areas.

Our study demonstrated clustered phylogenetic structure at community scale due to climate refugia and isolation between inselbergs, as well as random phylogenetic substitution at biome and landscape scale owing to dispersal limitations. In this way, we showed that isolation acts as a strong barrier to plant species, increasing the phylogenetic turnover with the increase of isolation, which supported the *in situ* diversification and later migrations in Atlantic Forest inselbergs. We demonstrated the negative relationship between climatic instability and phylodiversity, leading to high phylodiversity in communities with higher stability (climate refugia) and accumulation of evolutionary distinct lineages, as well as low phylodiversity in inselbergs with low stability and recent evolution clades. We believe this study and conservation strategies are necessary to drive practices for political, social, and economic purposes enabling the maintenance of phylogenetic connectivity in neglected climate refugia landscapes.

5. Conclusions

Our study demonstrated the existence of a latitudinal gradient in species richness and sesPD of plants species, across the Neotropical inselberg landscape, and greater isolation between the northeastern and southeastern core areas. Thus, the joint-effect of isolation by resistance and environmental filtering can create more isolated communities, composed by less phylogenetic diversity of closer species and functionally adapted to environmental conditions (impoverished soils and buffered climate), supporting the OCBIL theory. Our findings suggest that the Pleistocene Arc Hypothesis may have contributed to greater isolation of inselberg species and the existence of ancient connections between the northeastern and southeastern core areas, given to inselbergs climate stability areas (refugia) since the LGM. We highlight that the conservation of mountain vegetation is a key strategy to the maintenance of biodiversity and distinct phylogenetic lineage in inselbergs. We emphasize the need for more investment in research, mainly in biogeographic studies that combined different branches of science (botany, zoology, ecology, genetic and conservation) to explore the integrated effect of these sciences on biotic interactions of inselbergs species.

6. Acknowledgements

We acknowledge the Programa de Pós-Graduação em Botânica – UFV for supporting our research in Brazil and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing scholarships to the author. We would like to thank Gustavo Heringer, Écio S. Diniz and Pedro M. Villa for contributions in methodology, ideas and suggestions in the final version of this manuscript. We are also grateful to Rafael F. Lopes-Silva for kindly helped with images of the Caatinga inselbergs. We thank to Instituto Estadual do Meio Ambiente e Recursos Hídricos do Espírito Santo (IEMA) for the research license, Neotropical Grassland Conservancy (NGC) for financial supporting and Deutscher Akademischer Austauschdienst (DAAD) for providing scholarships as visiting researcher in Institute of Landscape Ecology (ILÖK) University of Münster (WWU).

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8. Supplementary Material

8.1. *Tables*

Table S1 – Complementary information about inselbergs sampled, including the biome, climate and geographic coordinates.

