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EPÍFITAS VASCULARES DA ILHA GRANDE, RJ: PADRÕES E REGRAS DE MONTAGEM DAS COMUNIDADES

Ana Carolina Rodrigues da Cruz

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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Botânica), Museu Nacional, da Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Doutora em Ciências Biológicas (Botânica).

Orientadores: Drª Lana da Silva Sylvestre
Dr. André Felippe Nunes-Freitas

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“A vida é muito mais que a ciência. Ciência é uma coisa entre outras, que empregamos na aventura de viver, que é a única coisa que importa. É por isto, além da ciência, é preciso a “*sapiência*”, ciência saborosa, que tem a ver com a arte de viver. Porque toda a ciência seria inútil se, por detrás de tudo aquilo que faz os homens conhecer, eles não se tornassem mais sábios, mais tolerantes, mais mansos, mais felizes, mais bonitos.”

Rubem Alves

RESUMO

EPÍFITAS VASCULARES DA ILHA GRANDE, RJ:
PADRÕES E REGRAS DE MONTAGEM DAS COMUNIDADES

Ana Carolina Rodrigues da Cruz

Orientadores: Dra. Lana da Silva Sylvestre & Dr. André Felippe Nunes-Freitas

Resumo da Tese de Doutorado submetida ao Programa de Pós-graduação em Ciências Biológicas, Museu Nacional, da Universidade Federal do Rio de Janeiro - UFRJ, como parte dos requisitos necessários à obtenção do título de Doutor em Ciências Biológicas (Botânica)**.**

Compreender como a heterogeneidade espacial afeta a biodiversidade em escalas diferentes é uma das questões fundamentais da ecologia. Assim, o objetivo desta tese é investigar como as condições ambientais associadas a disponibilidade de nichos ecológicos direcionam a montagem da comunidade de epífitas vasculares em uma abordagem multiescalas: em escala de paisagem (considerando florestas com características distintas), mesoescala (ao longo de cada floresta) e microescala (ao longo das zonas de altura das árvores). Foram amostradas cinco parcelas do RAPELD instaladas na Ilha Grande, Rio de Janeiro, Brasil. As florestas possuíam vegetações em diferentes estágios sucessionais e fitofisionomias distintas. Registramos 253 espécies para a área de estudo, incluindo dados de herbários online, pesquisas publicadas e trabalho de campo. A amostragem das parcelas resultou em 76 espécies e 1.735 indivíduos. As cinco fitofisionomias amostradas tiveram riqueza, abundância e composição de espécies particulares. A floresta ombrófila densa submontana em estado avançado de regeneração apresentou os maiores índices de riqueza e diversidade. Na macroescala, houve efeito positivo do número de árvores e efeito negativo da cobertura do dossel na diversidade de epífitas. As variáveis não influenciaram as epífitas na maioria das florestas quando analisadas em mesoescala e as principais famílias foram afetadas de diferentes maneiras tanto pelas condições ambientais quanto pela morfometria das árvores. Na microescala, a maior riqueza e abundância foram encontradas nos troncos das árvores. A copa alta apresentou menor diversidade e um conjunto característico de espécies. O padrão foi semelhante mesmo em florestas com diferentes fitofisionomias e as principais famílias exibiram diferentes padrões de diversidade ao longo do dossel. Demonstra-se a importância da abordagem multiescalas em estudos ecológicos para a compreensão dos padrões da biodiversidade, já que os fatores abióticos que afetam as epífitas operam de maneiras diferentes na macro e mesoescala. E, portanto, a teoria do nicho ecológico é a mais adequada para explicar a montagem de comunidades epífitas tanto ao longo das florestas horizontalmente como verticalmente. Assim, habitats e microhabitats mais úmidos e com maior disponibilidade de substratos adequados possuem maior diversidade e a composição de espécies varia de acordo com as características dos ambientes.

Palavras-chave: diferenciação de nicho, ecologia de comunidades, epifitismo, estratificação vertical, filtros ambientais.

ABSTRACT

VASCULAR EPIPHYTES FROM ILHA GRANDE, RJ:
PATTERNS AND ASSEMBLY RULES OF THE COMMUNITY

Ana Carolina Rodrigues da Cruz

Orientadores: Dra. Lana da Silva Sylvestre & Dr. André Felippe Nunes-Freitas

Abstract da Tese de Doutorado submetida ao Programa de Pós-graduação em Ciências Biológicas, Museu Nacional, da Universidade Federal do Rio de Janeiro - UFRJ, como parte dos requisitos necessários à obtenção do título de Doutora em Ciências Biológicas (Botânica)**.**

Understanding how spatial heterogeneity affects biodiversity at different scales is one of the fundamental questions of ecology. Thus, the aim of this dissertation is to investigate how the environmental conditions associated with the availability of ecological niches drive the assembly of the vascular epiphyte community in a multiscale approach: landscape scale (considering forests with distinct characteristics), mesoscale (along each forest), and microscale (along the tree height zones). Five RAPELD plots installed in Ilha Grande, Rio de Janeiro, Brazil, were sampled. The forests had vegetation in different successional stages and different phytophysiognomies. We registered 253 species for the study area, including data from online herbaria, published research, and fieldwork. The sampling of the plots resulted in 76 species and 1,735 individuals. Each phytophysiognomy had unique species richness, abundance, and composition. The submontane dense ombrophylous forest in an advanced state of regeneration showed the highest levels of richness and diversity. On the macroscale, there was a positive effect of the number of trees and a negative effect of canopy cover on epiphyte diversity. The variables did not influence epiphytes in most forests when analyzed at mesoscale and the main families were affected in different ways both by environmental conditions and tree morphometric. On the microscale, the highest richness and abundance were found in tree trunks. The upper crown showed less diversity and a characteristic set of species. The pattern was similar even in forests with different phytophysiognomies and the main families exhibited different patterns of diversity along the canopy. It demonstrates the importance of the multiscale approach in ecological studies to understand the patterns of biodiversity since the abiotic factors that affect epiphytes operate in different ways at the macro and mesoscale.Therefore, the ecological niche theory is the most adequate to explain the assembly of epiphytic communities both along the forests horizontally and vertically. Thus, wetter habitats and microhabitats with larger availability of suitable substrates have greater diversity and the species composition varies according to the characteristics of the environments.

Kew-words: community ecology, environmental filters, epiphytism, niche differentiation, vertical stratification.

SUMÁRIO

1. INTRODUÇÃO

1.1. Regras de montagem das comunidades ecológicas

As condições ambientais têm um papel central na distribuição das espécies ao redor do planeta, no entanto, o resultado desse efeito sobre as comunidades ecológicas em diferentes escalas geográficas ainda precisa ser melhor elucidado (Kraft et al., 2015). Os ecólogos quantificam e buscam entender a estrutura das comunidades desde antes da definição das chamadas “assembly rules”. Dentre os primeiros trabalhos destacam-se, como os mais notórios, o livro de Kershaw (1964), que discute técnicas para o estudo da estrutura de comunidades vegetais, Pielou (1972) que analisou a presença e ausência de espécies estabelecendo associações não aleatórias em comunidades, e Greig-Smith (1983), que aborda a correlação da distribuição de espécies com as condições do habitat. O termo regras de montagem foi primeiramente utilizado por Diamond (1975), pesquisando coocorrência de espécies de aves em ilhas, e foi abordado por Keddy (1992), que o definiu como processos ecológicos que atuam sobre um conjunto regional de espécies e que determinam a estrutura e os padrões da comunidade no tempo e em habitat específicos. Mais recentemente, Götzenberger et al. (2012) tornaram a definição de regras de montagem mais abrangente, explicando que a coocorrência das espécies é resultado tanto do acaso, como de padrões históricos de especiação, migração e dispersão, além de fatores abióticos e interações bióticas. Para estes autores, os processos ecológicos não são mutuamente excludentes e compreendê-los é fundamental para entender os seus efeitos nas comunidades e como estas se comportarão em diferentes cenários ambientais futuros (Götzenberger et al., 2012). O estudo das regras de montagem traz à tona a clássica questão ecológica sobre comunidades abertas, consideradas agregações aleatórias de espécies, recentemente elucidada na Teoria Neutra da Biodiversidade proposta por Hubbell (2001), em contraposição as comunidades fechadas, onde as espécies interagem fortemente entre si devido a processos coevolutivos, e que está relacionada à Teoria do Nicho de Hutchinson (1957).

Para entender a estrutura das comunidades e os padrões ecológicos observados é importante conhecer os mecanismos ecológicos que atuam sobre o *pool* regional de espécies. Em uma determinada comunidade local, as espécies do pool regional são selecionadas através de limitações na dispersão, de fatores ambientais e interações bióticas (Cadotte & Tucker, 2017). Algumas espécies do pool podem não alcançar determinado local por acaso ou podem não cumprir as necessidades ecológicas para sobreviver em qualquer um dos habitats (Webb et al., 2002). Para Keddy (1992), as comunidades vegetais são o resultado de processos abióticos e bióticos hierarquizados. O primeiro filtro corresponde as condições ambientais dos diferentes tipos de habitats e o segundo corresponde as habilidades competitivas daquele subconjunto de espécies previamente selecionado pelo ambiente (Keddy, 1992). Götzenberger et al. (2012) afirmaram que a montagem das comunidades está relacionada a quaisquer restrições impostas às espécies do pool regional e que impeçam a sua coocorrência em um habitat específico.

O conjunto de condições abióticas que seleciona espécies capazes de sobreviverem e persistirem num determinado local é chamado de filtro ambiental (Keddy, 1992). O conceito de filtros ambientais remonta aos anos 1970 e 1980, onde destacam-se os trabalhos de Noble & Slatyer (1977), analisando a sucessão pós-fogo em ecossistemas mediterrâneos, e Van Der Valk (1981), que propôs um modelo para dinâmica de comunidades em áreas úmidas baseado-se nas características das espécies e nas condições ambientais. O ambiente, nesses estudos, é descrito como a metáfora de uma “peneira” que permite algumas espécies prevalecerem devido a suas características específicas (Noble & Slatyer, 1977; Van Der Valk, 1981; Keddy, 1992; Kraft et al., 2015). Os filtros operam sobre as características das espécies eliminando do habitat aquelas “inadequadas” naquele momento, ou seja, todas as espécies da comunidade local são aquelas que sobreviveram e persistiram após a passagem pelo filtro ambiental (Keddy, 1992). Na última década o termo tem sido alvo de críticas porque dados observacionais podem ser resultado de efeitos combinados de filtros abióticos e de competição local (Kraft et al., 2015; Cadotte & Tucker, 2017). Além disso, se considerarmos somente o efeito da filtragem ambiental, isso acarreta o aumento das semelhanças fenotípicas na comunidade, o que leva a sobreposição de nichos e competição (Webb et al., 2002). Os dados observacionais, como o padrão de abundância das espécies, sejam estes fenotípicos e filogenéticos, podem mudar ao longo de um gradiente ambiental devido a outros processos ecológicos e não apenas condições abióticas (Kraft et al., 2015). Outra questão referida nas críticas é que a estruturação das comunidades não é sequencial, como proposto por Keddy (1992), mas as interações bióticas e a filtragem abiótica agem dinamicamente, direcionando os padrões observados (Kraft et al., 2015). Por isso, a definição mais adequada e rigorosa para filtros ambientais deve ser a determinação das espécies que chegam ao local, mas são incapazes de tolerar as condições abióticas na ausência de interações com outras espécies (Kraft et al., 2015).

Apesar das críticas, o papel dos filtros abióticos no direcionamento da estrutura das comunidades não deve ser invalidado, e, sim, melhor analisado, especialmente em condições de gradientes ambientais (Cadotte & Tucker, 2017). Uma forma de minimizar o erro na compreensão do papel das condições ambientais como filtros na estruturação das comunidades é determinar claramente a escala espacial. Definir a escala consiste em um dos maiores desafios em estudos ecológicos, pois os processos vão diferir de acordo com a escala analisada (Webb et al., 2002). Mudanças na abundância das espécies ao longo de um forte gradiente ambiental podem indicar atuação da filtragem abiótica, pois mostra que as espécies são incapazes de tolerar algumas condições específicas ao longo do gradiente (Kraft et al., 2015). Contudo, se a abundância muda em escala pequena de gradiente é mais provável que este seja impulsionado por uma combinação de efeitos, tanto bióticos como abióticos (Kraft et al., 2015), já que as regras de montagem bióticas são mais perceptíveis em escalas espaciais menores (Götzenberger et al., 2012). Muitas pesquisas concordam que filtros ambientais exercem maior influência em escalas espaciais maiores (Webb et al., 2002; Götzenberger et al., 2012; Sobral & Cianciaruso, 2012; Kraft et al., 2015; Cadotte & Tucker, 2017). Dessa forma, habitats com condições abióticas similares apresentarão composições e comunidades ecológicas com traços funcionais semelhantes, uma vez que se tratam das melhor adaptadas aquele ambiente (Webb et al., 2002; Sobral & Cianciaruso, 2012). Desse modo, ressalta-se que estudos integrando diferentes escalas espaciais e não apenas a escala local, são essenciais e permitem a compreensão de um maior número de processos que estruturam as comunidades ecológicas (Webb et al., 2002; Sobral & Cianciaruso, 2012). Ressalta-se ainda que o entendimento das regras de montagem aumenta a capacidade preditiva da ecologia de comunidades, levanta informações ecológicas mais confiáveis e possibilita a tomada de decisões políticas adequadas e efetivas para a conservação das espécies (Weiher & Keddy, 2004; Götzenberger et al., 2012).

1.2. As epífitas vasculares – panorama geral

A epibiota compreende organismos que vivem sobre outros seres vivos, como as cracas que se alojam nas grandes baleias, por exemplo, e dentro deste imenso grupo destacamos as plantas epífitas (Zotz, 2016). Mirbel (1815), em seu livro *Elementos de Fisiologia Vegetal e Botânica*, foi o primeiro a definir o termo epífitas e o fez da seguinte forma: “plantas que germinam em outras plantas sem tirar o alimento delas” (Mirbel, 1815 *apud* Zotz, 2016). O conceito mais comumente utilizado é o de Madison (1977), que definiu este grupo como plantas que se utilizam de outras plantas como forma de apoio em alguma fase da vida. Já Moffett (2000), define como epífita qualquer planta, fungo ou, até mesmo, micróbio, que seja sustentado inteiramente por água e nutrientes do dossel. Zotz (2016), uma das referências mais atuais e conceituadas sobre o tema, utiliza definição semelhante à de Madison (1977): “Epífitas são plantas que germinam e enraízam não parasiticamente em outras plantas em todas as fases da vida” (Zotz, 2016, p.1). As epífitas podem viver em qualquer superfície de outra planta que esteja acima do solo e qualquer efeito negativo que possa causar é indireto, como devido ao aumento de peso sobre os galhos (Moffett, 2000). As pesquisas sobre plantas epífitas começaram bem antes das definições de Madison (1977), remontando aos anos de 1884 e 1888 nas obras: *Sobre a estrutura e os hábitos das epífitas das Índias Ocidentais* (Schimper, 1884) e *A vegetação epifítica das Américas* (Schimper, 1888). No século XX destacam-se, devido ao pioneirismo na área, as obras clássicas de Oliver (1930), Went (1940), Hertel (1949), Johansson (1974), Madison (1977), Nadkarni (1981, 1984, 1986); Gentry & Dodson (1987); Benzing (1987, 1990, 1995); Lüttge (1989) e ter Steege & Cornelissen (1989). Muitos destes trabalhos são amplamente citados e utilizados como referência até os dias atuais.

No Brasil, apesar de terem sido amplamente retratadas na obra clássica *Flora Brasiliensis* (Martius, Eichler & Urban, 1840-1906), uma das primeiras pesquisas com epífitas foi a tese de Hertel (1949), seguida dos muitos trabalhos de Waechter (1980, 1986, 1992, 1998b, 1998a, 2006), todos realizados no sul do país. Para a década de 1980, além dos trabalhos de Waechter, há as publicações de Aguiar et al. (1981) e Cervi *et al.* (1988). Na década de 1990, há as publicações de Fontoura et al. (1997), Silva et al., (1997), Labiak et al. (1998), Dislich & Mantovani (1998) e Dittrich et al. (1999). A partir dos anos 2000 inúmeras pesquisas foram realizadas no país, especialmente nas regiões sul e sudeste, e todas reforçam a elevada riqueza da comunidade epifítica no domínio Atlântico (ver detalhes na revisão de Kersten, 2010). Nas últimas décadas as pesquisas tem aumentado consideravelmente e abordado temas tanto florísticos como de análises de padrões ecológicos e biogeográficos (Petean, 2009; Mania & Monteiro, 2010; Barbosa et al., 2015; 2020; Leitman et al., 2015; Cruz, 2017; Kurtz et al., 2017; Furtado & Menini Neto, 2018; Cruz & Nunes-Freitas, 2019; Marcusso et al., 2019;

Marcusso & Monteiro, 2016; Padilha et al., 2017; Santana et al., 2017; Cruz et al., 2021; Furtado & Menini Neto, 2021; ver mais em Ramos et al., 2019).

A obra clássica de Gentry & Dodson (1987), *Diversity and biogeography of neotropical vascular epiphythes*, registra que cerca de 29.000 espécies de plantas vasculares podem ocorrer como epífitas, o que corresponde a quase 10% de toda a flora de traqueófitas. Benzing (1990) cita que 84 famílias botânicas possuem pelo menos uma espécie de hábito epifítico. Zotz et al. (2021) atualiza os dados e aponta em torno de 28.000 espécies. A maioria das famílias, assim como apontavam Gentry & Dodson (1987) e Benzing (1990), é de monocotiledôneas e ressalta-se que a distribuição do número de espécies nos táxons é realmente bastante desigual (Zotz et al., 2021). Poucas famílias abrigam a grande maioria das espécies, sendo elas: Orchidaceae, Bromeliaceae e Polypodiaceae, respectivamente (Zotz et al. 2021). Orchidaceae é, sem dúvida alguma, a família que obteve maior sucesso na colonização da copa das árvores, com mais de 70% das espécies epífitas (Zotz, 2016; Zotz et al., 2021). Dentro de Orchidaceae destaca-se a subfamília Epidendroideae, onde praticamente todas as espécies são epífitas, ao passo que menos de 100 espécies epífitas são conhecidas nas outras subfamílias (Zotz, 2016). Bromeliaceae é uma família praticamente exclusiva do Novo Mundo e possui 60% das espécies com o hábito epifítico, especialmente nas subfamílias Tillandsioideae e Bromelioideae (Benzing, 1987; Zotz, 2016). Em samambaias e licófitas, aproximadamente 2.700 espécies, de cerca de 120 gêneros, são epífitas, sendo a família Polypodiaceae a de maior riqueza epifítica com quase 90% de suas espécies vivendo sobre as árvores (Zotz, 2016; Zotz et al., 2021).

A comunidade epifítica possui elevada importância nos ecossistemas. Segundo Nadkarni (1984), apesar de apresentarem pouca matéria seca, sua biomassa fotossintetizante se iguala a das árvores que as abrigam em florestas da Costa Rica e, além disso, a serapilheira produzida por esta comunidade contém elevada concentração de nutrientes (Clark et al., 1998; Nadkarni, 1992; Oliveira, 2004). Epífitas, vasculares ou não, afetam o ciclo hidrológico das florestas através da interceptação da água das chuvas, armazenamento e evapotranspiração (Holwerda et al., 2013). Epífitas também contribuem para a diversificação de microhábitats e nichos ecológicos no dossel florestal, aumentando a disponibilidade de espaço físico, umidade e alimentos disponíveis para a fauna, além de servirem como refúgio reprodutivo para muitos animais (Benzing, 1986; Rocha et al., 2000). Bromélias-tanque, por exemplo, podem acumular água em seu interior constituindo um micro-habitat para diversos seres vivos, estes ambientes são chamados de fitotelmata, sendo constituídos por água, serapilheira e detritos nas bases foliares sobrepostas das bromélias (Rocha et al., 2000, 2022; Zotz, 2016). Os habitats de fitotelmata formam ambientes limnéticos complexos com associações antigas das bromélias com linhagens específicas de protozoários, invertebrados e vertebrados e ainda podem funcionar como ampliadoras da biodiversidade, favorecendo o estabelecimento de vários organismos nas florestas (Rocha et al., 2000; Zotz, 2016).