Inselberg	Name	Biome	Climate (Alvares et al., 2013)	Geographic Coordinates
1	acucar	Atlantic Forest	Aw - Tropical zone with dry winter	S -22.93 W -43.15
2	agenor	Caatinga	As - Tropical zone with dry summer	S -12.71 W -39.77
3	aguia	Atlantic Forest	Aw - Tropical zone with dry winter	S -18.97 W -40.70
4	antonio	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.34 W -35.79
5	araras	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -22.41 W -43.23
6	cariri	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.20 W -36.16
7	cruzeiro	Caatinga	As - Tropical zone with dry summer	S -35.75 W -8.15
8	cve	Caatinga	As - Tropical zone with dry summer	S -8.39 W -36.01
9	elef	Atlantic Forest	Aw - Tropical zone with dry winter	S -18.76 W -40.45
10	espinho	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.06 W -37.29
11	falm	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.47 W -36.89
12	figueira	Atlantic Forest	Aw - Tropical zone with dry winter	S -18.64 W -40.55
13	fornog	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -20.51 W -41.09
14	furada	Caatinga	As - Tropical zone with dry summer	S -8.57 W -36.87
15	gamela	Atlantic Forest	Am - Tropical zone monsoon	S -20.29 W -40.30
16	guariba	Caatinga	As - Tropical zone with dry summer	S -8.38 W -35.84
17	helena	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -6.82 W -35.63
18	imbui	Atlantic Forest	Aw - Tropical zone with dry winter	S -22.93 W -43.11
19	itacoatiara	Atlantic Forest	Aw - Tropical zone with dry winter	S -22.96 W -43.01
20	itanhanga	Atlantic Forest	Aw - Tropical zone with dry winter	S -22.98 W -43.31
21	jiboiaf	Atlantic Forest	As - Tropical zone with dry summer	S -12.27 W -39.06
22	jiboias	Atlantic Forest	As - Tropical zone with dry summer	S -12.85 W -39.46
23	lagpe	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.01 W -35.88
24	lajinha	Atlantic Forest	Cwa - Humid subtropical zone with dry winter and hot summer	S -41.08 W -20.01
25	luzia	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -4.95 W -39.02
26	macumba	Atlantic Forest	Aw - Tropical zone with dry winter	S -23.03 W -43.48
27	madalena	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -21.93 W -42.01
28	misterioso	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -19.80 W -40.77
29	pab	Caatinga	As - Tropical zone with dry summer	S -8.33 W -35.83
30	papagaio	Caatinga	As - Tropical zone with dry summer	S -38.09 W -7.68
31	pedraazul	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -41.01 W -20.39
32	pedras1	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7 W -36.01
33	pedras2	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.08 W -36.06
34	pontoes	Atlantic Forest	Cwb - Humid subtropical zone with dry winter and temperate summer	S -20.93 W -41.54

35	puxinana	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.15 W -35.97
36	sta_terezinha	Atlantic Forest	Aw - Tropical zone with dry winter	S -40.78 W -18.5
37	submarino	Atlantic Forest	Cwa - Humid subtropical zone with dry winter and hot summer	S -41.29 W -20.18
38	teofilo	Atlantic Forest	Cwa - Humid subtropical zone with dry winter and hot summer	S -17.08 W -41.37
39	timbauba	Caatinga	BSh - Dry zone semi-arid with low latitude and altitude	S -7.01 W -35.88
40	trevo	Atlantic Forest	As - Tropical zone with dry summer	S -8.68 W -35.72
41	urca	Atlantic Forest	Aw - Tropical zone with dry winter	S -22.95 W -43.15
42	urucu	Atlantic Forest	As - Tropical zone with dry summer	S -8.79 W -35.84

Table S2 – Bioclimatic and topographic variables selected were after eliminating variables with strong biological correlation ($r > 0.9$).

Variable	Dataset	Status	References
Annual Mean Temperature (Bio 1)	Bioclimatic	Selected	Hijmans et al., 2005
Mean Diurnal Range (Bio 2)	Bioclimatic	Selected	Hijmans et al., 2005
Isothermality (Bio 3)	Bioclimatic	Selected	Hijmans et al., 2005
Temperature Seasonality (Bio 4)	Bioclimatic	Selected	Hijmans et al., 2005
Max Temp. of Warmest Month (Bio 5)	Bioclimatic	Selected	Hijmans et al., 2005
Min Temp. of Coldest Month (Bio 6)	Bioclimatic	Unselected	Hijmans et al., 2005
Temperature Annual Range (Bio 7)	Bioclimatic	Selected	Hijmans et al., 2005
Mean Temp. of Wettest Quarter (Bio 8)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temp. of Driest Quarter (Bio 9)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temp. of Warmest Quarter (Bio 10)	Bioclimatic	Unselected	Hijmans et al., 2005
Mean Temp. of Coldest Quarter (Bio 11)	Bioclimatic	Unselected	Hijmans et al., 2005
Annual Precipitation (Bio 12)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Wettest Month (Bio 13)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Driest Month (Bio 14)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation Seasonality (Bio 15)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Wettest Quarter (Bio 16)	Bioclimatic	Unselected	Hijmans et al., 2005
Precipitation of Driest Quarter (Bio 17)	Bioclimatic	Unselected	Hijmans et al., 2005
Precipitation of Warmest Quarter (Bio 18)	Bioclimatic	Selected	Hijmans et al., 2005
Precipitation of Coldest Quarter (Bio 19)	Bioclimatic	Selected	Hijmans et al., 2005
Aspect-eastness	Topographic	Selected	Amatulli et al., 2018
Aspect-northness	Topographic	Selected	Amatulli et al., 2018
Cloud Cover	Bioclimatic	Selected	Wilson & Jetz, 2016
Elevation	Topographic	Selected	Amatulli et al., 2018
Geology	Topographic	Selected	Our study
Global Aridity Index	Bioclimatic	Unselected	Zomer et al., 2008
Global Potential Evapotranspiration (PET)	Bioclimatic	Selected	Zomer et al., 2007
Mean Annual Actual Evapotranspiration (AET)	Bioclimatic	Unselected	Trabucco & Zomer, 2019
Roughness	Topographic	Selected	Amatulli et al., 2018
Slope	Topographic	Selected	Amatulli et al., 2018
Solar Radiation	Bioclimatic	Selected	Fick & Hijmans, 2017
Terrain Ruggedness Index (TRI)	Topographic	Unselected	Amatulli et al., 2018
Topographic Position Index (TPI)	Topographic	Selected	Amatulli et al., 2018