1.3. Padrões de distribuição da comunidade epifítica

A distribuição global e regional das plantas epífitas apresenta particularidades em comparação com outras formas de vida vegetal devido a sua forte ligação com a umidade atmosférica, pluviosidade e temperatura (Madison 1977; Gentry & Dodson 1987; Zotz 2016), esses fatores explicam os padrões de distribuição latitudinal e altitudinal das epífitas. Como é esperado devido a alta pluviosidade, a comunidade apresenta forte associação com os trópicos e alguns autores até as incluem como definidoras das florestas tropicais (Zotz 2016). Nos neotrópicos, especificamente, a diversidade de epífitas é muito maior do que no Velho Mundo e Australásia (Madison, 1977; Gentry & Dodson, 1987; Benzing, 1990; Taylor et al., 2021). Segundo Gentry & Dodson (1987), a diferença nesta diversidade se deve a especiações rápidas das principais famílias epifíticas nos neotrópicos. Tais radiações são principalmente associadas às extensas áreas de florestas úmidas, a alta heterogeneidade topográfica e até a fertilidade do solo (Gentry & Dodson, 1987). Para Benzing (1990), a diversidade desproporcional também tem relação com fatores paleoclimáticos, uma vez que as áreas de florestas residuais durante as glaciações do Pleistoceno foram mais extensas nas Américas. Taylor et al. (2021) demonstraram com dados atuais que as epífitas contribuem com quase 40% da flora neotropical, abrigando 63% de todas as epífitas do mundo e, segundo Marcusso et al. (2022), há regiões biogeográficas com padrões florísticos característicos nos neotrópicos e estes respondem as variáveis climáticas. Além do padrão latitudinal, há um padrão altitudinal onde a diversidade de epífitas é maior em altitudes intermediárias (Gentry & Dodson 1987) e este padrão mostra-se muito bem estabelecido, havendo mudanças na estrutura da comunidade com o aumento da elevação, especialmente na composição das espécies (Cardelús et al., 2006; Ramos et al., 2021). Além disso, ressalta-se que as florestas nebulares, aquelas associadas a montanhas e que se encontram em meio a nuvens e nevoeiros a maior parte do ano, apresentam o maior número de espécies epifíticas (Küper et al., 2004; Gehrig-Downie et al., 2011; Furtado & Neto, 2018; Taylor et al., 2021).

Quanto à distribuição regional, a variação na estrutura da comunidade de epífitas depende das diferenças climáticas entre florestas, umidade, luminosidade e temperatura, assim como do tipo de formação vegetal e arquitetura das árvores (ter Steege & Cornelissen, 1989; Zotz & Büche, 2000; Benavides et al., 2011; Leitman et al., 2015; Dislich & Mantovani, 2016; Marcusso & Monteiro, 2016; Marcusso et al., 2019; Zotarelli et al., 2019; Amici et al., 2020; Furtado & Menini Neto, 2021; Ramos et al., 2021). Estágio sucessional e mudanças no uso da terra, como desmatamento e corte seletivo de árvores, alteram o microclima e outras condições e, consequentemente, também afetam fortemente a distribuição, diversidade e composição de epífitas (Borgo & Silva, 2003; Bonnet & Queiroz, 2006; Hietz et al., 2006; Dettke et al., 2008; Geraldino et al., 2010; Padilha et al., 2017; Parra-Sanchez & Banks-Leite, 2020; Richards et al., 2020; Parra-Sanchez & Banks-Leite, 2022). O estudo realizado por Janzen et al. (2020) mostrou que alguns padrões para a comunidade de epífitas podem ser causados devido a estocasticidade relacionada a limitações da dispersão, visto em florestas de terras baixas na Amazônia.

Em escala local, as mudanças na estrutura da comunidade ocorrem horizontalmente, ao longo das formações vegetais, e verticalmente, da base até a copa das árvores. A distribuição horizontal está relacionada às diferenças locais nas condições ambientais, principalmente umidade e luminosidade (Benzing, 1995; Nunes-Freitas & Rocha, 2007), características das árvores, como arquitetura, tipo de casca e idade, e até interações bióticas facilitadoras, como associações específicas com espécies de árvores ou de formigas (Rocha et al., 2000; Zotz & Büche, 2000; Nieder et al., 2001; Zotz & Vollrath, 2003; Laube & Zotz, 2006; Zotz & Schultz, 2008; Benavides et al., 2011; Paula & Lopes, 2013; Sáyago et al., 2013; Sanger & Kirkpatrick, 2014; Vicente et al., 2020). A distribuição vertical está associada a condições microclimáticas, como umidade, luminosidade e temperatura (ou radiação), que sofre variações desde o solo até a alta copa das árvores (Hallé et al., 1978; Richards, 1996; Anhuf & Rollenbeck, 2001; Stark et al., 2012; Fauset et al., 2017; Murakami et al., 2022). Estudos clássicos, assim como os mais recentes, mostram que as epífitas possuem um padrão heterogêneo de distribuição vertical, o que parece ter relação com os microclimas particulares das zonas de altura das árvores e o nicho ecológico das espécies (Johansson, 1974; Benzing, 1995, 1990; Nieder et al., 2000; Krömer et al., 2007; Zotz, 2007; Martínez-Meléndez et al., 2008; Woods et al., 2015, 2019). Além do efeito das variáveis ambientais, a distribuição local, tanto horizontal como vertical, também está associada à fatores bióticos, dos quais podemos citar a dispersão, a facilitação e a competição entre as espécies (Wolf, 2005; Hietz et al., 2006). Por exemplo, há maior similaridade entre comunidades de epífitas em árvores vizinhas do que o esperado ao acaso, isso devido a limitações na dispersão das espécies (Zotz, 2016).

1.4. As síndromes epifíticas

O termo síndrome epifítica se refere, de acordo com Zotz (2016) no epílogo da principal obra atual sobre o assunto, às características mais frequentemente encontradas nos táxons com maior número de epífitas. Ressalta-se que as características são traços vantajosos para a vida no dossel, e não adaptações exclusivas do epifitismo. Os traços funcionais são muito variados, uma vez que há grande diversidade taxonômica no grupo e o habitat do dossel é bastante complexo e, por isso, “there are many ways of being an epiphyte” (Zotz 2016, p. 267). Apesar da copa das árvores ser um habitat com maior disponibilidade de luz que o sub-bosque, o que é uma vantagem, as plantas enfrentam muitas outras condições limitantes, como nutrientes insuficientes, substrato instável e baixa disponibilidade de água (Lüttge, 1989; Sillett & Van Pelt, 2007). Por isso, espera-se que as epífitas sejam pequenas e leves, de modo a reduzir o estresse mecânico e a atingir a maturidade sexual antes que os substratos, no caso cascas da árvore ou galhos, caiam. Além disso, precisam ter alta tolerância ao estresse hídrico e à radiação (Hietz et al., 2022). Por isso, nas plantas epífitas há um determinado grau de resistência à seca com a presença de mecanismos diversos para obtenção e armazenamento de água (Benzing, 1990). Muitas orquídeas possuem pseudobuldos, caules com grande quantidade de parênquima aquífero, folhas suculentas e algumas ainda possuem tricomas absorventes (Pridgeon, 1981). Em cactos é comum a presença de caules suculentos com alta razão área/volume, o que eleva a capacidade de armazenamento de água (Andrade & Nobel, 1997). Em samambaias dos gêneros *Cyclophorus* Desv. e *Pyrrosia* Mirb., foi descrito um tecido especializado no armazenamento de água (Pande, 1935), enquanto em outras, como em *Aglaomorpha* Schott, *Phlebodium* (R.Br.) J.Sm. e *Pleopeltis* Alderw, o próprio rizoma é espessado e mais extenso, permitindo a reserva de água (Mehltreter et al., 2010).

Estudos comparando o tamanho de plantas terrestres e epífitas de um mesmo táxon demonstraram que as epífitas são significativamente menores por causa da seleção por motivos mecânicos de ancoragem, especialmente observado em orquídeas e samambaias (Carlsward et al., 2006; Porembski et al., 2006; Creese et al., 2011). Em muitas bromélias, a redução vegetativa, como a perda quase completa de raízes e caules, é associada à nutrição atmosférica, realizada exclusivamente pelos tricomas localizados nas pequenas e estreitas folhas (Benzing, 2000). Além disso, observa-se que brotos e inflorescências pendentes são hábitos comuns dentre as epífitas, assim como o alto desenvolvimento de raízes adventícias, pois estas possibilitam que as plantas possam se ancorar de forma eficiente no tronco e galhos da árvore (Zotz, 2016) e ainda maximizar a absorção de nutrientes (Andrade & Nobel, 1997).

Com relação as folhas, há espécies de epífitas com estratégias para desenvolvimento a sombra, folhas escuras com alto teor de clorofila e outras com proteção da radiação solar direta, com desenvolvimento de antocianina na epiderme adaxial atuando como filtro solar (Benzing, 1990). Hietz et al. (2022) demonstraram que folhas de epífitas possuem menor área foliar específica, são mais espessas e com maior teor de água quando comparadas com árvores e ervas enraizadas no solo. Estudos com orquídeas epífitas mostram que os estômatos, estruturas fundamentais para as relações hídricas das plantas, são xeromórficos com bordas cuticulares externas bem desenvolvidas, células-guarda espessadas e câmaras subestomáticas estreitas (Zotz 2016). Quanto aos tricomas foliares, estruturas epidérmicas multicelulares complexas, a maioria possui morfologia variada e reconhecido papel da absorção de água e sais minerais (Benzing et al., 1976; Benzing, 2000; Zotz, 2016). Especialmente em Bromeliaceae, os tricomas garantem a absorção através das folhas (Benzing et al., 1976) e experimentos mostraram que em Tillandsioideae de folhas cinzentas tais tricomas são altamente refletivos, fornecendo fotoproteção a planta (Pierce, 2007). Além disso, a morfologia dos tricomas foliares em algumas espécies de *Tillandsia* L. parece facilitar a ventilação foliar e a condensação de vapor de água na cutícula, favorecendo a aquisição de água (Pierce, 2007). Muitas samambaias epífitas também apresentam alta cobertura de tricomas ou escamas, com formas bastante variadas e que podem refletir a luz, diminuir a temperatura da folha, reduzir a transpiração e influenciar outras trocas gasosas (Mehltreter et al., 2010)

Nas bromélias há duas formas principais de absorção de água, ambas com independência do sistema radicular: através da fitotelmata com a formação de tanques, pela estrutura foliar imbricada, ou unicamente por tricomas absorventes das folhas (Benzing, 2000). No primeiro tipo a absorção é realizada também pelos tricomas, mas estes se localizam na base das folhas dentro do tanque, especialmente na subfamília Bromelioideae, enquanto o segundo tipo ocorre somente por tricomas foliares, por isso, são chamadas de bromélias atmosféricas, comuns em Tillandsioideae (Benzing, 2000; Benzing et al., 1976). Também apresentam a formação de cestos coletores de detritos outras espécies e grupos fora de Bromeliaceae, como as samambaias *Asplenium nidus* L. (Aspleniaceae) e *Niphidium crassifolium* (L.) Lellinger (Polypodiaceae), e algumas espécies de *Anthurium* e *Philodendron* (Araceae), ressaltando a vantagem desta característica para a vida do dossel (Zona & Christenhusz, 2015; Zotz, 2016).

As raízes de plantas epífitas enfrentam um forte desafio por crescerem completamente expostas nos troncos e galhos das árvores. Uma das estratégias epifíticas de raiz mais bem conhecida é o velame, uma epiderme múltipla, esponjosa e com muitas células mortas, que ocorre principalmente nas orquídeas, mas também aparece em alguns antúrios (Araceae) (Arditti, 1992). O velame tem como funções a absorção de água e sais minerais e a redução da perda hídrica (Zotz & Winkler, 2013), mas também pode realizar fotossíntese em espécies com redução de folhas e proteger os tecidos internos contra a radiação UV-B, como mostram experimentos com muitas espécies (Chomicki et al., 2015). Esta última função do velame das orquídeas pode ser considerada, de acordo Chomicki et al. (2015), uma adaptação essencial ao hábito epifítico limitado pela água. Em outros táxons de epífitas, como cactos e samambaias, as raízes apresentam como funções principais a fixação da planta ao tronco, armazenamento de água e, algumas, apresentam tolerância a seca e podem estar sujeitas a dessecação entre as chuvas (Andrade & Nobel, 1997; Mehltreter et al., 2010). Pande (1935), ao descrever a anatomia da raiz de *Pyrrosia lanceolata* (L.) Farw. (Polypodiaceae), registrou duas ou três camadas de parênquima cortical com espessamentos em espiral nas paredes que, segundo o autor, apresentam uma semelhança impressionante com o velame das orquídeas epífitas. Em algumas samambaias há a redução do sistema radicular, como uma forma de economizar nutrientes, e em Hymenophyllaceae, por exemplo, a fixação no tronco é realizada por pelos adesivos e a absorção de água e sais ocorre pelo rizoma e folhas (Schneider, 2000). Em outras, como *Asplenium nidus* L., há um grande volume de raiz que realiza a função de absorção e armazenamento de água, também comparáveis ao velame das orquídeas (Zona & Christenhusz, 2015; Zotz, 2016).

Intensidade luminosa, umidade e elementos nutricionais, especialmente o nitrogênio, são os principais fatores que influenciam a seleção dos variados mecanismos fotossintéticos das plantas no dossel (Benzing, 1990). O estudo recente realizado por Hietz et al. (2022) mostrou que a maioria das epífitas realizam a fixação de carbono via C3, não sendo registradas epífitas C4 e quase 30% apresentaram metabolismo ácido das crassuláceas (CAM). Esta via fotossintética ocorre na maioria das espécies das principais famílias de epífitas: Orchidaceae, especialmente na subfamília Epidendroideae, Bromeliaceae, Polypodiaceae, e em Cactaceae está presente em todas as espécies (Zotz & Ziegler, 1997; Silvera et al., 2009; Rodrigues et al., 2013; Crayn et al., 2015). Para Hietz et al. (2022), o resultado elevado de epífitas com metabolismo CAM é fortemente influenciado pelas bromélias, uma vez que excluindo-as, apenas 10% das epífitas do seu estudo apresentaram essa via fotossintética. Para Benzing (1990), os microambientes no dossel podem ser de úmidos, frios e sombreados envoltos por nevoeiros recorrentes, mais apropriados para a atividade de C3, até locais bastante áridos, que favorecem a via CAM. Kerbauy et al. (2012) ressaltam que há relação da altura do dossel das florestas com o epifitismo e o metabolismo CAM. Até em um mesmo local da floresta a presença de epífitas CAM aumenta com as zonas de altura da árvore, indo de 7% das epífitas no sub-bosque a 50% na alta copa (Zotz & Ziegler, 1997). Zotz & Ziegler (1997) avaliaram toda a flora epifítica vascular de uma floresta no Panamá quanto à presença de metabolismo CAM e verificaram que 25% das epífitas são CAM obrigatórias. Quanto à distribuição do metabolismo nas famílias epifíticas, os resultados foram um pouco diferentes do esperado. Os autores registraram que 100% de Cactaceae, 50% de Bromeliaceae e 42% de Orchidaceae são CAM e não foi registrada esta via em Araceae, Piperaceae ou Polypodiaceae (Zotz & Ziegler, 1997). Segundo os autores, tais resultados podem estar associados ao fato destas famílias utilizarem outras estratégias nessa floresta ou de serem CAM facultativas ou intermediárias, o que dificulta a avaliação direta do metabolismo pelos métodos utilizados (Zotz & Ziegler, 1997). Além disso, o carbono pode ser fixado por vias diferentes em uma mesma epífita, como já registrado em *Peperomia camptotricha* Miq. (Piperaceae), que apresentou padrões fotossintéticos diferentes dependendo da idade das folhas, umidade local e outras características do ambiente (Benzing, 1990).

Outra estratégia xeromórfica para lidar com o estresse hídrico é a tolerância a dessecação e a poiquiloidria. Para Mehltreter et al. (2010), a tolerância à dessecação é a capacidade que algumas plantas possuem de sobreviver a uma perda de quase 90% do teor de água do tecido de uma folha saturada. Watkins et al. (2007), definem como plantas tolerantes à dessecação aquelas que podem perder a água de suas estruturas vegetativas e recuperar-se posteriormente, havendo a interrupção da atividade metabólica como consequência do baixo conteúdo de água intracelular. Já plantas poiquiloídricas são aquelas que não controlam seu teor celular de água, se desidratam rapidamente e, para aquelas tolerantes a dessecação, podem se reidratar e sobreviver a longos períodos de seca (Benzing, 1990). Tolerância à dessecação não é sinônimo de poiquiloidria, visto que muitas plantas poiquiloídricas não conseguem resistir a dessecação severa e algumas outras de folha coriácea, tolerantes à dessecação, não são poiquiloídricas (Mehltreter et al., 2010). A maioria dos casos de poiquiloidria ocorre em samambaias, principalmente em Hymenophyllaceae e Polypodiaceae (Mehltreter et al., 2010; Zotz 2016). Um dos principais exemplos, citado por Benzing (1990), é a espécie *Pleopeltis minima* (Bory) J. Prado & R.Y. Hirai (Polypodiaceae), que fica completamente seca e enrolada. Quando as folhas dessa espécie são reidratadas, elas adquirem, em cerca de 40 minutos, a capacidade fotossintética (Mehltreter et al., 2010). Isso é possível porque há conservação da integridade citoplasmática devido à seiva vacuolar se solidificar e evitar o colapso completo do protoplasto (Benzing 1990). A tolerância à dessecação tem se mostrado mais frequente do que os pesquisadores supunham e deve compreender 5-10% das samambaias e licófitas (Mehltreter et al., 2010). Muitas samambaias tolerantes à dessecação, especialmente *Pleopeltis* e *Polypodium*, apresentam tricomas absorventes de água e podem se reidratar rapidamente após entrarem em contato com a chuva sem precisarem transportar de água de suas raízes ou rizoma (Mehltreter et al., 2010).

É importante lembrar que em samambaias há ocorrência de alternância de gerações que inclui duas gerações de vida livre, sendo um gametófito haplóide e um esporófito diploide, nas análises ecológicas muitas vezes a fase do gametófito é esquecida (Zotz, 2016). O gametófito, responsável pela fecundação, é pequeno, sem tecido vascular e com cutícula ausente ou pouco desenvolvida (Watkins et al., 2007). Já o esporófito, agente responsável pela dispersão, apresenta sistema vascular bem desenvolvido e cutícula cerosa completa com estômatos (Watkins et al., 2007). Essas diferenças em suas características por si só já levam a estratégias ecológicas diversas no que se refere às relações hídricas e ecológicas. Experimentos demonstram que a tolerância à intensidade de dessecação está fortemente ligada à ecologia das espécies, sendo que gametófitos de plantas epífitas apresentaram alta recuperação à dessecação e menor sensibilidade à sua intensidade (Watkins et al., 2007). A maior tolerância à dessecação está relacionada a mecanismos bioquímicos celulares e a aspectos anatômicos da parede celular, como a maior espessura da mesma, perder água mais lentamente e resistir melhor ao colapso (Watkins et al., 2007). Além disso, o gametófito de plantas epífitas geralmente tem a forma de “fita”, podem produzir gemas como um meio de reprodução vegetativa e ter vida mais longa, diferentemente dos gametófitos cordiformes com vida curta das espécies terrestres (Farrar et al., 2008).