Wind Speed		Bioclimatic	Selected	Fick & Hijmans, 2017

Table S3 – Regression between the β mean pairwise distance (βMPD) and β mean nearest taxon distance and (βMNTD) indices and their standardized effect size (ses) from the unresolved and resolved phylogeny.

Index	r^2	slope
βMPD	1	0.99 ± 0.00009
sesβMPD	0.99	1 ± 0.001
βMNTD	0.99	0.99 ± 0.0002
sesβMNTD	0.99	0.99 ± 0.001

8.2. *Figures*

Figure S1 – Beta regression between Jaccard distance and the resistance distance (best model – 4) to test the effect of isolation among inselbergs from each of the six models of Jaccard dissimilarity.

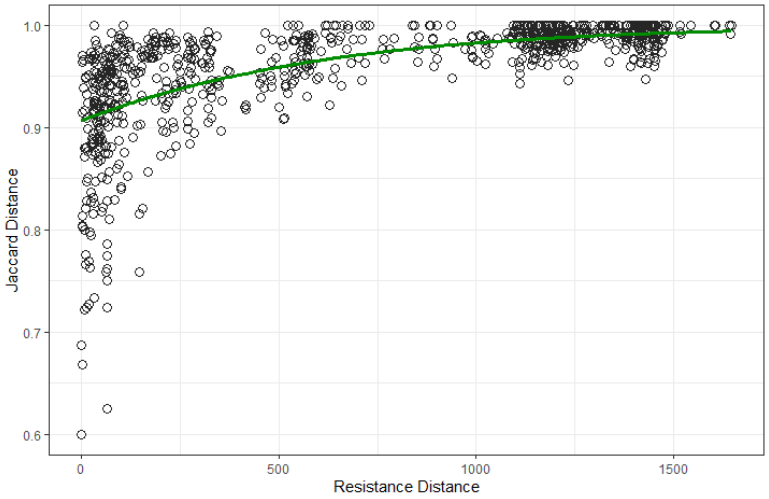


Figure S2 – Geographic distributions of conservation metrics across Atlantic Forest and Caatinga inselbergs at eastern Brazil.