Assim, diante do exposto, percebe-se que as características mais importantes para a vida no dossel estão relacionadas às relações hídricas das plantas. Segundo Zotz (2016), as “síndromes epifíticas” envolvem toda ontogenia, desde aspectos germinativos, passando pela anatomia, morfologia e fisiologia, variando entre os indivíduos, espécies e microhabitats.

1.5. Estudos de epífitas na Mata Atlântica e lacunas

Para a Mata Atlântica do Brasil, Argentina, Paraguai e Uruguai foram compiladas, incluindo hemiepífitas, 2.095 espécies por Ramos et al. (2019), registradas a partir de dados de fontes publicadas (incluindo artigos, livros e teses revisadas por pares), não publicados e informações de herbários. Segundo dados atuais da Flora e Funga do Brasil 2022, constam registradas 2.128 espécies de epífitas vasculares para o Domínio Atlântico, sendo 1.880 angiospermas e 248 samambaias e licófitas. Ainda há 173 espécies classificadas como hemiepífitas, com 145 angiospermas e 28 samambaias e licófitas (Flora e Funga do Brasil, 2022). Há bastante confusão com relação a classificação das hemiepífitas e não há uma padronização no uso dos termos (hemiepífitas primárias, secundárias e trepadeiras nômades) e, por isso, existem muitas críticas a sua inclusão nos estudos epifíticos (ver Moffett 2000; Zotz 2013; Sperotto et al. 2020; Zotz et al. 2021a). Independente da inclusão das hemiepífitas, todos os dados supracitados corroboram com o fato de a Mata Atlântica brasileira ser considerada um centro de diversidade para as plantas epífitas, concentrando alta riqueza e elevada taxa de endemismos, conforme corroborado por muitos outros autores (Nieder et al., 1999; Nunes-Freitas et al., 2016; Menini Neto et al., 2016; Furtado & Menini Neto, 2021; Ramos et al., 2021; Taylor et al., 2021). As florestas do Domínio Atlântico correspondem ao centro de dispersão e diversidade para as famílias mais ricas em espécies de epífitas: Orchidaceae, Bromeliaceae, Polypodiaceae e Araceae (Tryon 1986; Mayo et al. 1997; Siqueira Filho & Félix 2006; Martinelli et al. 2008). Além disso, reúnem condições ideais para o desenvolvimento e estabelecimento das plantas epífitas, como alta umidade atmosférica, temperatura e precipitação, assim como oferece alta heterogeneidade de habitats (Nieder et al., 2001; Leitman et al., 2015; Furtado & Menini Neto, 2021). Quanto ao padrão taxonômico, os dados referentes à Mata Atlântica são semelhantes ao observado para o mundo, sendo as principais famílias: Orchidaceae (856 spp.), Bromeliaceae (527 spp.), Araceae (83 spp.), Polypodiaceae (79 spp.) e Piperaceae (65 spp.) (Ramos et al., 2019).

A diversidade de epífitas não é igualmente distribuída pelas regiões da Mata Atlântica. De acordo com Menini Neto et al. (2016) as regiões sudeste e sul são as mais ricas em número de espécies e, segundo Ramos et al. (2019), soma-se a elas o sul da Bahia. Os estados do Rio de Janeiro e Espírito Santo, ao longo da Serra do Mar, ainda destacam-se dentro dessas regiões pela elevada riqueza de espécies associada a altos valores de endemismo (Furtado & Menini Neto, 2021; Menini Neto et al., 2016; Ramos et al., 2021). Para o estado do Rio de Janeiro são registradas 972 espécies de epífitas e 77 hemiepífitas angiospemas, somado a 200 espécies epífitas e 20 hemiepífitas em samambaias e licófitas (Flora e Funga do Brasil, 2022). Entretanto, o número de publicações específicas sobre esta comunidade no estado ainda é baixo, quando comparado a outras formas de vida e outras regiões (Fontoura et al., 1997; Couto et al., 2017; Dornelas et al., 2017; Cruz & Nunes-Freitas, 2019; Cruz et al., 2021; Furtado & Menini Neto, 2022). De acordo com Araujo & Ramos (2021) os maiores esforços de amostragem futuras precisam se concentrar em áreas negligenciadas, entre elas regiões de altitudes intermediárias (200 a 600 metros) em florestas submontanas, uma vez que tais ambientes podem conter espécies altamente ameaçadas. Florestas submontanas e montanas podem ter sido negligenciadas, entre outros motivos, por apresentarem dosséis mais altos, o que dificulta o acesso as epífitas da alta copa.

A maior parte das pesquisas na Mata Atlântica correspondem a levantamentos florísticos (Kersten, 2010; Ramos et al., 2019b). As publicações que incluem a análise de padrões e regras que regem a montagem de comunidades epifíticas apoiam que predominam processos baseados no nicho ecológico das espécies, como a estrutura das florestas e microclima dos ambientes (Borgo & Silva, 2003; Nunes-Freitas & Rocha, 2007; Dettke et al., 2008; Kersten et al., 2009; Kersten & Kuniyoshi, 2009; Bataghin et al., 2010; Mania & Monteiro, 2010; Blum et al., 2011; Freitas & Assis, 2013; Geraldino et al., 2010; Marcusso & Monteiro, 2016; Dislich & Mantovani, 2016; Padilha et al., 2017; Barbosa et al., 2019; Zotarelli et al., 2019; Parra-Sanchez & Banks-Leite, 2020; Alvim et al., 2021). Assim, apesar da alta diversidade na Mata Atlântica brasileira ser amplamente reconhecida e das pesquisas terem aumentado nas últimas décadas, ainda se sabe pouco sobre a dinâmica das comunidades de epífitas nos diferentes tipos de florestas e como os processos ocorrem nas diferentes escalas espaciais. Pesquisas ecológicas devem integrar escalas espaciais para que informações sobre as variáveis que influenciam os processos de distribuição das espécies não sejam perdidas (Talley, 2007) e, além disso, entender como a heterogeneidade espacial afeta a diversidade em escalas diferentes é considerada uma das fundamentais da ecologia atualmente, de acordo com Sutherland et al. (2013). Como já mencionado, a compreensão das regras de montagem aumenta a capacidade preditiva da ecologia de comunidades e permite entender como as comunidades se comportarão em cenários futuros, o que é essencial para a elaboração de estratégias eficientes de conservação das espécies (Götzenberger et al., 2012).

Diante disso, o objetivo desta tese consiste em analisar como as condições abióticas associadas a disponibilidade de nichos ecológicos direcionam a montagem da comunidade de epífitas vasculares ao longo de gradientes ambientais localizados nas florestas da Ilha Grande, Rio de Janeiro, em uma abordagem em multiescalas: na macroescala (fatores determinantes da estrutura da comunidade na escala da paisagem levando em conta florestas com características distintas), mesoescala (fatores determinantes ao longo de cada floresta) e microescala (distribuição espacial e a estrutura da comunidade ao longo do gradiente vertical das florestas). Testa-se a seguinte hipótese: habitats mais úmidos e com maior disponibilidade de substratos adequados (mais árvores, árvores de grande porte e maior superfície ao longo da árvore), apresentam maior diversidade e composição florística diferenciada porque os táxons respondem de formas diferentes às variações ambientais. A hipótese é testada na macro, meso e microescala e visa corroborar com a teoria do nicho ecológico (Hutchinson, 1957; Chase & Leibold, 2004). Segundo Chase & Leibold (2004), o nicho ecológico de uma espécie pode ser definido como um conjunto de condições e recursos ambientais que permitem que as espécies satisfaçam seus requisitos mínimos de crescimento populacional. Dessa forma, previmos que a distribuição das epífitas vasculares será heterogênea entre as florestas da ilha, ao longo de cada fitofisionomia e, também, ao longo do gradiente vertical no dossel conforme afirmam os estudos clássicos de Benzing (1990) e Johansson (1974).

A tese está estruturada em três capítulos:

- Capitulo 1: Diversity of vascular epiphytes from Ilha Grande, Rio de Janeiro, Brazil

- Capítulo 2: Assembly of the vascular epiphyte community in protected areas of the Atlantic Forest in Southeastern Brazil
- Capítulo 3: Importance of the vertical gradient in the variation of epiphyte community structure in the Brazilian Atlantic Forest

O capítulo 1 traz a lista de espécies atualizada de epífitas vasculares da Ilha Grande, Rio de Janeiro, com seus estados de conservação e principais ameaças, o objetivo é contribuir com o conhecimento desta parcela da biodiversidade na área de estudo. O capítulo 2 testa a hipótese na macro e na mesoescala, com objetivo de investigar o papel de fatores ambientais e morfométricos das árvores na montagem de comunidades de epífitas em escala de paisagem, em diferentes fitofisionomias e em grupos taxonômicos individuais. Enquanto o capítulo 3 verifica a hipótese em microescala, com o objetivo de investigar como a estrutura da comunidade varia ao longo do gradiente vertical e se o padrão de estratificação é semelhante entre florestas com características distintas e entre as famílias de epífitas com maior número de espécies.

2. MATERIAL E MÉTODOS

2.1. Área de estudo – A Ilha Grande

2.1.1. Contexto histórico

A Ilha Grande, localizada no litoral sul do Rio de Janeiro nas coordenadas geográficas 23º 09’ 26,77’’ S e 44º 13’ 53,72’’ O, apresenta área de 65.258 ha e perímetro de aproximadamente 350 km (Creed et al., 2007), está inserida na baía de mesmo nome e pertence ao município de Angra dos Reis. A ilha possui um longo histórico de ocupação que remonta há cerca de três mil anos com os paleoíndios coletores-caçadores, o “povo do sambaqui” e o “povo da pedra polida”, que deixaram suas marcas em alguns pontos da ilha (INEA - Instituto Estadual do Ambiente, 2011). Posteriormente os índios Tupinambás (ou Tamoios) batizaram-na de “Ipaum Guaçu”, que significa Ilha Grande e, após muitas lutas no século XVI, os colonizadores praticamente exterminaram os índios e deram início a povoação por europeus (INEA, 2011). O estabelecimento de fazendas levou ao desmatamento para plantação de alimentos para autoconsumo (mandioca, feijão, milho etc.) e a criação de animais (boi, porco, galinha etc.), bem como demandavam de grandes volumes de madeira e lenha para construções e tarefas diárias (INEA, 2011). No século XX, a pesca deu lugar a agricultura como atividade econômica primordial dos moradores da ilha, juntamente com o trabalho nas fábricas de processamento de sardinhas, no Lazareto e nos dois presídios ali estabelecidos, a Colônia Agrícola do Distrito Federal e a Colônia Penal Cândido Mendes (INEA, 2011).

O Parque Estadual da Ilha Grande (PEIG) foi criado em 1971 e a Reserva Biológica Estadual da Praia do Sul (RBEPS) em 1981. Já em 1982, mais de 40% da ilha estava sob proteção destas Unidades de Conservação (UC). Devido a sua vegetação de Mata Atlântica costeira, em 1988, a Ilha Grande passou a ser Patrimônio Nacional, em 1989, tornou-se área de relevante interesse ecológico e, em 1992, foi reconhecida pela UNESCO ao integrar Reserva da Biosfera da Mata Atlântica (INEA, 2011). No fim do século XX e início do século XXI, atividades turísticas tornaram-se um dos pontos fortes da economia dos moradores da ilha levando a grande pressão antrópica sobre a biodiversidade. Em 2001, a Ilha Grande passa a ser parte do polo ecoturístico da Costa Verde do Rio de Janeiro e em 2019 é reconhecida, juntamente com Paraty, como

Patrimônio Mundial da UNESCO, um sítio misto devido à excepcionais riquezas naturais e culturais (ONU, 2019).

Atualmente a ilha é uma das maiores áreas preservadas de Mata Atlântica no sudeste brasileiro e é uma importante região de preservação e pesquisa a respeito da biodiversidade (Alho et al., 2002) e possui quatro UC, duas classificadas como de Proteção Integral e duas de Uso Sustentável. As UC de Proteção Integral são o PEIG e a RBEPS, abrangendo quase 80% da ilha, e as UC de Uso Sustentável são a Área de Proteção Ambiental (APA) Tamoios e a Reserva de Desenvolvimento Sustentável do Aventureiro, estabelecida após a recategorização do Parque Marinho do Aventureiro. O PEIG foi criado pelo Decreto Estadual nº 15273, de 26 de junho de 1971 e ampliado pelo Decreto Estadual nº 40 602, de 12 de fevereiro de 2007. A RBEPS foi criada pelo Decreto Estadual n° 4972, de 2 de dezembro de 1981 e está localizada na área da Praia do Sul, vertente oceânica da ilha (INEA 2019) (ver Figura 1).

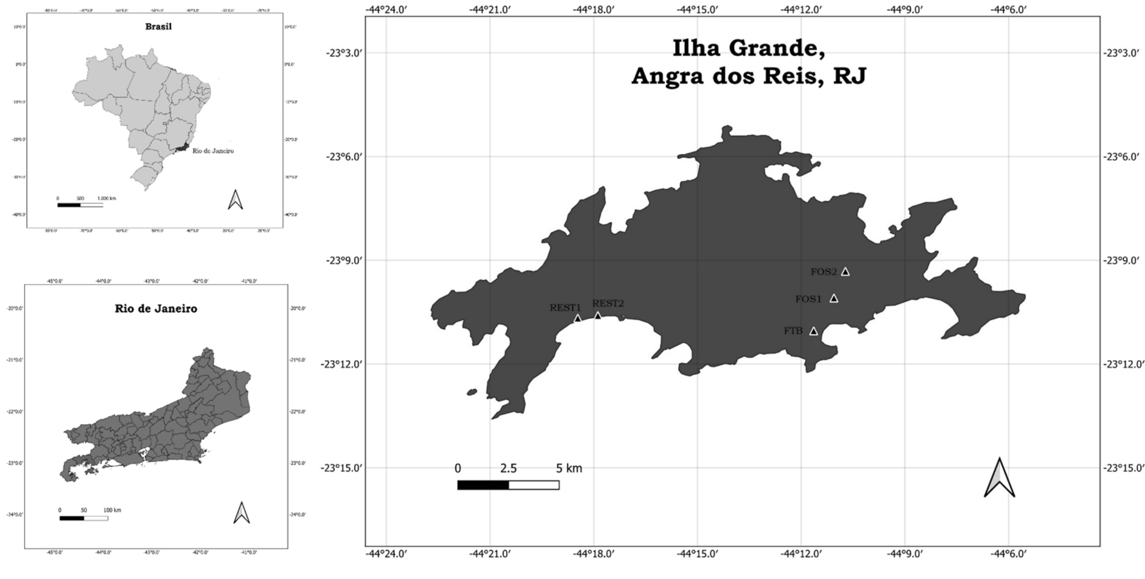

Figura 1: Mapa da Ilha Grande e demais ilhas associadas, localizadas no município de Angra dos Reis, estado do Rio de Janeiro. Fonte: a autora.

2.1.2. Relevo, solos e clima

A Ilha Grande e suas demais ilhas associadas constituem-se de afloramentos rochosos de regiões mais proeminentes do embasamento rochoso da Serra do Mar (UFRRJ/IEF/PRO-NATURA, 1992), sendo que a separação total da ilha com o continente é recente e se deu por volta de 5100 anos atrás com o último evento de transgressão marinha com a subida nível do mar (último máximo transgressivo) (Gama et al., 2009). O substrato geológico da ilha é formado por rochas ígneas de dois tipos principais: granito e charnockito, sendo que em alguns locais podem aflorar ortognaisses, rochas metamórficas mais antigas, e diques de diabásio, rocha da família dos basaltos (Gama et al., 2009).

A Ilha Grande faz parte de um dos maciços costeiros da Serra do mar e apresenta relevo montanhoso orientado na direção nordeste-sudoeste, com a maior parte de seu território situado abaixo de 500 metros de altitude (Gama et al., 2009). As maiores cotas altimétricas ocorrem na região centro-leste e varia de 0 a 1031 metros, na Pedra D’água, o ponto máximo da ilha, com destaque para o Pico do Papagaio, com 959 m, e o Morro do Ferreira, com 735 m (INEA - Instituto Estadual do Ambiente, 2011). São reconhecidos e destacados dois domínios geomorfológicos: as encostas formadas pela degradação das rochas ígneas; e áreas de depósitos sedimentares, originadas do intemperismo das rochas em áreas de baixadas (Gama et al., 2009). As vertentes ainda podem ser classificadas como encostas íngremes, afloramentos rochosos, grandes depósitos de tálus e colúvios ou canais fluviais em vales (Gama et al., 2009). Os solos de cada área variam de acordo com o tipo de rocha, relevo e clima local (INEA, 2011). Predominam os solos do tipo Cambissolos, bastante variáveis, são pouco profundos ou rasos e ocorrem associados ao relevo montanhoso e vegetação de Floresta Ombrófila Densa Submontana e Montana, e Espodossolos, pouco variáveis, minerais hidromórficos, rasos e saturados, com textura arenosa e caráter distrófico ou hálico, ocorrem associados a florestas de baixada e restingas arbóreo-arbustivas (Gama et al., 2009).

O clima é tropical úmido Af de Köppen, quente e úmido, sem estação seca (INEA - 2011). Toda a região de Angra dos Reis apresenta clima tropical, com altas temperaturas e precipitação bastante elevada no verão (Salgado & Vasquez, 2009). A temperatura média anual é de 23,2ºC com médias máximas superiores a 30ºC, com umidade do ar média anual de 82%, sem grandes variações ao longo do ano (Salgado and Vasquez, 2009). As características climáticas da ilha estão relacionadas à latitude tropical, à maritimidade, à presença da cobertura vegetal e ao avanço de massas polares na região (Salgado & Vasquez, 2009). A precipitação na ilha é desigual por causa do relevo acidentado e pode atingir até 4.500 mm de chuva em algumas regiões (Oliveira & Neto, 2000), mas, em média, a pluviosidade anual é de 2.242 mm nas baixadas próximas ao nível do mar, sendo janeiro o mês mais chuvoso e julho o mais seco (INEA 2011). Os ventos da Ilha Grande têm direção variável durante o ano com ligeiro predomínio de ventos leste e sudeste (Salgado & Vasquez, 2009).

2.1.3. Flora e cobertura vegetal

A flora da ilha constitui-se de várias formações vegetacionais associadas ao Domínio da Mata Atlântica (Callado et al., 2009) (Figura 2). As fitofisionomias predominantes são Floresta Ombrófila Densa Submontana e Montana, mas ainda ocorrem Floresta Ombrófila Densa de Terras Baixas, áreas de formação pioneira de influência marinha (restingas) e fluviomarinha (matas alagadiças e manguezais), além de vegetações em afloramentos rochosos (Oliveira & Neto, 2000). A ilha possui um dos mais importantes remanescentes de Mata Atlântica do sudeste brasileiro com um diversificado conjunto de habitats (Alho et al., 2002). As Florestas Ombrófilas Densas abrangem mais de 90% da ilha, formando um mosaico em estágios sucessionais diferentes com dossel de cerca de 15 m de altura e alta copa com 25 a 30 m (Alho et al., 2002). A vertente sul e centro da ilha apresentam melhor estado de conservação, enquanto as áreas mais próximas às vilas e povoados estão cobertas por vegetação degradada e capoeiras recentes – 5 a 25 anos (Oliveira, 2002).

Figura 2: Florestas de Mata Atlântica da Ilha Grande, município de Angra dos Reis, RJ.

A Floresta Ombrófila Densa Montana encontra-se em bom estado de conservação, devido ao difícil acesso e, consequentemente, com menor impacto humano e a sua rápida capacidade de regeneração (Alho et al., 2002). A Floresta Ombrófila Densa Submontana ocupa a maior parte da ilha e possuem dossel entre 20 e 30 m com algumas árvores emergentes (Oliveira, 2002). As florestas ombrófilas possuem matas secundárias em diferentes estágios de regeneração, desde áreas climáxicas, como as próximas ao pico do Papagaio, com muitas árvores de grande porte, áreas em estágio secundário tardio, como na RBEPS e a mata da Jararaca, no PEIG, áreas em estágio secundário inicial, como as matas próximas ao Caxadaço, a Mãe D'água e a Parnaioca, até áreas em estágio inicial de sucessão como as capoeiras recentes próximas às vilas (Callado et al., 2009). Nas proximidades das vilas ocorrem muitas plantas exóticas, como lembranças dos ciclos econômicos que passaram pela ilha, dentre as principais destacam-se pela maior frequência de ocorrência: *Artocarpus heterophyllus* Lam., *Mangifera indica* L. e *Coffea* sp. (Callado et al., 2009). A Floresta Ombrófila Densa de Terras Baixas é a que se apresenta mais altamente antropizada e com vegetação mais degradada, com predomínio de vegetação herbácea e plantas ruderais, como *Imperata brasiliensis* Trin., *Panicum racemosum* (P. Beauv.) Spreng. e *Psidium guineense* SW. (Callado et al., 2009).

As fitofisionomias de restinga da ilha são encontradas nas praias de Dois Rios, Lopes Mendes, Parnaioca, do Leste e do Sul. Em Dois Rios, a vegetação de restinga encontra-se bastante antropizada devido às atividades do antigo presídio nas proximidades (Callado et al., 2009). Não foram registrados trabalhos florísticos específicos realizados para as restingas de Lopes Mendes, Parnaioca e Praia do Leste. Para a Praia do Sul há três publicações que abrangem a restinga. Araujo & Oliveira (1987), que registraram 144 espécies para a área e classificaram a restinga em vegetação psamófila reptante de anteduna e mata de cordão arenoso (classificação utilizada pelos demais pesquisadores). Nunes-Freitas et al. (2006) que registraram 16 espécies de bromélias e Cruz & Nunes-Freitas (2019) que levantaram 31 espécies de epífitas vasculares na mata de cordão arenoso. Já as matas alagadiças ocorrem em Lopes-Mendes e na Praia do Sul, esta última foi descrita por Araújo & Oliveira (1987) com a presença de substrato úmido a muito encharcado na época das chuvas. É uma formação robusta com árvores de até 20 m de altura, com muitas palmeiras, plantas epífitas e "gravatás" (*Bromelia antiacantha* Bertol.) (Araújo & Oliveira 1987). Os manguezais ocorrem em Dois Rios, na Praia do Sul e do Leste e no interior do Saco do Céu e no Sítio Forte. Não foram encontrados trabalhos florísticos específicos sobre as áreas de manguezal.

Quanto a números relacionados à flora, no plano de manejo do Parque Estadual da Ilha Grande são citadas mais de 1.000 espécies de plantas, com 684 angiospermas, pertencentes a 106 famílias (INEA 2011), das quais se destacam Orchidaceae, Bromeliaceae, Myrtaceae, Rubiaceae e Fabaceae como as mais ricas em número de espécies, e 115 pteridófitas (INEA, 2011). Ainda de acordo com o plano de manejo do PEIG, baseado nos critérios do IBAMA, IUCN e Biodiversitas, 25 espécies ocorrentes na ilha se encontram ameaçadas de extinção.

2.2. Metodologia

2.2.1. O método RAPELD

Foram utilizadas as parcelas do método RAPELD, sigla que une as duas escalas que o método abrange: inventários rápidos (RAP) e projetos ecológicos de longa duração (PELD) (ver Magnusson et al. 2005), para a realização da amostragem e coleta de dados. O método se trata de uma modificação do desenvolvido por Gentry, em 1982. O sistema é fundamentado em parcelas permanentes alocadas em uma rede de sítios, baseado em grade, módulo, trilhas e parcelas. Os módulos são constituídos por grades. Cada grade abrange 25 km^2, sendo composta por trilhas com 5 km de comprimento cada, distantes um km entre si. Nas trilhas, há parcelas permanentes de 250 m com largura variável. As parcelas são longas e estreitas, minimizando a variação da topografia e do solo em cada parcela, assim, estes fatores podem ser avaliados como preditores da estrutura das comunidades (Figura 3).

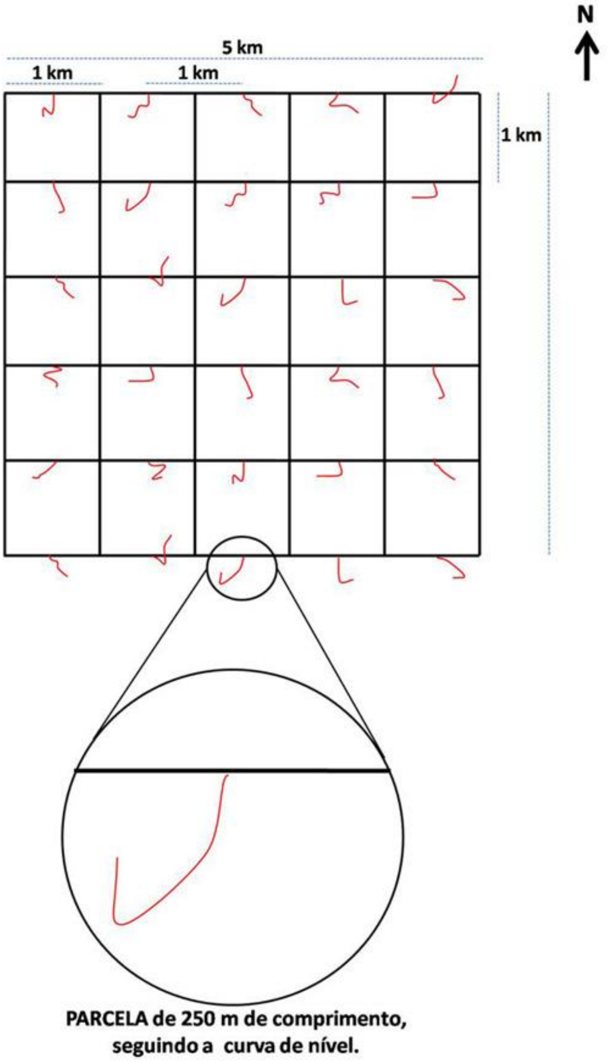

Figura 3: Estrutura do método RAPELD indicando grade com módulos, trilhas e parcelas (em destaque). Fonte: Programa de Pesquisa em Biodiversidade (PPBio, 2022).

Há dois módulos do RAPELD instalados na Ilha Grande. O módulo leste possui dez parcelas e está inserido no PEIG, em áreas de Floresta Ombrófila Densa Submontana e Montana. O módulo oeste possui nove parcelas e abrange áreas de Formação Pioneira de influência marinha (restinga), fluvio-marinha (mata alagadiça e manguezal) e de Floresta Ombrófila Densa Submontana (Figura 4) (PPBio, 2022). Com o início das atividades do RAPELD na Ilha Grande, o conhecimento sobre as espécies foi ampliado, uma vez que novas áreas são amostradas (PPBio, 2022).

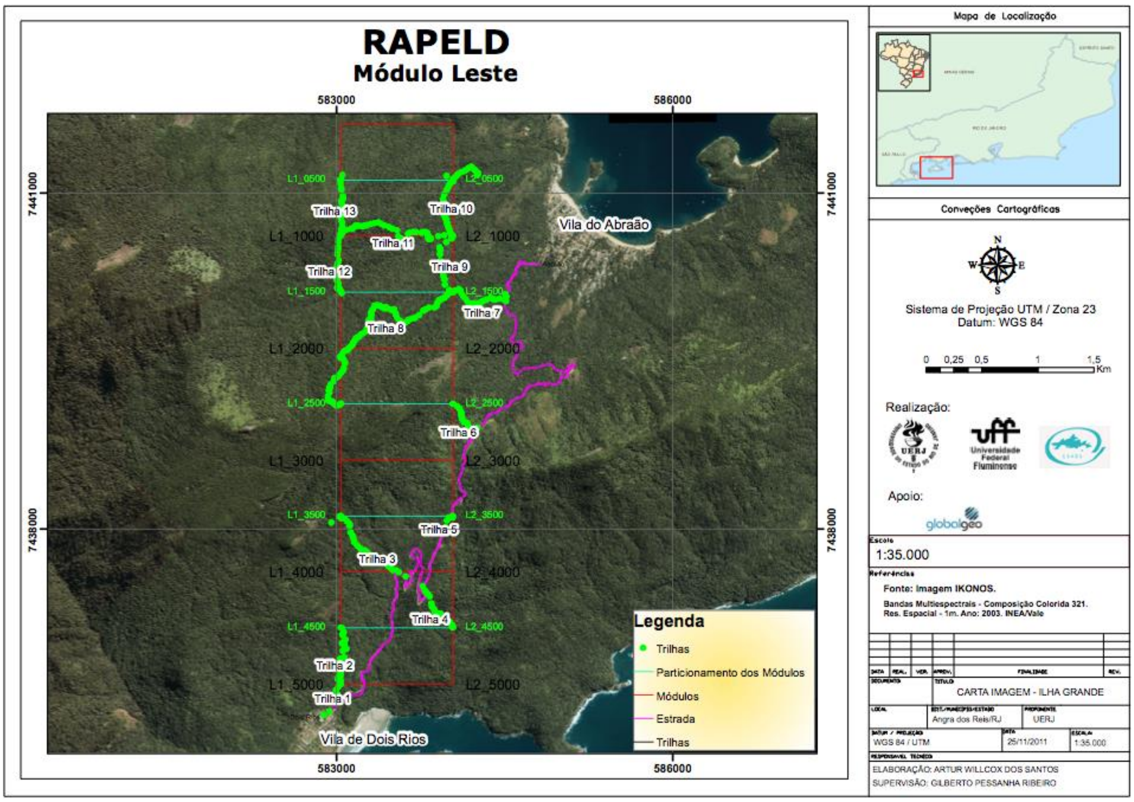

Figura 4: Carta imagem do módulo leste do RAPELD da Ilha Grande. Fonte: Programa de Pesquisa em Biodiversidade (PPBio 2022).

2.2.2. Fitofisionomias amostradas nas parcelas do RAPELD

Florestas de restinga

A mata de cordão arenoso, ou de restinga, se estende por toda a Praia do Sul, vertente oceânica da ilha, e consiste em uma floresta baixa. O dossel é relativamente fechado (contínuo e a copa possui cerca de 10 m de altura, mas que permite luminosidade suficiente para o estabelecimento de um estrato inferior com rica diversidade de várias famílias botânicas (Araujo & Oliveira, 1987; Nunes-Freitas et al., 2006; Cruz & Nunes-Freitas, 2019). A vegetação natural da mata de restinga foi modificada no passado pelos ciclos agrícolas ocorridos nesta parte da ilha. As alterações podem ser percebidas pela presença de áreas com moitas de arbustos, locais sem vegetação ou com vegetação muito esparsa (Araujo & Oliveira, 1987). Além disso, Cruz & Nunes-Freitas (2019), que registraram as epífitas vasculares da mata de restinga, verificaram diferenças na distribuição do número de espécies entre as famílias de epífitas mais comuns, havendo baixa riqueza de Orchidaceae e alta de Araceae, padrão já identificado para vegetações secundárias.

São localizadas duas parcelas do RAPELD na mata de restinga, nas trilhas Oeste 1 (O1) e Oeste 2 (O2), cada uma com exatamente 250 m de comprimento e distantes 1 km entre si. Apesar da proximidade, a estrutura da vegetação nas duas parcelas difere. A parcela 1 (como será chamada ao longo da tese), é mais próxima ao costão e possui as seguintes coordenadas geográficas: latitude: -23,17795 e longitude: -44,30768, apresenta poucas árvores de médio e grande porte, altura média das árvores é de 10 m com Diâmetro a Altura do Peito médio (DAP) de 17 cm, troncos relativamente finos e bastante tortuosos (Figura 5 – a e b). Já a parcela 2, assim tratada ao longo da tese, é localizada pouco a frente da Lagoa do Sul, mais próxima a Praia do Leste, e possui as coordenadas: latitude: -23,17668333 e longitude: -44,29798. A parcela 2 apresenta muitas árvores de médio porte, com altura média de 8 m e DAP médio de 18 cm (Figura 5 – c e d). Em ambas as parcelas há muitas lianas e epífitas. Especialmente na parcela 2, a abundância destas plantas estruturalmente dependentes é maior e o sub-bosque é rico e constituído por grande diversidade de bromélias, aráceas, samambaias e outras, destacando-se as espécies *Aechmea nudicaulis* (L.) Griseb., *Bromelia antiacantha* Bertol., *Philodendron cordatum* Kunth ex Schott, *P. crassinervium* Lindl. e *Neomarica etabol* (Hassl.) Sprague.

Figura 5: Fotografias da mata de restinga na Reserva Biológica Estadual da Praia do Sul onde estão instaladas as parcelas 1 e 2 do RAPELD da Ilha Grande, Rio de Janeiro. As fotografias (a) e (b) correspondem a parcela 1, enquanto as (c) e (d) correspondem a parcela 2. Fonte: a autora.

Segundo a Resolução VI do Conselho Nacional do Meio Ambiente (CONAMA) de 1994 (Brasil, 1994), os parâmetros definidos para classificação do estágio sucessional de restingas devem ser definidos por regulamentação específica. Não foram encontradas resoluções específicas para o estado do Rio de Janeiro e, por esta razão, utilizou-se a Resolução VII do CONAMA (Brasil, 1996) que traz a análise dos estágios de sucessão de vegetação de restinga para o Estado de São Paulo. De acordo com a referida resolução, ambas as parcelas podem ser classificadas como floresta alta em estágio avançado de regeneração. Esta classificação se deve aos seguintes elementos: estrato predominante arbóreo, com árvores de até 12 metros de altura, amplitude diamétrica de 10 a 15 centímetros, comunidade de epífitas formada por líquens, briófitas, pteridófitas, bromélias, orquídeas, piperáceas e aráceas. Além disso, há presença de várias trepadeiras, camada espessa de serapilheira, presença de sub-bosque semelhante ao original e espécies indicadoras pertencentes às famílias Myrtaceae, Lauraceae, Arecaceae e Rubiaceae.

Floresta Ombrófila Densa de Terras Baixas

A parcela em Floresta Ombrófila Densa de Terras Baixas, que será referida como parcela 3 nesta tese, corresponde a uma mata ripária e está estabelecida fora da grade do RAPELD a fim de abranger outro tipo de fitofisionomia que não estava sendo contemplada. A parcela se localiza na trilha entre a Vila de Dois Rios e a praia da Parnaioca, latitude: -23,18405 e longitude: -44,19394, altitude média de 10 m e vegetação classificada como Floresta Ombrófila Densa de Terra Baixas em estágio médio de regeneração, segundo os parâmetros da Resolução VI do CONAMA (Brasil, 1994) (Figura 6). A fisionomia é arbórea e arbustiva prevalecendo sobre a herbácea, exceto em alguns pontos isolados, com estratos diferenciados e altura média das árvores em cerca de 18 m, com média de DAP de 30 cm, algumas árvores emergentes com até 40 m e DAP de 65 cm, muitas epífitas, de famílias variadas e presença de trepadeiras lenhosas. As principais espécies de árvores registradas foram: *Clitoria fairchildiana* R.A.Howard (“Sombreiro”), *Tapirira guianensis* Aubl. (“pau-pombo”) e *Miconia calvescens* DC. A parcela se localiza à montante do riacho que apresenta no máximo 2 m de largura em algumas áreas, águas claras e pouca profundidade.

Figura 6: Fotografias da parcela 3 do RAPELD da Ilha Grande, Rio de Janeiro, instalada em Floresta Ombrófila Densa de Terras Baixas entre a Vila de Dois Rios e a Praia da Parnaioca. Fonte: a autora.

Floresta Ombrófila Densa Submontana

Foram amostradas duas parcelas em Floresta Ombrófila Densa Submontana. Uma delas, parcela 4, se trata de mata ripária localizada próximo à estrada que vai da Vila do Abraão para a Vila de Dois Rios, nas seguintes coordenadas geográficas: latitude: -23,16821 e longitude: -44,18418, com altitude média de 142 m. A vegetação está em estágio médio de regeneração, de acordo os parâmetros da Resolução VI do

CONAMA (Brasil, 1994). A fitofisionomia é predominantemente arbórea e arbustiva com diferentes estratos, altura média do dossel de 21 m e DAP médio de 21,5 cm, com algumas árvores emergentes com até 30 m de altura e DAP de 70 cm (Figura 7). As principais árvores identificadas foram: *Cupania oblongifolia* Mart., *Cupania emarginata* Cambess., *Tapirira guianensis* Aubl. ("pau-pombo") e outras espécies de Fabaceae e Melastomataceae. Foi observada uma alta riqueza de trepadeiras lenhosas e epífitas, especialmente das famílias Bromeliaceae, Araceae e Polypodiaceae, inclusive as mesmas famílias apresentam alta diversidade no solo e sobre pedras a beira do riacho, juntamente com densas populações de briófitas. O riacho possui cerca de quatro metros de largura e desce em meio a grandes e numerosas pedras cobertas por briófitas e samambaias.

Figura 7: Fotografias da parcela 4 do RAPELD da Ilha Grande, Rio de Janeiro, instalada em Floresta Ombrófila Densa Submontana próximo à estrada que vai da Vila do Abraão para a Vila de Dois Rios. Fonte: a autora.

A segunda parcela em Floresta Ombrófila Densa Submontana, parcela 5, é uma mata de encosta localizada nas seguintes coordenadas geográficas: latitude: -23,15536 e longitude -44,17866, com altitude média de 380 m. A parcela apresenta vegetação classificada como estágio avançado de regeneração, segundo os parâmetros da Resolução VI do CONAMA (Brasil, 1994). A fitofisionomia é arbórea, sub-bosque mais denso em apenas alguns pontos, altura média do dossel de 23 m, predominantemente fechado e uniforme, DAP médio de 43 cm, com árvores emergentes frequentes com até 40 m de altura e DAP de 95,5 cm (Figura 8). Quanto às árvores, foi observada alta diversidade de Fabaceae, Melastomataceae, Arecaceae, Anacardiaceae e Sapindaceae. A mata apresenta elevada densidade de trepadeiras, lianas e epífitas, especialmente Fabaceae, Bromeliaceae, Araceae e samambaias.

Figura 8: Fotografias da parcela 5 do RAPELD da Ilha Grande, RJ, instalada em Floresta Ombrófila Densa Submontana no módulo Leste. Fonte: a autora.

2.2.3. Coleta e análise de dados

Nas parcelas do módulo Leste e Oeste do RAPELD foram demarcadas subparcelas de 100 m^2 de um ou de ambos os lados do corredor central intercalando-se segmentos de 10 m e respeitando-se a faixa sensível, de acordo com o proposto por Cruz (2017) (Figura 9). Nas subparcelas, todas as árvores com DAP ≥ 15 cm tiveram as espécies de epífitas vasculares registradas e abundância estimada. Nas parcelas 3, 4 e 5 foram amostradas subparcelas apenas à montante devido à presença de riachos em 3 e 4, e à declividade acentuada em 5.