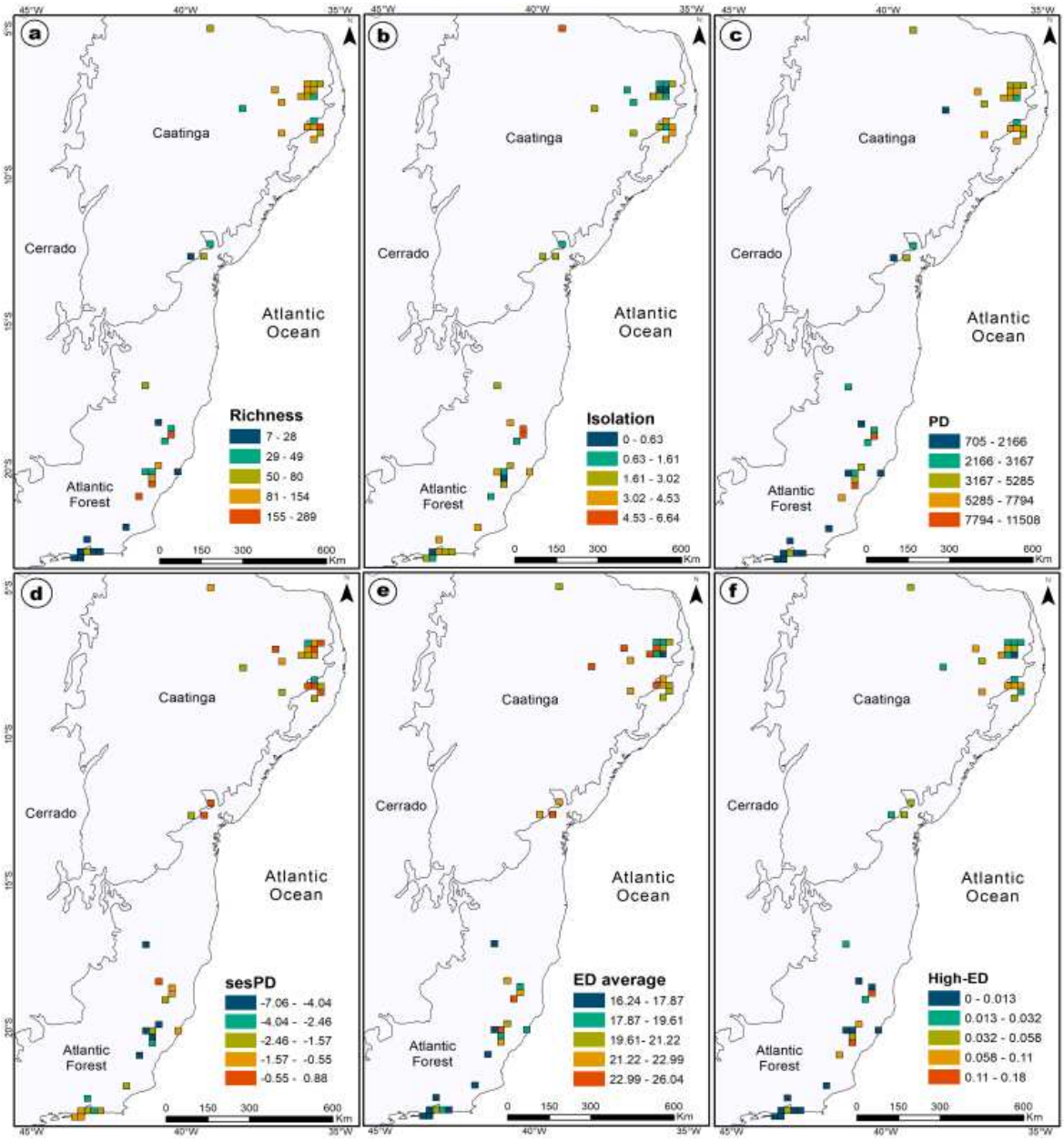
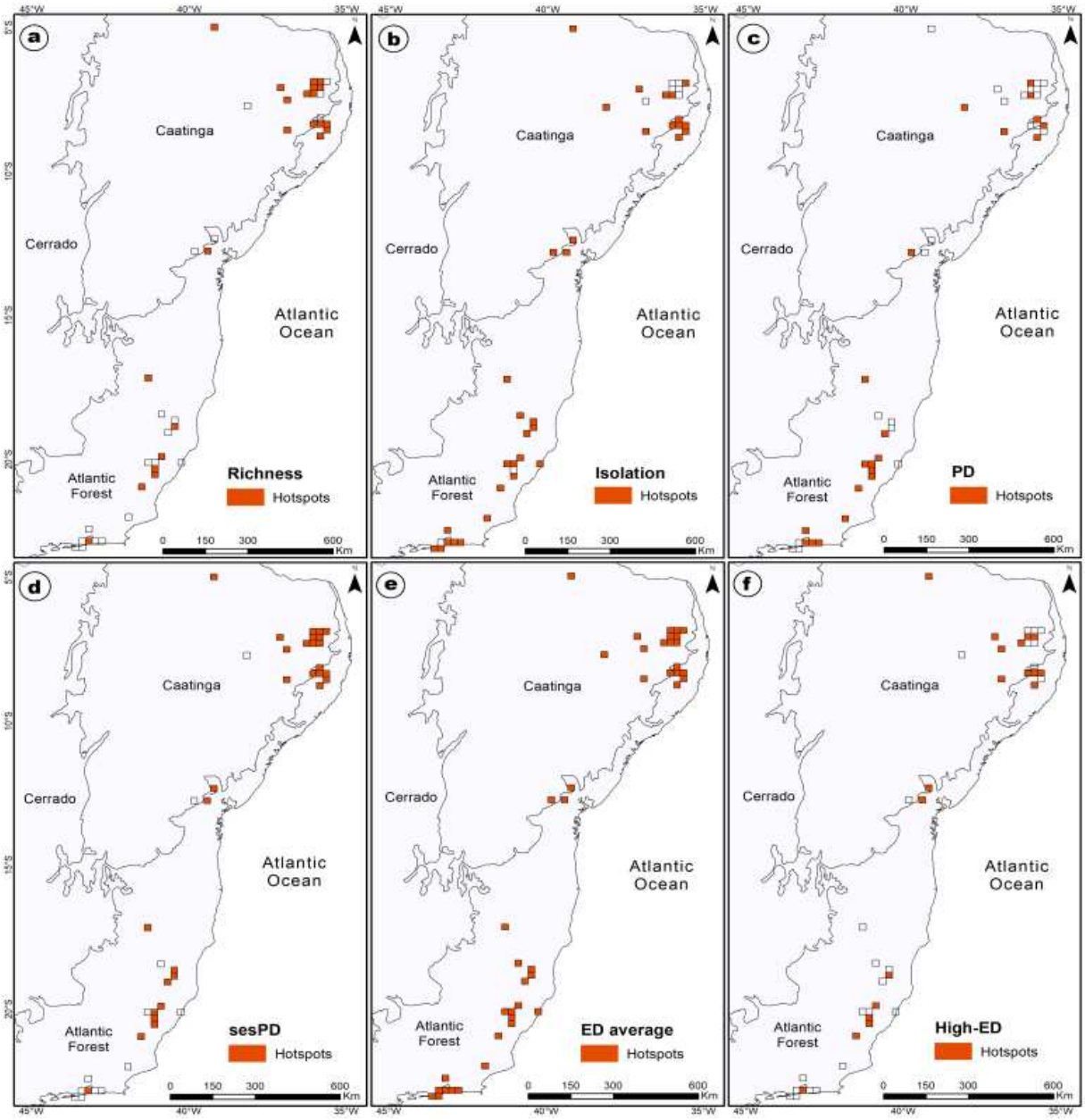