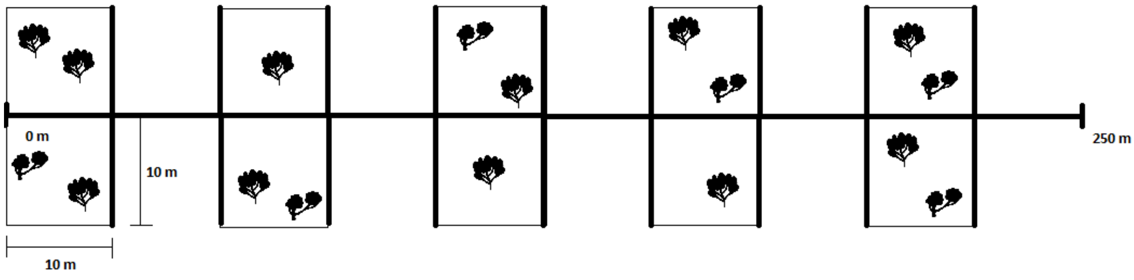

Figura 9: Representação esquemática das subparcelas de 100 m^2 que foram utilizadas para a amostragem de epífitas vasculares em parcelas do RAPELD da Ilha Grande, Rio de Janeiro. Fonte: Cruz (2017)

Em cada subparcela foram mensurados os seguintes dados de características ambientais com as respectivas ferramentas:

1. Coordenadas geográficas, latitude e longitude, e altitude: uso de GPS Garmin Etrex.

2. Cobertura do dossel: uso do aplicativo Canopeo, que avalia a porcentagem (%) de cobertura verde no dossel florestal (Patrignani & Ochsner, 2015).
3. Inclinação da parcela: uso do aplicativo Clinometer, que permite avaliar o ângulo de inclinação das superfícies.
4. Morfometria das árvores: altura total, altura do fuste, diâmetros maior e menor da copa, medidas em metros (m), e circunferência a altura do peito (CAP), em centímetros (cm), medidas com trena convencional ou fita métrica e comparação com podão telescópico de cinco metros.
5. Densidade de árvores: número de árvores com DAP ≥ 15 cm.

As informações ambientais foram mensuradas no centro de cada subparcela. Foi calculada a profundidade da copa dos forófitos através da diferença entre a altura total e a altura do fuste (tronco até as primeiras ramificações). Também foi calculado o diâmetro médio da copa pela média aritmética dos valores do diâmetro maior e menor da copa. Foram calculadas as médias das variáveis morfométricas das árvores em cada subparcela, pois estas foram consideradas unidades amostrais nas análises. Além disso, todas as variáveis foram transformadas em unidades de desvio padrão, uma vez que se foram mensuradas em diferentes unidades de medida. As especificidades da metodologia e análise dos dados encontram-se nos capítulos da tese.

Todo o material botânico coletado foi depositado nos herbários R e RBR, do Museu Nacional e da Universidade Federal Rural do Rio de Janeiro, respectivamente.

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CAPÍTULO I

Diversity of vascular epiphytes from Ilha Grande, Rio de Janeiro, Brazil

ABSTRACT

The Atlantic Forest stands out among the Brazilian domains for its high rate of epiphytes, making it possible to estimate more than 3,000 species of vascular epiphytes, highlighting its taxonomic and ecological importance for ecosystems. Despite the increase in the number of studies on epiphytes in recent decades, many regions do not even have a floristic survey of this community. Thus, the present study aims to contribute to the knowledge about the flora of vascular Epiphytes of Ilha Grande, Angra dos Reis, RJ, gathering information on the diversity and conservation status of the species. The species list was prepared from consultations with herbarium collections, published species lists for the study area, and fieldwork. A total of 253 species were surveyed, and field sampling resulted in 76 species. The most representative botanical families were Orchidaceae, Bromeliaceae, and Polypodiaceae. The conservation status of most species is unknown, four are considered vulnerable and five are threatened with extinction. *Neoregelia hoehneana* L.B.Sm., *Octomeria alexandri* Schltr., *Wittrockia superba* Lindm., and *Rauhiella silvana* Toscano are endangered and *Vriesea rubyae* E. Pereira is critically endangered. Therefore, the island can be considered an important area for the preservation of the biodiversity of epiphytes and there is a need for urgent population studies to support the elaboration of strategies for the conservation of the species.

Keywords: Atlantic Forest, bromeliads, ferns, floristic inventory, insular biodiversity.

1. INTRODUCTION

The forest canopy is an important part of the overall structure and functioning of ecosystems and there has been a large and rapid increase in research into this environment in recent decades (Barker & Pinard, 2001). The increase is due, among other reasons, to the high species richness associated with this compartment (Allen, 1996). Among the communities that make the forest canopy one of the most complex ecosystems on the planet, vascular epiphytes stand out (Gentry & Dodson, 1987; Zotz, 2016). Epiphytes are plants that germinate and root nonparasitically in other plants at all stages of life (Madison, 1977; Zotz, 2016). According to Gentry & Dodson (1987), epiphytism occurs in 84 families, 876 genera and about 29,000 species, recently published data update this number to 28,000 species, which corresponds to almost 10% of all tracheophytes on the planet (Zotz et al., 2021). Epiphytes form a very diverse group from a taxonomic point of view, with representatives in all major groups of vascular plants (Madison, 1977; Benzing, 1990). However, most species belong to a few families of angiosperms, especially Orchidaceae, Bromeliaceae and Polypodiaceae, respectively, with the greatest richness (Zotz et al., 2021). Epiphytes have essential roles in tropical and subtropical forest ecosystems. We can highlight the high photosynthetic rate (Nadkarni, 1984), litter with a high concentration of nutrients (Clark et al., 1998; Nadkarni, 1992; Oliveira, 2004), interception, and storage of water and moisture in the canopy (Holwerda et al., 2013), diversification of niches, microhabitats, and food sources for the fauna (Benzing, 1986; Rocha et al., 2000).

The Atlantic Forest, which occurs along the Brazilian coast extending from the state of Rio Grande do Sul to Rio Grande do Norte (Morellato & Haddad, 2000), it has more than 8,000 endemic plant species and is one of the biodiversity hotspots with a large number of endangered species (Myers et al., 2000; Mittermeier et al., 2004). This phytogeographic domain corresponds to one of the world's regions where the epiphytic habit is more highly pronounced, along with Central and South America and the Sub-Andean Belt (Nieder et al., 1999; Taylor et al., 2022). Ramos et al. (2019) compiled 2,095 species of epiphytes and hemiepiphytes for the Atlantic Domain and in Flora e Funga do Brasil (2022) 2,128 species of vascular epiphytes are recorded for the Atlantic Forest. Many floristic surveys and research on the ecology of vascular epiphytes have been carried out in the forests of southern and southeastern Brazil in recent decades (see Kersten 2010; Ramos et al. 2019). In addition to the high diversity, there is also the high rate of endemism that has been endorsed in several studies (Freitas et al., 2016; Menini Neto et al., 2016; Furtado & Menini Neto, 2021; Araujo & Ramos, 2021).

The diversity of epiphytes is not evenly distributed in the forests of the Atlantic Forest and the southeastern and southern regions are the richest in number of species (Menini Neto et al., 2016), along with southern Bahia (Ramos et al., 2019). Despite the high richness and endemism index, the number of specific publications on epiphytes in the state of Rio de Janeiro is still low when compared to other life forms and regions (Fontoura et al., 2012; Couto et al., 2017; Dornelas et al., 2017; Cruz & Nunes-Freitas, 2019; Cruz et al., 2021; Furtado & Menini Neto, 2022). For Araujo & Ramos (2021) the greatest sampling efforts need to focus on neglected regions, since these areas may contain highly threatened species. Ilha Grande, in the municipality of Angra dos Reis, Rio de Janeiro, represents one of the most important remnants of Atlantic Forest in the state, both because of its size and the high biodiversity and state of preservation (Alho et al., 2002; Rocha, 2003). Many studies point to a high richness of epiphytes on the island (Araujo & Oliveira, 1987; Nunes-Freitas et al., 2006; Braga, 2011; Cruz & Nunes-Freitas, 2019; Cruz et al., 2021; Rocha et al., 2022). However, there should be more publications providing specific information on the diversity of vascular epiphytes for the island as a whole to support the development of adequate strategies for the conservation of the species. In this context, the present research aims to contribute to the knowledge about the flora of vascular epiphytes of Ilha Grande, gathering information on patterns of diversity and the conservation status of the species.

2. MATERIAL AND METHODS

2.1. Study area

Ilha Grande is the largest island on the southern coast of the State of Rio de Janeiro and has a very complex history of occupation (INEA - Instituto Estadual do Ambiente 2011; UFRRJ (Universidade Federal Rural do Rio de Janeiro 1992). The island was once the scene of resistance struggles between Indians and colonizers, it housed farms of different cultures, whale traps, a lazaretto and even two prisons (INEA 2011). As it represents one of the largest preserved areas of Atlantic Forest in the Southeast, the site has become an important preservation and research region in the 21st Century (Alho et al., 2002). Currently, the island has four Conservation Units: the Ilha Grande State Park, the Praia do Sul State Biological Reserve, the Tamoios

Environmental Protection Area, and the Aventureiro Sustainable Development Reserve. Forests occupy more than 90% of the island and form a mosaic in different successional stages, and in some locations the high canopy reaches 30 m in height (INEA, 2011). Ilha Grande has Dense Ombrophilous Forest and extensive secondary forests, as well as vegetation formed by herbaceous, herbaceous rocky outcrops, restingas, mangroves and beaches (Oliveira & Neto, 2000; Alho et al., 2002; Callado et al., 2009).

The relief is quite rugged, consisting mainly of mountains and coastal plains, with altitudes ranging from 0 to 1,031 meters, the highest point being Pedra D'água (INEA, 2011). The soils vary according to the type of rock, relief, and climate, especially red-yellow alitic latosols, Cambisols, and rocky outcrops (INEA, 2011). The climate is hot and humid, with no dry season, due to its geographical location and topography (INEA, 2011). The entire region of Angra dos Reis has a tropical climate, with high temperatures and very high rainfall in the summer (Salgado & Vasquez, 2009). The average annual temperature is 23.2ºC, with maximum averages above 30ºC and minimums below 10ºC, with average annual air humidity of 82%, without major variations throughout the year (Salgado & Vasquez, 2009).

2.2. Methodology

To prepare the species list, three different methodologies were used:

a) Survey of species occurring in Ilha Grande, RJ, by consulting the database in online herbaria, through speciesLink (speciesLink, 2022) and REFLORA – Database of Brazilian Flora (Reflora, 2022).

b) Floristic listings published for Ilha Grande (Bastos & Callado, 2009; Braga, 2011; Cruz, 2017; Cruz & Nunes-Freitas, 2019; Cruz et al., 2021; Rocha et al., 2022);

c) Sampling of five RAPELD plots installed on Ilha Grande, RAPELD is an acronym that unites the two scales that the method covers: rapid inventories (RAP) and long-term ecological projects (PELD) (*see* Magnusson et al., 2005).

All epiphyte species present in the databases were surveyed for families with floristic representation greater than 1% in the surveys of vascular epiphytes in the Atlantic Forest according to Kersten et al. (2010). Only species that were identified to a specific level and whose collection area corresponds to Ilha Grande, Angra dos Reis, RJ, were listed. Data were collected for the following families: Orchidaceae, Bromeliaceae, Polypodiaceae, Araceae, Piperaceae, Cactaceae, Dryopteridaceae, Gesneriaceae, Hymenophylaceae, Aspleniaceae, Begoniaceae, Melastomataceae, and Lycopodiaceae. In the publications, all species with epiphytic or hemiepiphyte habits present in the floristic surveys were considered, according to information from Flora and Funga do Brasil (2022) and observed as epiphyte in the study areas.

All field collections were carried out in RAPELD plots installed on Ilha Grande. RAPELD is a method that combines rapid inventories (RAP) and long-term ecological projects (PELD) (see Magnusson et al., 2005). Two plots located in restinga vegetation, two in submontane dense ombrophylous forest, and one in lowland forest were sampled. The visualization of the epiphytes was made from the ground and, when necessary, with the use of a photographic camera. The botanical material was collected with the aid of pruning shears and with a telescopic pruner in higher areas of the tree, it was pressed, oven dried and the exsiccates were deposited in the R and RBR herbaria. Species identification was based on specific literature, on the study of herborized material, and with the help of specialists. Scientific names have been verified in Flora and Funga do Brasil (2022).

Sampling sufficiency was verified through accumulation and rarefaction curves based on the species recorded as a function of the subplots sampled in the fieldwork. We used the following richness estimators: Chao 1, Jacknife 1 and Bootstrap. In addition, we calculated the Shannon and Simpson Diversity Indices for each of the RAPELD plots. All of these analyses were conducted with the Vegan and BiodiversityR packages (Kindt & Coe, 2005; Oksanen et al., 2020). All treatments and analyses were performed using the program R version 4.10 (R Core Team, 2020).

Species were classified according to substrate use into epiphytes and hemiepiphytes (those that can connect to the soil at some stage of life), according to Benzing (1990). This classification was chosen because there is no consensus in the literature in the use of the terms hemiepiphytes primary or secondary and nomadic climbing, used for plants that connect to the soil at different stages of life (Moffett, 2000; Zotz, 2013; Sperotto et al., 2020; Zotz et al., 2021).

The contribution of epiphytes to the total flora of Ilha Grande was verified through the epiphytic index (or epiphytic quotient), which corresponds to the percentage of epiphytes in relation to the total number of vascular plant species in the area (Hosokawa, 1950). The conservation status was verified on the website of the National Center for the Conservation of Flora (CNC Flora, 2022), the Red List of Brazilian Flora

(Martinelli & Moraes, 2013), and the Red Book of Endemic Flora of the State of Rio de Janeiro (Martinelli et al., 2018).

3. RESULTS

A total of 253 species from 16 botanical families were recorded, 21 of which were classified as hemiepiphytes (Table 1). The sampling of the RAPELD plots resulted in the survey of 76 species, which represents 30% of the total surveyed considering secondary data sources. Richness estimators indicated the following values: Chao 1 = 123.4 ± 23.7, Jackknife 1 = 106.6 ± 9.9, and Bootstrap = 89.1 ± 5.2. The diversity indices for each plot were, respectively: Shannon Index: 1.96, 2.07, 1.87, 2.38, and 3.54. Simpson Index: 0.82, 0.83, 0.67, 0.79, and 0.95.

Table 1 List of vascular epiphytes and hemiepiphytes species occurring in Ilha Grande, Angra dos Reis, RJ, by botanical family, ecological category (Benzing, 1990) and conservation status, according to the National Flora Conservation Center (CNC Flora, 2022). NE = Not evaluated; LC= Least concern; DD = Data Deficient; NT = Nearly in danger; VU = Vulnerable; EN = Endangered; CR = Critically endangered. It also contains the reference from where the information was extracted and/or the voucher. NC = not collected, due to difficult access or because it was sterile. The vouchers presented are the numbers of herbarium records, whose acronyms follow Thiers (2022, continuously updated), or last name of the collectors followed by the collect number.

Family	**Species**	**Ecological category**	**Conservation status**	**Reference and/or *voucher***
Araceae	*Anthurium intermedium* Kunth	Epiphyte	NE	RBR 42711
Araceae	*Anthurium pentaphyllum* (Aubl.) G.Don	Hemiepiphyte	NE	RB 470950
Araceae	*Anthurium scandens* (Aubl.) Engl.	Epiphyte	NE	Cruz & Correa 128
Araceae	*Anthurium minarum* Sakur. & Mayo	Epiphyte	NE	NC
Araceae	*Anthurium urvilleanum* Schott	Epiphyte	NE	Cruz & Correa 106
Araceae	*Monstera adansonii* Schott	Hemiepiphyte	NE	RBR 42693; Cruz & Correa 100
Araceae	*Monstera praetermissa* E.G.Gonç. & Temponi	Hemiepiphyte	NE	Cruz (2017)
Araceae	*Philodendron cordatum* Kunth ex Schott	Hemiepiphyte	NE	RBR 42726
Araceae	*Philodendron crassinervium* Lindl.	Hemiepiphyte	NE	RBR 42703
Araceae	*Philodendron curvilobum* Schott	Hemiepiphyte	NE	RBR 42715
Araceae	*Philodendron eximium* Schott	Hemiepiphyte	NE	Cruz & Correa 103
Araceae	*Philodendron hastatum* K.Koch & Sello	Hemiepiphyte	NE	Cruz & Correa 88
Araceae	*Philodendron martianum* Engl.	Epiphyte	NE	RB 473560; Cruz et al. 2019

Araceae	*Philodendron oblongum* (Vell.) Kunth	Hemiepiphyte	NE	Cruz et al. 2021
Araceae	*Philodendron ornatum* Schott	Hemiepiphyte	NE	HRJ 7341; HRJ 7342
Araceae	*Philodendron propinquum* Schott	Hemiepiphyte	NE	Cruz et al. 2019
Araceae	*Syngonium podophyllum* Schott	Hemiepiphyte	NE	Bastos & Callado (2009)
Araceae	*Thaumatophyllum bipinnatifidum* (Schott ex Endl.) Sakur., Calazans & Mayo	Hemiepiphyte	NE	Bastos & Callado (2009)
Aspleniaceae	*Asplenium auriculatum* Sw.	Epiphyte	NE	NY 809769; Cruz et al. 186
Aspleniaceae	*Asplenium lacinulatum* Schrad.	Epiphyte	LC	Bastos & Callado (2009)
Aspleniaceae	*Asplenium mucronatum* C.Presl	Epiphyte	NE	Bastos & Callado (2009)
Aspleniaceae	*Asplenium serratum* L.	Epiphyte	NE	CESJ 26725
Begoniaceae	*Begonia integerrima* Spreng.	Hemiepiphyte	LC	Cruz et al. 146
Begoniaceae	*Begonia herbacea* Vell.	Epiphyte	LC	Cruz et al. 159; Bastos & Callado (2009)
Bromeliaceae	*Aechmea coelestis* (K. Koch) E.Morren	Epiphyte	NE	RB 484381; Rocha et al. (2022)
Bromeliaceae	*Aechmea distichantha* Lem.	Epiphyte	NE	RBR 44219; Rocha et al. (2022)
Bromeliaceae	*Aechmea gracilis* Lindm.	Epiphyte	LC	Cruz & Correa 85; Rocha et al. (2022)

Bromeliaceae	*Aechmea nudicaulis* (L.) Griseb.	Epiphyte	LC	RBR 42714; Rocha et al. (2022)
Bromeliaceae	*Aechmea organensis* Wawra	Epiphyte	NE	RFA 30691; Rocha et al. (2022)
Bromeliaceae	*Aechmea pectinata* Baker	Epiphyte	LC	RBR 44208; Rocha et al. (2022)
Bromeliaceae	*Aechmea weilbachii* Didrich	Epiphyte	NE	RBR 44745; Rocha et al. (2022)
Bromeliaceae	*Billbergia amoena* (Lodd.) Lindl.	Epiphyte	NE	RBR 42713; Rocha et al. (2022)
Bromeliaceae	*Billbergia pyramidalis* (Sims) Lindl.	Epiphyte	DD	RBR 44749; Rocha et al. (2022)
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	Epiphyte	LC	RBR 44603; Rocha et al. (2022)
Bromeliaceae	*Canistropsis billbergioides* (Schult. & Schult. f.) Leme	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Canistropsis microps* (E. Morren ex Mez) Leme	Epiphyte	LC	Cruz et al. 184; Rocha et al. (2022)
Bromeliaceae	*Edmundoa ambigua* (Wand. & Leme) Leme	Epiphyte	NE	RBR 44604; Rocha et al. (2022)

Bromeliaceae	*Edmundoa lindenii* (Regel) Leme	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Neoregelia cruenta* (R. Graham) L.B.Sm.	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Neoregelia hoehneana* L.B.Sm.	Epiphyte	EN	RBR 44741; Rocha et al. (2022)
Bromeliaceae	*Neoregelia johannis* (Carrière) L.B.Sm.	Epiphyte	NE	RBR 42701; Rocha et al. (2022)
Bromeliaceae	*Nidularium innocentii* Lem.	Epiphyte	LC	RBR 44591; Rocha et al. (2022)
Bromeliaceae	*Portea petropolitana* (Wawra) Mez	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009); Rocha et al. (2022)
Bromeliaceae	*Quesnelia marmorata* (Lem.) R.W. Read	Epiphyte	NE	RFA 28317; Rocha et al. (2022)
Bromeliaceae	*Quesnelia quesneliana* (Brongn.) L.B.Sm.	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009); Rocha et al. (2022)
Bromeliaceae	*Tillandsia dura* Baker	Epiphyte	NE	RBR 42716; Rocha et al.

				(2022)
Bromeliaceae	*Tillandsia gardneri* Lindl.	Epiphyte	LC	Cruz & Correa 126; Rocha et al. (2022)
Bromeliaceae	*Tillandsia geminiflora* Brongn.	Epiphyte	LC	Cruz & Correa 150; Rocha et al. (2022)
Bromeliaceae	*Tillandsia mallemontii* Glaziou ex Mez	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Tillandsia recurvata* (L.) L.	Epiphyte	NE	RBR 44746; Rocha et al. (2022)
Bromeliaceae	*Tillandsia stricta* Sol.	Epiphyte	NE	RBR 44761; Rocha et al. (2022)
Bromeliaceae	*Tillandsia tenuifolia* L.	Epiphyte	LC	Cruz & Correa 129; Rocha et al. (2022)
Bromeliaceae	*Tillandsia tricholepis* Baker	Epiphyte	LC	RBR 44607; Rocha et al. (2022)
Bromeliaceae	*Tillandsia usneoides* (L.) L.	Epiphyte	LC	Cruz & Correa 131; Rocha et al. (2022)
Bromeliaceae	*Vriesea bituminosa* Wawra	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)

Bromeliaceae	*Vriesea carinata* Wawra	Epiphyte	LC	RBR 44576; Rocha et al. (2022)
Bromeliaceae	*Vriesea drepanocarpa* (Baker) Mez	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea gigantea* Gaudich.	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea gradata* (Baker) Mez	Epiphyte	NE	RBR 44575; Rocha et al. (2022)
Bromeliaceae	*Vriesea jonghei* (K. Koch) E. Morren	Epiphyte	NE	R 214526; Rocha et al. (2022)
Bromeliaceae	*Vriesea longiscapa* Ule	Epiphyte	NE	Cruz (2017) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea lubbersii* (Baker) E. Morren	Epiphyte	LC	Cruz & Correa 120; Rocha et al. (2022)
Bromeliaceae	*Vriesea pauperrima* E. Pereira	Epiphyte	LC	RBR 44596; Rocha et al. (2022)
Bromeliaceae	*Vriesea philippocoburgii* Wawra	Epiphyte	LC	RBR 44212; Rocha et al. (2022)
Bromeliaceae	*Vriesea procera* (Mart. ex Schult. & Schult.) f. Wittm.	Epiphyte	LC	RBR 44232; Rocha et al.

				(2022)
Bromeliaceae	*Vriesea rodigasiana* E. Morren	Epiphyte	LC	RBR 42704; RBR 42705; Rocha et al. (2022)
Bromeliaceae	*Vriesea rubyae* E. Pereira	Epiphyte	CR	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea scalaris* E. Morren	Epiphyte	LC	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea secundiflora* Leme	Epiphyte	NE	RBR 44754; Rocha et al. (2022)
Bromeliaceae	*Vriesea simplex* (Vell.) Beer	Epiphyte	NE	RBR 44601; Rocha et al. (2022)
Bromeliaceae	*Vriesea unilateralis* (Baker) Mez	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009) ; Rocha et al. (2022)
Bromeliaceae	*Vriesea vagans* (L.B. Sm.) L.B. Sm.	Epiphyte	NE	RBR 44570; Rocha et al. (2022)
Bromeliaceae	*Wittrockia superba* Lindm.	Epiphyte	EN	RBR 44225
Cactaceae	*Hatiora salicornioides* (Haw.) Britton & Rose	Epiphyte	NE	NY 645335

Cactaceae	*Selenicereus setaceus* (Salm-Dyck) Berg	Epiphyte	LC	RBR 42722; Cruz & Nunes-Freitas 68
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	Epiphyte	LC	NY 645354; Cruz & Nunes-Freitas 68
Cactaceae	*Rhipsalis clavata* F.A.C.Weber	Epiphyte	NE	Cruz et al. 153
Cactaceae	*Rhipsalis crispata* (Haw.) Pfeiff.	Epiphyte	DD	NC
Cactaceae	*Rhipsalis elliptica* G.Lindb. ex K.Schum.	Epiphyte	LC	SPF 111985; RBR 44233; Cruz & Murakami, 40; Cruz & Correa 114
Cactaceae	*Rhipsalis grandiflora Haw.*	Epiphyte	NE	Bastos & Callado (2009)
Cactaceae	*Rhipsalis oblonga* Loefgr.	Epiphyte	NT	RBR 42707
Cactaceae	*Rhipsalis pachyptera* Pfeiff.	Epiphyte	NE	RBR 42707; Cruz & Correa 178
Cactaceae	*Rhipsalis teres* (Vell.) Steud.	Epiphyte	NE	SPF 111987; NY 645743; Cruz & Nunes-Freitas 58
Commelinaceae	*Tradescantia fluminensis* Vell.	Epiphyte	NE	Cruz & Correa 127
Commelinaceae	*Tradescantia zebrina* Heynh. ex Bosse	Epiphyte	NE	NC
Dryopteridaceae	*Polybotrya pilosa* Brade	Hemiepiphyte	NE	Cruz (2017)
Dryopteridaceae	*Polybotrya semipinnata* Fée	Hemiepiphyte	NE	HRJ 4279
Gesneriaceae	*Codonanthe devosiana* Lem.	Epiphyte	LC	RBR 42718;

				Cruz & Sylvestre 71; Cruz & Correa 113
Gesneriaceae	*Codonanthe gracilis* (Mart.) Hanst.	Epiphyte	LC	RBR 42698
Gesneriaceae	*Nematanthus fissus* (Vell.) L.E.Skog	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009)
Hymenophillaceae	*Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara	Epiphyte	NE	Bastos & Callado (2009)
Hymenophillaceae	*Didymoglossum krausii* (Hook. & Grev.) C. Presl	Epiphyte	NE	Bastos & Callado (2009)
Hymenophillaceae	*Hymenophyllum caudiculatum* Mart.	Epiphyte	NE	Bastos & Callado (2009)
Hymenophillaceae	*Hymenophyllum polyanthos* (Sw.) Sw.	Epiphyte	NE	Bastos & Callado (2009)
Hymenophillaceae	*Trichomanes polypodioides* L.	Epiphyte	NE	Bastos & Callado (2009)
Hymenophillaceae	*Vandenboschia radicans* (Sw.) Copel.	Hemiepiphyte	NE	Cruz et al. 143
Lomariopidaceae	*Lomariopsis marginata* (Schrad.) Kuhn	Hemiepiphyte	NE	HRJ 7203
Lycopodiaceae	*Phlegmariurus mandiocanus* (Raddi) B.Øllg.	Epiphyte	NE	Cruz & Correa 133
Melastomataceae	*Bertolonia acuminata* Gardner	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009)
Orchidaceae	*Acianthera aphthosa* (Lindl.) Pridgeon & M.W.Chase	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Acianthera saundersiana* (Rchb.f.) Pridgeon & M.W.Chase	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Acianthera sonderiana* (Rchb.f.) Pridgeon & M.W.Chase	Epiphyte	NE	Cruz (2017); Braga (2009)

Orchidaceae	*Acianthera subrotundifolia* (Cogn.) F.Barros & V.T.Rodrigues	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Anathallis brevipes* (H.Focke) Pridgeon & M.W.Chase	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Anathallis paranapiacabensis* (Hoehne) F.Barros	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Anathallis sclerophylla* (Lindl.) Pridgeon & M.W.Chase	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Bifrenaria racemosa* (Hook.) Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Bifrenaria tetragona* (Lindl.) Schltr.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Brasiliorchis consanguinea* (Klotzsch) R.B.Singer et al.	Epiphyte	NT	Cruz (2017); Braga (2009)
Orchidaceae	*Catasetum hookeri* Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Catasetum macrocarpum* Rich. ex Kunth	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Cattleya cernua* (Lindl.) Van den Berg	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Cattleya coccinea* Lindl.	Epiphyte	NE	Cruz (2017); Braga

				(2009)
Orchidaceae	*Cattleya crispa* Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Cattleya forbesii* Lindl.	Epiphyte	NE	RBR 42719; Bastos & Callado (2009)
Orchidaceae	*Cattleya guttata* Lindl.	Epiphyte	VU	Cruz (2017); Bastos & Callado (2009)
Orchidaceae	*Christensonella pumila* (Hook.) Szlach. et al.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Christensonella subulata* (Lindl.) Szlach. et al.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Cirrhaea dependens* (Lodd.) Loudon	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Dichaea cogniauxiana* Schltr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Dichaea pendula* (Aubl.) Cogn.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Dryadella edwallii* (Cogn.) Luer	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Elleanthus brasiliensis* (Lindl.) Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)

Orchidaceae	*Encyclia patens* Hook.	Epiphyte	NE	Cruz & Correa 121
Orchidaceae	*Epidendrum avicula* Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum filicaule* Lindl.	Epiphyte	LC	Cruz et al. 149; Cruz & Correa 160
Orchidaceae	*Epidendrum flexuosum* G.Mey.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum hololeucum* Barb.Rodr.	Epiphyte	NT	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum nutans* Sw.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum paranaense* Barb.Rodr.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum proligerum* Barb.Rodr.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum pseudodifforme* Hoehne & Schltr.	Epiphyte	NE	RBR 44214
Orchidaceae	*Epidendrum ramosum* Jacq.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum rigidum* Jacq.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Epidendrum strobiliferum* Rchb.f.	Epiphyte	NE	Cruz (2017); Braga

				(2009)
Orchidaceae	*Eurystyles actinosophila* (Barb.Rodr.) Schltr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Eurystyles cotyledon* Wawra	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa ciliata* (Lindl.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa flexuosa* (Lodd.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa glaziovii* Cogn.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa jucunda* (Rchb.f.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa microphyta* (Barb.Rodr.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa recurva* R.Br.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa sarcodes* (Lindl.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Gomesa uniflora* (Booth ex Lindl.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)

Orchidaceae	*Gongora bufonia* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Grandiphyllum auricula* (Vell.) Docha Neto	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Grandiphyllum hians* (Lindl.) Docha Neto	Epiphyte	VU	Cruz (2017); Braga (2009)
Orchidaceae	*Heterotaxis valenzuelana* (A.Rich.) Ojeda & Carnevali	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Huntleya meleagris* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Laelia gloriosa* (Rchb.f.) L.O.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Lankesterella ceracifolia* (Barb.Rodr.) Mansf.	Epiphyte	LC	Cruz (2017); Cruz & Correa 107
Orchidaceae	*Lockhartia lunifera* (Lindl.) Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Masdevallia infracta* Lindl.	Epiphyte	NE	Cruz (2017); Cruz & Nunes-Freitas 54
Orchidaceae	*Maxillaria bradei* Schltr. ex Hoehne	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria brasiliensis* Brieger & Illg	Epiphyte	NE	Cruz (2017); Braga

				(2009)
Orchidaceae	*Maxillaria imbricata* Barb.Rodr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria marginata* (Lindl.) Fenzl	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria parviflora* (Poepp. & Endl.) Garay	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria phoenicanthera* (Barb.Rodr.)	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria picta* (Hook.) R.B.Singer et al.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria robusta* Barb.Rodr.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillaria rodriguesii* Cogn.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Maxillariella robusta* (Barb.Rodr.) M.A.Blanco & Carnevali	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Miltonia candida* Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Miltonia flavescens* (Lindl.) Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)

Orchidaceae	*Miltonia regnellii* Rchb.f.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Miltonia russelliana* (Lindl.) Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Miltonia spectabilis* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Mormolyca rufescens* (Lindl.) M.A.Blanco	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Myoxanthus exasperatus* (Lindl.) Luer	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Myoxanthus punctatus* (Barb.Rodr.) Luer	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Notylia lyrata* S.Moore	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria alexandri* Schltr.	Epiphyte	EN	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria crassifolia* Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria decumbens* Cogn.	Epiphyte	DD	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria gracilis* Lodd. ex Lindl.	Epiphyte	NE	Cruz (2017); Braga

				(2009)
Orchidaceae	*Octomeria grandiflora* Lindl.	Epiphyte	NE	RBR 42720
Orchidaceae	*Octomeria juncifolia* Barb.Rodr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria rotundiglossa* Hoehne	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Octomeria tricolor* Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Ornithidium rigidum* (Barb.Rodr.) M.A.Blanco & Ojeda	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Ornithocephalus myrticola* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Pabstiella colorata* (Pabst) Luer & Toscano	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Pabstiella ephemera* (Lindl.) Luer	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Pabstiella fusca* (Lindl.) Chiron & Xim.Bols.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Phymatidium falcifolium* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Polystachya caespitosa* Barb.Rodr.	Epiphyte	NE	Cruz (2017); Braga

				(2009)
Orchidaceae	*Polystachya concreta* (Jacq.) Garay & Sweet	Epiphyte	NE	Cruz & Correa 112
Orchidaceae	*Polystachya estrellensis* Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Promenaea guttata* (Rchb.f.) Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Promenaea stapelioides* (Link & Otto) Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Promenaea xanthina* (Lindl.) Lindl.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Prosthechea bulbosa* (Vell.) W.E.Higgins	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Prosthechea fragrans* (Sw.) W.E.Higgins	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Prosthechea pachysepala* (Klotzsch) Chiron & V.P.Castro	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Prosthechea pygmaea* (Hook.) W.E.Higgins	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Prosthechea vespa* (Vell.) W.E.Higgins	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Rauhiella silvana* Toscano	Epiphyte	EN	Cruz (2017); Braga

				(2009)
Orchidaceae	*Rhetinantha notylioglossa* (Rchb.f.) M.A.Blanco	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Rodriguezia bracteata* (Vell.) Hoehne	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Scaphyglottis modesta* (Rchb.f.) Schltr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Specklinia grobyi* (Batem. ex Lindl.) F.Barros	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Stelis palmeiraensis* Barb.Rodr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Stelis papaquerensis* Rchb.f.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Stelis triangularis* Barb.Rodr.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Trichocentrum fuscum* Lindl.	Epiphyte	LC	Cruz (2017); Braga (2009)
Orchidaceae	*Trichocentrum pumilum* (Lindl.) M.W.Chase & N.H.Williams	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Vanilla bahiana* Hoehne	Hemiepiphyte	NE	Cruz (2017); Braga (2009)

Orchidaceae	*Vanilla chamissonis* Klotzsch	Hemiepiphyte	LC	RBR 42694
Orchidaceae	*Warczewiczella wailesiana* (Lindl.) Rchb.f. ex E.Morren	Epiphyte	DD	Cruz (2017); Braga (2009)
Orchidaceae	*Xylobium variegatum* (Ruiz & Pav.) Garay & Dunst.	Epiphyte	NE	Cruz (2017); Braga (2009)
Orchidaceae	*Zootrophion atropurpureum* (Lindl.) Luer	Epiphyte	NT	Cruz (2017); Braga (2009)
Orchidaceae	*Zygostates grandiflora* (Lindl.) Mansf.	Epiphyte	NE	Cruz (2017); Braga (2009)
Piperaceae	*Peperomia armondii* Yunck.	Epiphyte	NE	RB 523517
Piperaceae	*Peperomia corcovadensis* Gardner	Epiphyte	NE	Cruz (2017); Cruz & Correa 118
Piperaceae	*Peperomia elongata* Kunth	Epiphyte	NE	RB 874453; Cruz & Murakami 38
Piperaceae	*Peperomia nitida* Dahlst.	Epiphyte	LC	RB 523486
Piperaceae	*Peperomia obtusifolia* (L.) A.Dietr.	Epiphyte	NE	RB 274075
Piperaceae	*Peperomia rotundifolia* (L.) Kunth	Epiphyte	NE	RB 874397; Cruz et al. 157; Cruz et al. 142.
Piperaceae	*Peperomia rubricaulis* (Nees) A.Dietr.	Epiphyte	NE	Cruz (2017)
Piperaceae	*Peperomia serpens* (Sw.) Loudon	Epiphyte	LC	RB 874396

Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	Epiphyte	NE	RBR 42695; Cruz & Nunes-Freitas 62; Cruz & Correa 87
Polypodiaceae	*Campyloneurum aglaolepis* (Alston) de la Sota	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Campyloneurum angustifolium (Sw.) Fée*	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Campyloneurum atlanticum* R.C. Moran & Labiak	Epiphyte	NE	Cruz & Correa 105
Polypodiaceae	*Campyloneurum lapathifolium* (Poir.) Ching	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	Epiphyte	NE	Cruz & Nunes-Freitas 66
Polypodiaceae	*Campyloneurum rigidum* Sm.	Epiphyte	NE	Cruz et al. 152; Cruz & Correa 84
Polypodiaceae	*Cochlidium serrulatum* (Sw.) L.E.Bishop	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Microgramma crispata* (Fée) R.M.Tryon & A.F.Tryon	Epiphyte	LC	RBR 42708; Cruz & Nunes-Freitas 70; Cruz & Nunes-Freitas 60
Polypodiaceae	*Microgramma geminata* (Schrad.) R.M.Tryon & A.F.Tryon	Epiphyte	NE	RBR 42706
Polypodiaceae	*Microgramma percussa* (Cav.) de la Sota	Epiphyte	NE	Cruz (2017); Bastos & Callado (2009)
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	Epiphyte	NE	Cruz & Correa 132
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	Epiphyte	NE	RBR 42710; Cruz et al. 154; ACR

				Cruz & AF Nunes-Freitas 60
Polypodiaceae	*Microgramma tecta* (Kaulf.)Alston	Hemiepiphyte	NE	Cruz & Correa 83
Polypodiaceae	*Pecluma pectinatiformis* (Lindm.) M.G.Price	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Pecluma recurvata* (Kaulf.) M.G.Price	Epiphyte	NE	RB 579175
Polypodiaceae	*Pecluma sicca* (Lindm.) M.G. Price	Epiphyte	NE	Cruz & Nunes-Freitas 59
Polypodiaceae	*Pecluma singeri* (de la Sota) M.G.Price	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Phlebodium pseudoaureum* J.Sm.	Epiphyte	NE	Cruz & Correa 134
Polypodiaceae	*Pleopeltis astrolepis* (Liebm.) E.Fourn.	Epiphyte	NE	Cruz & Nunes-Freitas 56; Cruz & Correa 101
Polypodiaceae	*Pleopeltis minima* (Bory) J.Prado & R.Y.Hirai	Epiphyte	NE	Cruz & Correa 137
Polypodiaceae	*Pleopeltis pleopeltifolia* (Raddi) Alston	Epiphyte	NE	RBR 42709; Cruz & Nunes-Freitas 61
Polypodiaceae	*Pleopeltis polypodioides* (L.) Andrews & Windham	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota	Epiphyte	NE	Cruz & Nunes-Freitas 125
Polypodiaceae	*Serpocaulon catharinae* (Langsd. & Fisch.) A.R.Sm.	Epiphyte	NE	Bastos & Callado (2009)
Polypodiaceae	*Serpocaulon fraxinifolium* (Jacq.) A.R.Sm.	Epiphyte	NE	Cruz & Nunes-Freitas 123
Polypodiaceae	*Serpocaulon menisciifolium* (Langsd. & Fisch.) A.R.Sm.	Epiphyte	NE	Cruz & Nunes-Freitas 67
Polypodiaceae	*Serpocaulon triseriale* (Sw.) A. R. Sm.	Epiphyte	NE	RBR 42727
Pteridaceae	*Polytaenium cajenense* (Desv.) Benedict	Epiphyte	NE	Bastos & Callado (2009)
Pteridaceae	*Polytaenium lineatum* (Sw.) J.Sm.	Epiphyte	NE	Bastos & Callado (2009)

Pteridaceae	*Vittaria lineata* (L.) Sm.	Epiphyte	NE	Bastos & Callado (2009)

Most recorded species belong to angiosperms, which have nine families and 209 species (82.6%), while ferns and lycophytes are represented by seven families and 44 species (17.4%). The richest families were Orchidaceae (S = 115; 45.5%), Bromeliaceae (S = 49; 19.4%), and Polypodiaceae (S = 27; 10.7%) (Figure 1).