Figure S3 – Geographic distributions of hotspots conservation metrics across Atlantic Forest and Caatinga inselbergs at eastern Brazil.



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Conclusões Gerais

Nossos resultados demonstram a importância do entendimento das diversas facetas presentes na biodiversidade dos ecossistemas rupestres, bem como a compreensão destes padrões, que podem variar no tempo (passado, presente e futuro) e na escala de espaço (comunidade, região e paisagem). Destacamos ainda, a necessidade cada vez maior da junção das técnicas de medição da diversidade, tornando os resultados mais robustos e expressivos, o que pode permitir interpretações evidentes dos processos ecológicos modeladores da biodiversidade. Dessa forma, os resultados do Capítulo 1 permitem destacar as diferenças na estrutura e diversidade das comunidades, bem como evidenciar que as comunidades dos inselbergs não possuem uma espécie hiperdominante, mas sim vários codominantes, o que possibilita o domínio de certas espécies de acordo com a disponibilidade de recursos e espaço preenchido. Em relação às métricas de diversidade avaliadas pelo Capítulo 1, nós revelamos que a maior diversidade β-taxonômica e funcional é impulsionada por um maior *turnover* funcional e taxonômico nos inselbergs do Estado do Espírito Santo, portanto este padrão pode ser o resultado de um forte processo de filtragem de nicho ao longo de um gradiente ambiental.