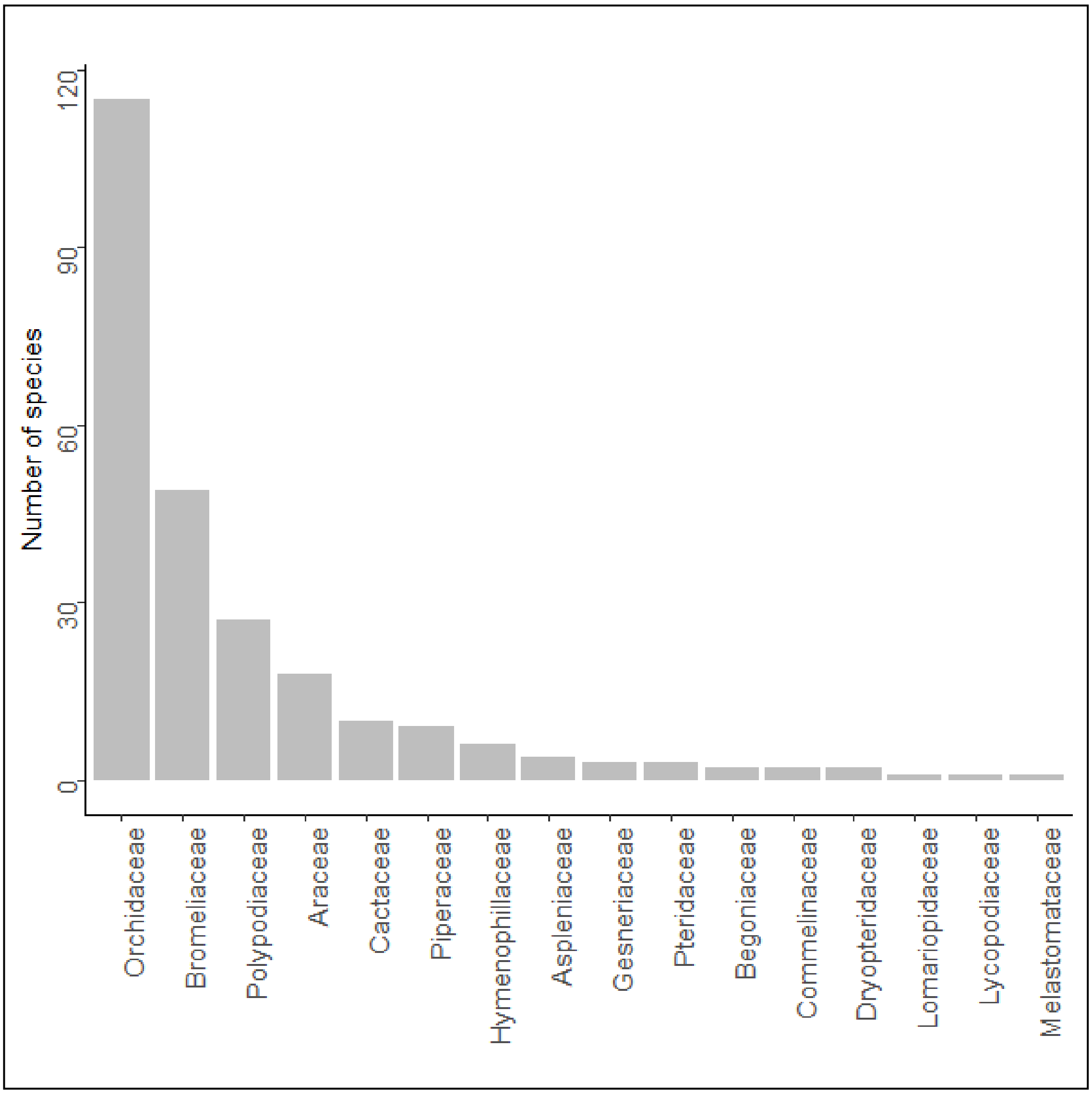

Figure 1 Species richness by families of vascular epiphytes recorded for Ilha Grande, Rio de Janeiro, Brazil.

The sampling of the RAPELD plots showed higher richness of Bromeliaceae (S = 18; 23.7%), Polypodiaceae (S = 15; 19.7%), and Orchidaceae (S = 13; 17.1%) (Figure 2).

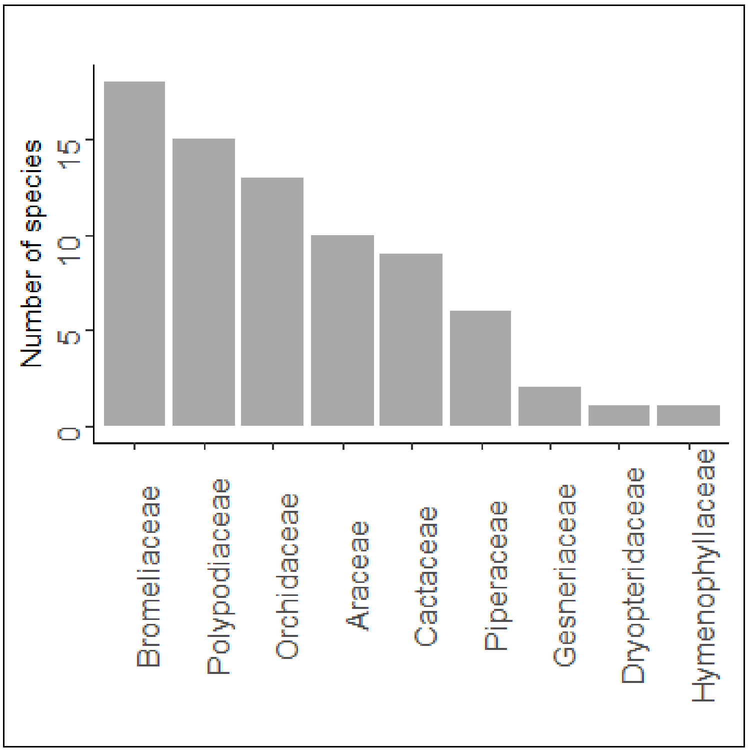

Figure 2 Species richness by families of vascular epiphytes from the RAPELD plots on Ilha Grande, Rio de Janeiro, Brazil.

Ilha Grande has 799 species of vascular plants, according to the Ilha Grande State Park Management Plan, of which 684 are angiosperms and 115 pteridophytes (INEA - Instituto Estadual do Ambiente, 2011), which makes it possible to calculate an epiphytic index of 31.7%. The state of Rio de Janeiro has 1,269 species of vascular epiphytes, including hemiepiphytes (Flora and Funga do Brasil, 2022). The richness found in this study shows that 20.2% of the total species in the state are on Ilha Grande.

Most of the species surveyed on Ilha Grande were not evaluated regarding the degree of threat of extinction (NE; S = 173; 71.1%) and seven are threatened, two of them vulnerable (VU), four endangered (EN), and one critically endangered (CR). In addition, there are four data deficient (DD).

4. DISCUSSION

The richness of epiphytes on Ilha Grande is quite high when compared to other studies carried out in the Southeast (Fontoura et al., 1997; Mania & Monteiro, 2010; Couto et al., 2017; Dornelas et al., 2017; Furtado & Menini Neto, 2022). The island concentrates on several factors that favor the establishment of a high diversity of epiphytes, such as the good state of conservation of the forests, the high heterogeneity of habitats, humidity, and rainfall, in addition to the high density of trees. The rarefaction curve and the values of expected richness for the study area show that the number of species recorded in the sample is still below the richness that can be found in its forests. It is noticed that the curve continues to grow even after a high number of subplots sampled, this indicates that the sampling of more environments would result in the inclusion of new species in the checklist. This richness may be a reflection of the good state of conservation of its ecosystems. Epiphytes can be used to assess the conservation status of forests (Bonnet and Queiroz, 2006; Dislich and Mantovani, 2016). As they are sensitive and slow-growing plants, the group is one of the most vulnerable in environments, being an adequate indicator of changes in the structure, climate, and health of ecosystems (Zotz, 2016). The vegetation of Ilha Grande presents a low degree of disturbance, with secondary forests in an advanced state of succession covering most of the island (Alho et al., 2002). However, some factors threaten the local biodiversity, mainly those related to illegal occupation, disorderly tourism, and the introduction of exotic and invasive species (Alho et al., 2002; Callado et al., 2009; Martinelli et al., 2018).

The epiphytes are taxonomically very diverse, but a few botanical families concentrate most of the species (Madison, 1977; Benzing, 1990) and, in the Ilha Grande, the community followed this general trend of the group. Most species are angiosperms and the two most representative families on Ilha Grande, Orchidaceae and Bromeliaceae, account for 65% of the total richness. This result corroborates the majority of studies carried out in Brazil and worldwide (Kersten, 2010; Ramos et al., 2019; Zotz et al., 2021). Orchidaceae is the most successful family in the epiphytic habit, with over 70% of its species living above ground (Benzing, 1990). This success is guaranteed through vegetative and reproductive adaptations such as pseudobulb stems and complex aerial root systems (Pridgeon, 1981; Benzing, 1990). In Bromeliaceae, epiphytism is also quite common, with half of its species formed by epiphytes that have adaptations to this way of life (Benzing et al., 1976; Benzing, 2000). They may have leaves arranged in rosettes forming a tank to accumulate water and nutrients (e.g. *Neoregelia*), as well as the ability to absorb them through the trichomes of their leaves (e.g. *Tillandsia*) (Benzing et al., 1976; Benzing, 1990; 2000; Hietz et al., 2022). Bromeliads are more important in the number of species in the Atlantic Forest than anywhere else in the world due to their essentially neotropical distribution (Gentry & Dodson, 1987). Ilha Grande is particularly rich in bromeliads (Nunes-Freitas et al., 2006; Rocha et al., 2022), especially with an epiphytic habit (Cruz et al., 2021).

However, when only species recorded in fieldwork are considered, the pattern of richness distribution per family does not correspond to the main one found in the Atlantic Forest. It is likely that this is related to the fact that the sampled environments correspond to secondary forests in different stages of succession, which affects the richness of particular families (Zotz & Bader, 2008; Kartzinel et al., 2013). According to Araujo & Ramos (2021), taxons rich in epiphytes, such as orchids and bromeliads, are better sampled while other families, such as Cactaceae, Piperaceae, and Araceae, may be undersampled in the environments. This is corroborated in this research since the number of records in herbarium or floristic surveys of species belonging to other families was low when compared to Bromeliaceae and Orchidaceae.

The distribution of abundance of epiphytic individuals in inverted J with few dominant species and many rare species also occurs in other areas of the Atlantic Forest. Similar results were observed in studies carried out in seasonal semideciduous and ombrophilous forests (Dettke et al., 2008; Kersten et al., 2009; Bataghin et al., 2010; Geraldino et al., 2010; Freitas & de Assis, 2013), as well as in the Colombian Amazon (Benavides et al., 2011b). The ten most abundant species on Ilha Grande were: *Philodendron cordatum*, *Pleopeltis pleopeltifolia*, *Aechmea gracilis*, *Monstera adansonii*, *Microgramma vacciniifolia*, *Neoregelia johannis*, *Rhipsallis clavata*, *Anthurium urvileanum*, *Epidendrum filicaule*, and *Peperomia elongata*. Bataghin et al. (2010) also recorded a high occurrence of *Pleopeltis pleopeltifolia* in São Paulo.

In this study, less than 10% of the species are considered as hemiepiphytes. There is a discussion about the classification of Benzing (1990) for the so-called hemiepiphytes and many researchers defend that these are categorized as hemiepiphytes only when they germinate on trees (Zotz, 2013; Zotz et al., 2021). In this case, those that germinate in the soil and then establish themselves in trees would be classified as nomadic vines and should not be included in epiphytic studies (Moffett, 2000; Sperotto et al., 2020). However, most bibliographies do not provide enough information for this distinction. Furthermore, recent studies show that the ontogeny of many Araceae species considered hemiepiphytes is quite complex and variable, being able to germinate in the soil and climb trees, breaking or not the connections with the soil, but the same species can also germinate in trees, therefore, it is not possible to draw conclusions with specific Observed as epiphyte in the study areas (Bautista-Bello et al., 2021).

For most epiphytes, the conservation status of the species is unknown, since they were not evaluated by the National Center for the Conservation of Flora (2022) in relation to the degree of threat of extinction. Only 23% (58 species) are in a situation of least concern (LC) because they are abundant and widely distributed species (CNC Flora, 2022). Four species are near threatened (NT) because they are likely to be classified in some category of threat in the near future (CNC Flora, 2022). These are the orchids *Brasiliorchis consanguinea*, *Epidendrum hololeucum* and *Zootrophion atropurpureum* and the Cactaceae *Rhipsalis oblonga*. Four species are categorized as data deficient: orchids *Octomeria decumbens* and *Warczewiczella wailesiana*; Piperaceae *Peperomia distachya*; and the bromeliad *Billbergia pyramidalis*. Only the latter was recorded in the fieldwork. These species do not have enough information on distribution and/or population status to classify them in some category of extinction risk (CNC Flora, 2022).

Red lists represent fundamental tools for establishing priorities for species conservation. Of the epiphytes raised for Ilha Grande, seven are found in the Red Book of Flora of Brazil (Martinelli and Moraes, 2013). *Cattleya guttata* and *Grandiphyllum hians* are in a vulnerable situation (VU), as they are at high risk of extinction in nature. Both face problems related to habitat loss and fragmentation, as well as predatory collection pressure due to ornamental value (Martinelli and Moraes, 2013). Endangered species (EN) are those that face a very high risk of extinction in the wild. In the study area they are: *Octomeria alexandri*, *Rauhiella Silvana*, *Neoregelia hoehneana*, and *Wittrockia superba*. In general, these species suffer from the loss and threat of their habitats (Martinelli and Moraes, 2013). *Vriesea rubyae* is critically endangered (CR) and faces an extremely high risk of extinction in the wild. It is threatened by the disorderly tourist growth of the Petrópolis mountains, RJ, and by commercial exploitation for ornamental purposes (Martinelli and Moraes, 2013).

In the Red Book of Endemic Flora of the State of Rio de Janeiro there are three species of epiphytes that occur on Ilha Grande, two orchids and one bromeliad. *Acianthera subrotundifolia* and *Stelis palmeiraensis* (Orchidaceae) are classified as vulnerable (VU). Both are endemic to the state of Rio de Janeiro and, despite being within the state park, it is threatened by habitat loss due to plantations, disorderly tourism, and irregular occupations (Alho et al., 2002; Martinelli et al., 2018). *Acianthera subrotundifolia* occurs exclusively on Ilha Grande and *Stelis palmeiraensis* occurs on Ilha Grande and Macaé de Cima. This last species can be included in categories of greater risk of extinction in a short period of time due to its reduced area of occupation and its particular characteristics (Martinelli et al., 2018). *Vriesea rubyae* (Bromeliaceae) is categorized as endangered (EN), as there are collections only for Petrópolis and Ilha Grande, RJ, and it suffers from loss of habitat quality, tourism, and fire (Martinelli et al., 2018). None of the species included in the red lists were collected in the fieldwork in the RAPELD plots.

5. CONCLUSION

Ilha Grande has one of the highest richness of vascular epiphytes in the state of Rio de Janeiro and the pattern for the most representative families is similar to the general trends for the community in the Atlantic Forest. Some botanical families are well represented in herbaria and publications, such as Orchidaceae and Bromeliaceae, but there are still many knowledge gaps for others, such as Cactaceae, Dryopteridaceae, Gesneriaceae, Hymenophyllaceae, and Polypodiaceae, since they are underrepresented in herbaria collections. We emphasize that most species have not been assessed for risk of extinction, there are four vulnerable species and seven that are threatened. Thus, the island can be considered an important area for the preservation of vascular epiphyte biodiversity in Rio de Janeiro. We point out the need for population studies to be carried out urgently in order to support the elaboration of strategies for the conservation of species.

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Photo board of vascular epiphyte species from Ilha Grande, Rio de Janeiro, Brazil.

Figure 1: Epiphytic Araceae species occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Anthurium intermedium* Kunth; B) Detail of the inflorescence of *Anthurium intermedium* Kunth; C) *Anthurium minarum* Sakur. & Mayo; D) *Anthurium pentaphyllum* (Aubl.) G.Don; E) *Anthurium scandens* (Aubl.) Engl.; F) *Anthurium urvilleanum* Schott; G) Detail of *Anthurium urvilleanum* Schott; H) *Monstera adansonii* Schott; I) *Philodendron cordatum* Kunth ex Schott.

Figure 2: Epiphytic Araceae species occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Philodendron crassinervium* Lindl.; B) Detail of the inflorescence of *Philodendron crassinervium* Lindl.; C) *Philodendron curvilobum* Schott; D) *Philodendron eximium* Schott; E) *Philodendron hastatum* K.Koch & Sello; F) *Philodendron martianum* Engl.; G) *Philodendron ornatum* Schott; H) *Syngonium podophyllum* Schott; I) *Thaumatophyllum bipinnatifidum* (Schott ex Endl.) Sakur., Calazans & Mayo.

Figure 3: Species of epiphytic Aspleniaceae, Begoniaceae, and Bromeliaceae occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Asplenium auriculatum* Sw. (Aspleniaceae); B) *Begonia integerrima* Spreng. (Begoniaceae); C) *Begonia herbacea* Vell. (Begoniaceae); D) *Aechmea gracilis* Lindm. (Bromeliaceae); E) Detail of the inflorescence of *Aechmea gracilis* Lindm. (Bromeliaceae); F) *Aechmea nudicaulis* (L.) Griseb. (Bromeliaceae); G) *Billbergia amoena* (Lodd.) Lindl. (Bromeliaceae); H) *Billbergia pyramidalis* (Sims) Lindl. (Bromeliaceae); I) *Billbergia zebrina* (Herb.) Lindl. (Bromeliaceae).