Conforme os resultados do Capítulo 2, podemos indicar que nos inselbergs amostrados, a vegetação apresenta uma elevada tolerância ao estresse, bem como evidentes traços funcionais conservativos. Ademais, nossos resultados indicam que mesmo não direcionando nossas amostras entre os habitats presentes nos inselbergs, o efeito do ambiente sobre as características funcionais foi capaz de explicar as pequenas diferenças funcionais entre as espécies e sua resposta à variabilidade dos microhabitats. Por fim, podemos concluir que as estratégias encontradas no Capítulo 2 estão de acordo com as observações fitossociológicas das respostas da vegetação a um gradiente ambiental ao longo de uma sucessão primária, assim como afirmar que o método CSR é suficientemente sensível para descobrir as diferenças entre as estratégias de plantas em condições ambientais semelhantes. De acordo com os resultados apresentados pelo Capítulo 3, os efeitos das mudanças climáticas serão extremos sob a vegetação rupícola dos inselbergs, nossos modelos mostraram que os inselbergs presentes na Mata Atlântica e na Caatinga terão perdas severas em áreas com adequabilidade ambiental para as espécies, inseridas ou não em áreas protegidas, caso esforços para reduzir os gases de efeito estufa não sejam adotados. Ressaltamos ainda que a conservação da vegetação rupestre tem papel fundamental na manutenção dos serviços ecossistêmicos prestados pelos inselbergs à flora, fauna e seres humanos de todos os biomas.

Os resultados referentes ao Capítulo 4 demonstram a existência de um gradiente latitudinal na riqueza de espécies e na diversidade filogenética (*sesPD*) da flora dos inselbergs, e um maior isolamento entre as áreas de núcleo do nordeste e do sudeste. Portanto, o efeito conjunto de isolamento provocado pela resistência da paisagem e a filtragem ambiental pode criar comunidades mais isoladas, compostas por menor diversidade filogenética de espécies mais próximas e funcionalmente adaptadas às condições ambientais (solos empobrecidos e clima estável), corroborando a teoria OCBIL. Por fim, nossos resultados sugerem que a Hipótese do Arco do Pleistoceno pode ter contribuído para um maior isolamento das espécies dos inselberg, assim como à existência de conexões antigas entre as áreas centrais do nordeste e do sudeste, dadas às áreas de estabilidade climática dos inselbergs (refúgios) desde o último máximo glacial.

De acordo com os resultados apresentados acima, é evidente que o entendimento das multifacetas da diversidade (taxonômica, funcional e filogenética) pode ajudar a priorizar os esforços para a conservação na vegetação rupestre dos inselbergs e de outros ecossistemas rupícolas. Assim, as ações de conservação devem ser direcionadas para a proteção de espécies endêmicas e/ou ameaçadas através de programas de conservação *ex situ* e educação ambiental; criação de áreas protegidas com o foco na proteção principalmente de inselbergs isolados, bem como grupos de cada uma das áreas centrais. A execução de medidas mitigadoras e/ou de compensação ambiental através de estratégias de restauração eficazes que minimizam o efeito do isolamento entre as áreas centrais, e que levem em consideração a manutenção de distintas linhagens filogenéticas, assim como as evidentes especializações das espécies para os microhabitats dos inselbergs. Com isso, acreditamos que este estudo possa contribuir para o desenvolvimento de uma legislação internacional para a conservação da flora dos inselbergs. Por fim, enfatizamos a necessidade de mais investimentos em pesquisas, principalmente em estudos biogeográficos que combinem diferentes ramos da ciência (botânica, zoologia, ecologia, genética e conservação) para explorar o efeito integrado destes ramos nas interações bióticas das espécies rupícolas dos inselbergs.