Figure 4: Epiphytic Bromeliaceae species occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Canistropsis microps* (E. Morren ex Mez) Leme; B) Detail of the inflorescence of *Canistropsis microps* (E. Morren ex Mez) Leme; C) *Neoregelia johannis* (Carrière) L.B.Sm.; D) Detail of the inflorescence of *Neoregelia johannis* (Carrière) L.B.Sm.; E) *Tillandsia dura* Baker; F) *Tillandsia gardneri* Lindl.; G) *Tillandsia geminiflora* Brongn.; H) Detail of the inflorescence of *Tillandsia geminiflora* Brongn.; I) *Tillandsia mallemontii* Glaziou ex Mez.

Figure 5: Epiphytic Bromeliaceae species occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Tillandsia stricta* Sol.; B) *Tillandsia tricholepis* Baker; C) *Tillandsia usneoides* (L.) L.; D) *Vriesea gigantea* Gaudich.; E) *Vriesea lubbersii* (Baker) E. Morren; F) *Vriesea philippocoburgii* Wawra; G) *Vriesea procera* (Mart. ex Schult. & Schult.) f. Wittm.; H) *Vriesea unilateralis* (Baker) Mez; I) Detail of the inflorescence of *Vriesea unilateralis* (Baker) Mez.

Figure 6: Species of epiphytic Cactaceae, Dryopteridaceae, and Gesneriaceae occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Lepismium cruciforme* (Vell.) Miq. (Cactaceae); B) *Rhipsalis clavata* F.A.C.Weber (Cactaceae); C) *Rhipsalis crispata* (Haw.) Pfeiff. (Cactaceae); D) *Rhipsalis elliptica* G.Lindb. ex K.Schum. (Cactaceae); E) *Rhipsalis pachyptera* Pfeiff. (Cactaceae); F) *Rhipsalis teres* (Vell.) Steud. (Cactaceae); G) *Polybotrya semipinnata* Fée (Dryopteridaceae); H) *Codonanthe devosiana* Lem. (Gesneriaceae); I) *Codonanthe gracilis* (Mart.) Hanst. (Gesneriaceae).

Figure 7: Species of epiphytic Hymenophyllaceae, Lomariopsidaceae, Lycopodiaceae, and Orchidaceae occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Vandenboschia radicans* (Sw.) Copel. (Hymenophyllaceae); B) *Lomariopsis marginata* (Schrad.) Kuhn (Lomariopsidaceae); C) *Phlegmariurus mandiocanus* (Raddi) B.Øllg. (Lycopodiaceae); D) *Cattleya forbesii* Lindl. (Orchidaceae); E) *Dichaea cogniauxiana* Schltr. (Orchidaceae); F) *Encyclia patens* Hook. (Orchidaceae); G) *Epidendrum filicaule* Lindl. (Orchidaceae); H) Detail of *Epidendrum filicaule* Lindl. (Orchidaceae); I) *Eurystyles actinosophila* (Barb.Rodr.) Schltr. (Orchidaceae).

Figure 8: Species of epiphytic Orchidaceae, Piperaceae, and Polypodiaceae occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Lankesterella ceracifolia* (Barb.Rodr.) Mansf. (Orchidaceae); B) *Eurystyles cotyledon* Wawra (Orchidaceae); C) *Polystachya concreta* (Jacq.) Garay & Sweet (Orchidaceae); D) *Scaphyglottis modesta* (Rchb.f.) Schltr. (Orchidaceae) E) *Vanilla chamissonis* Klotzsch. (Orchidaceae); F) *Peperomia rotundifolia* (L.) Kunth (Piperaceae); G) *Peperomia urocarpa* Fisch. & C.A.Mey. (Piperaceae); H) *Campyloneurum atlanticum* R.C. Moran & Labiak (Polypodiaceae); I) *Campyloneurum rigidum* Sm. (Polypodiaceae).

Figure 9: Species of epiphytic Polypodiaceae occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Microgramma crispata* (Fée) R.M. Tryon & A.F. Tryon; B) *Microgramma crispata* (Fée) R.M. Tryon & A.F. Tryon, in detail; C) *Microgramma squamulosa* (Kaulf.) de la Sota; D) *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.; E) *Pecluma sicca* (Lindm.) M.G. Price; F) *Phlebodium pseudoaureum* (Cav.) Lellinger; G) *Phlebodium pseudoaureum* (Cav.) Lellinger leaf detail; H) *Pleopeltis astrolepis* (Liebm.) E. Fourn.; I) *Pleopeltis minima* (Bory) J. Prado & R.Y. Hirai.

Figure 10: Epiphytic species occurring in Ilha Grande, municipality of Angra dos Reis, RJ. A) *Pleopeltis pleopeltifolia* (Raddi) Alston (Polypodiaceae); B) *Pleopeltis hirsutissima* (Raddi) de la Sota (Polypodiaceae); C) *Pleopeltis hirsutissima* (Raddi) de la Sota (Polypodiaceae), leaf detail; D) *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (Polypodiaceae); E) *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm. (Polypodiaceae), leaf detail; F) *Serpocaulon menisciifolium* (Langsd. & Fisch.) A.R. Sm. (Polypodiaceae); G) Community of epiphytes with several species in a tree isolated from an avenue in Vila do Abraão; H) Epiphyte community with bromeliad species in an isolated tree in the church square in Vila Dois; I) Vegetation in a secondary forest around a stream near Vila Dois Rios.

CAPÍTULO II

Assembly of the vascular epiphyte community in protected areas of the Atlantic Forest in Southeastern Brazil

ABSTRACT

One of the central issues of community ecology is to understand how spatial heterogeneity influences patterns of biodiversity, but a minimum number ecological research in this regard is published for epiphytic plants. Because of this knowledge gap, the objective of this research was to investigate the role of environmental and tree morphometric factors in the assembly of vascular epiphyte communities in different phytophysiognomies in a multiscale approach and in individual taxonomic groups. For this, five RAPELD plots installed in Atlantic Forest environments in different successional stages located in Ilha Grande, state of Rio de Janeiro, Brazil, were sampled. We recorded 76 species and 1,735 individuals of epiphytes in 75 subplots. Each Atlantic Forest phytophysiognomy had a unique richness, abundance, and composition of epiphytes. The submontane dense ombrophylous forest in an advanced state of regeneration was the one with the highest levels of richness and diversity. On a landscape scale, there was a positive effect of the number of trees and a negative effect of the canopy cover on the richness and abundance of epiphytes. The variables analyzed do not influence epiphyte diversity in most forests at a local scale. The main families of epiphytes are affected in different ways by both environmental conditions and tree morphometry. With our results, we reinforce the importance of a multiscale approach to understanding biodiversity patterns, since we demonstrate that the factors that affect epiphytes on a large scale do not act in the same way on a local scale. In addition, we emphasize the importance of analyzing taxa or groups individually, especially those considered hemiepiphytes that can mask certain ecological patterns due to their particular ecological characteristics.

Keywords: assembly rules, aroids, bromeliads, community ecology, ferns, orchids.

1. INTRODUCTION

Environmental conditions play an important role in the distribution of species (Kraft et al., 2015) and there are two main theories to explain the ecological patterns shaped by the assembly rules of communities: the niche theory (Hutchinson, 1957; Chase & Leibold, 2004) and the neutral theory of biodiversity (Hubbell, 2001). Although their definitions seem to contrast, they are not so obviously opposed because of the great complexity of ecosystems. According to the first, the ecological niche, the multivariate space of abiotic conditions and species resources, is the main force responsible for the distribution of living beings in environments (Hutchinson, 1957; Chase & Leibold, 2004)(Chase and Leibold, 2004; Hutchinson, 1957). Thus, communities are assembled by deterministic models of biotic and abiotic filters related to the ecological niches of the component species (Weiher and Keddy, 2004). In the neutral theory, proposed by Hubbell (2001), the dynamics of assembling populations and communities is mainly based on processes of colonization, dispersion and extinction of species.

In order to describe and understand the structure and patterns observed in communities, it is necessary to keep in mind the ecological mechanisms that act on the species pool on a larger geographic scale. To compose the local community, species from the regional pool are selected through limitations in dispersal, environmental (abiotic) factors, and biotic interactions (Cadotte and Tucker, 2017). Some species in the pool may not reach a certain location by chance or may not fulfill the ecological needs to survive in any of the habitats (Webb et al., 2002). Keddy (1992) and Weiher & Keddy (2004) states that plant communities are the result of such hierarchical abiotic and biotic processes, the first filter being the environmental conditions of different habitats and the second the competitive abilities of that subset of species previously selected by the environment. Götzenberger et al. (2012) state that the assembly of communities is related to any restrictions imposed on species in the regional pool that prevent their co-occurrence in a specific habitat. For this author, assembly rules can be separated into phylogeographic, associated with historical patterns of dispersion and migration, and ecological assembly, corresponding to ecological filters, such as dispersion, biotic and abiotic factors (Götzenberger et al., 2012). The construction and interpretation of scientific models, especially the analytical ones, simplify the reality that they represent (Pickett et al., 2007), and show the relationships of species with their environments, which has much to contribute to the understanding of the rules of assembly of ecological communities.

Epiphytes are mechanically dependent plants that live on trees without parasitizing them and that differ from vines in that they have no connection with the soil (Moffett, 2000; Zotz, 2016; Sperotto et al., 2020). Zotz et al. (2021) lists 31000 species as epiphytes (including true and facultative epiphytes, and hemiepiphytes, those that germinate on trees) in 79 taxonomic families, this corresponds to about 10% of all tracheophytes. Epiphytism appeared several times throughout the evolution of plants and is present in very different taxa, of which the monocots, ferns and lycophytes stand out, which are by far the most important groups as they incorporate most of the species (Taylor et al., 2021; Zotz et al., 2021). The global and regional distribution of epiphytes show particulars when compared to other plant groups, epiphytes are much more likely to suffer from climatic variations because of their high dependence on atmospheric humidity (Gentry & Dodson, 1987; Zotz, 2016; Taylor et al., 2021). Thus, the lowest latitudes tend to concentrate greater richness, however, the distribution in the tropics is also quite uneven and the neotropics encompass the greatest diversity of the main epiphytic groups (Gentry & Dodson, 1987; Nieder et al., 2001; Taylor et al., 2021). Epiphytes represent 39% of Ecuador's flora and more than a quarter of plants in Panama, southern Brazil, Costa Rica, Colombia, and other Latin American countries (Taylor et al., 2021). The Atlantic Forest, a biodiversity hotspot in South America (Mittermeier et al., 2004), is considered one of these centers of richness and endemism and recent works indicate the occurrence of more than 2,000 species in the forests of this phytogeographic domain with more than ten percent of them threatened with extinction (Freitas et al., 2016; Ramos et al., 2019; Ramos et al., 2021). According to Furtado & Menini Neto (2021) the most conserved areas of the Atlantic Forest have greater diversity and the highest values of endemism occur in the Brazilian States of Espírito Santo, Rio de Janeiro, São Paulo, and Paraná.

The local distribution and occurrence of vascular epiphytes are associated with the ecological niche of the species that make up the community (Benzing, 1990; Mendieta-Leiva and Zotz, 2015; Wagner et al., 2015). However, neutral processes of dispersion and colonization cannot be ruled out and contribute to explaining the colonization of certain environments (Janzen et al., 2020; Nieder et al., 2000). The dynamics and patterns of epiphytic communities depend on variation in tree characteristics and in the areas where they are located (Mendieta-Leiva and Zotz, 2015).

There is an influence of the microclimate, especially humidity and temperature, as well as the proximity of the source of propagules, spatial orientation, and nutrient availability (Zotz & Buche 2000, Zotz & Hietz 2001, Zotz & Vollrath 2003, Benavides et al. 2005, Zotz & Schultz 2008, Flores-Palacios & Garcia 2008, Benavides et al. 2011, Kartzinel et al. 2013). Of these, the architecture and age of the host tree have been the best corroborated in the literature (Zotz & Büche, 2000; Nieder et al., 2001; Zotz & Vollrath, 2003; Zotz & Schultz, 2008; Benavides et al., 2011; Sáyago et al., 2013). However, most current ecological studies are focused on just a few taxa, such as bromeliads and orchids, and the pattern for the community as a whole and other epiphytic groups is still unclear (Zotz & Hietz, 2001).

Epiphytes have a high photosynthetic rate (Nadkarni, 1984), leaf litter with a high concentration of nutrients (Nadkarni, 1992; Oliveira, 2000), intercept rainwater and store it along with the forest canopy (Holwerda et al., 2013). In addition, they diversify the micro-habitats and ecological niches along the trunks and in the treetops and provide food resources for the fauna (Zotz, 2016). Some epiphytes, such as tank bromeliads, can work as biodiversity enhancers (Rocha et al., 2000). Due to all these ecological functions in ecosystems, understanding how epiphyte communities are structured and determining which factors are relevant to their richness and abundance becomes of paramount importance to developing strategies that lead to the conservation of the group and associated biodiversity.

Understanding how spatial heterogeneity influences patterns of diversity at different scales is a fundamental question of ecology (Götzenberger et al., 2012; Sutherland et al., 2013), however, most research on epiphyte ecology in Brazil corresponds to floristic surveys (see Kersten, 2010; Ramos et al. 2019), and few address the rules of assembly of epiphytic communities. Research that does this shows that the patterns of local communities are determined by processes based on the ecological niche of the species, such as the structure of the host tree and the microclimate of the environments (Nunes-Freitas & Rocha 2007, Petean et al. 2009, Dislich & Mantovani 2016, Padilha et al. 2017, Zotarelli et al. 2019). Therefore, despite the high diversity in the Brazilian Atlantic Forest, little is known about the dynamics of communities in these forests. The objective of this research is to understand the role of environmental factors and tree morphometric in the assembly of vascular epiphyte communities in different phytophysiognomies in a multiscale approach and in individual taxonomic groups. Studies that do not integrate spatial scales lead to the loss of useful information about important variables in species distribution processes (Talley, 2007). Thus, we test two hypotheses. Firstly, it is hypothesized that the best-preserved forests and the most humid habitats and shaded, with the most suitable substrates available for epiphytes (more trees and larger trees), have greater diversity and composition is differentiated because the taxons respond in different ways to environmental variations, corroborating what was proposed by Benzing (1990) and the ecological niche theory (Hutchinson, 1957; Chase & Leibold, 2004). The second hypothesis is that on a local scale the epiphytes also respond to variations in the available humidity and substrates, but not exactly to the same factors because the forest structures are different. We aim to answer the following questions specifically:

i. How do forest structure, abiotic conditions and tree morphometric affect the richness, abundance and species composition of vascular epiphytes at landscape scale?
ii. How do epiphytic communities in forests with different phytophysiognomies and successional stages of regeneration respond to these same variables at a local scale?
iii. How do these factors effect the diversity of major taxonomic groups of epiphytes?

We predict that differences in environmental conditions and tree structure between forests act as filters directing the assembly of communities and the distribution of vascular epiphytes across the landscape. In this way, the community pattern and the ecological processes that act in its assembly will be distinct and unique in each Atlantic Forest environment and will vary according to the epiphytic taxon and its functional characteristics. Our null hypothesis is that the epiphyte community is randomly distributed across environments and trees regardless of their characteristics.

2. MATERIAL AND METHODS

2.1. Study site

Ilha Grande is located on the coast of the state of Rio de Janeiro, has an area of 65,258 hectares and is part of the municipality of Angra dos Reis (23º09’26,77’’ S e 44º13’53,72’’ O) (Bastos and Callado, 2009) (Figure 1). There are two integral protection conservation units located on the island, they are the Ilha Grande State Park and the Praia do Sul State Biological Reserve and constitute one of the largest preserved areas in southeastern Brazil (Alho et al., 2002). Ilha Grande is one of the coastal massifs of Serra do Mar, with mountainous relief and a maximum altitude of 1,031 m, although most of the territory is below 500 m (Bastos and Callado, 2009). The climate is tropical with an average annual temperature of 23.2ºC, high relative humidity, on average 82%, and annual rainfall of 1,977 mm, with no dry season (Bastos and Callado, 2009). Due to the great variation in relief along the island, some points can receive up to 4,500 mm of rain (Oliveira & Neto, 2000).

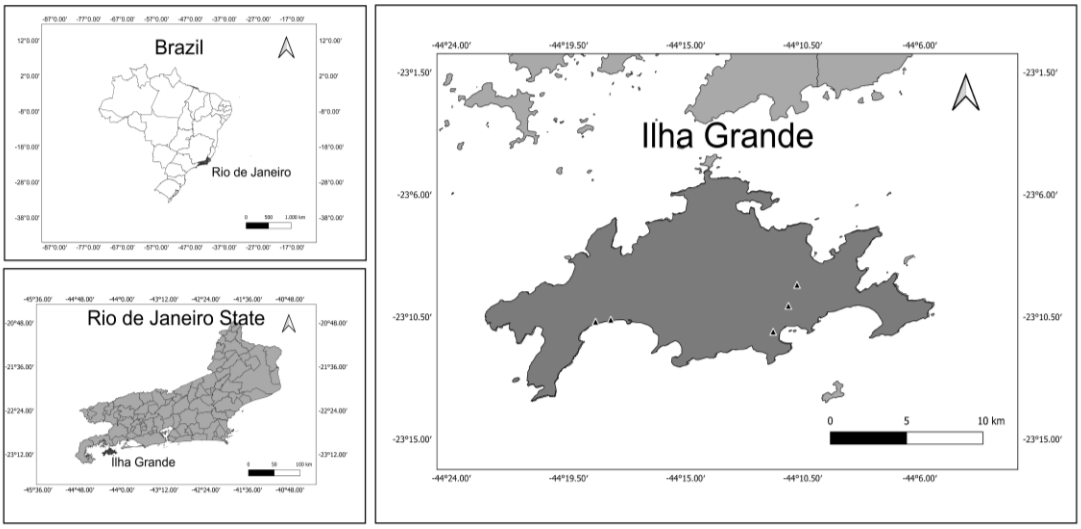


Figure 1 Location of Ilha Grande, municipality of Angra dos Reis, state of Rio de Janeiro, Brazil. Filled triangles correspond to RAPELD plots.

The vegetation of the study area can be classified as belonging to the Atlantic Forest Domain with ombrophilous forests in different successional stages, restinga forests, wetlands and mangroves (Oliveira & Neto, 2000; Oliveira, 2002; Bastos & Callado, 2009;). There is a high richness of plant species (Almeida et al., 1998; Araujo & Oliveira, 1987; Alho et al., 2002; Bastos & Callado, 2009; Nunes-Freitas et al., 2009; Cruz et al., 2021), especially epiphytic (Nunes-Freitas, 2004; Braga, 2011; Cruz & Nunes-Freitas, 2019; Miranda et al., 2020; Cruz et al., 2021; Rocha et al., 2022). In this research, data were collected in RAPELD plots, a method that combines the preparation of rapid inventories (RAP) and long-term ecological projects (PELD) (see Magnusson *et al.* 2005). We analyzed the diversity of epiphyte communities in five different environments: two in restinga forest, one in lowland dense ombrophilous forest, and two in submontane dense ombrophilous forest, following the classification of Veloso *et al.* (1991) e Brazilian Institute of Geography and Statistics (IBGE, 2012). The characteristics of each plot are summarized in figure 1 and table 1.

2.2. Data collection

In the RAPELD plots, subplots of 100 square meters were delimited, interspersed by 10 meters, and all trees with a diameter at breast height greater than or equal to 15 centimeters were sampled (see details about RAPELD methodology at

Magnusson et al., 2005). Fieldwork was carried out between 2018 and 2020. We considered all epiphytic species, including holoepiphytes and hemiepiphytes according to Benzing (1990). The authors are aware that the current recommendation is that primary and secondary hemiepiphytes be classified as hemiepiphytes and nomadic vines, respectively, and that the latter are not included in epiphytic studies (Moffett, 2000; Zotz, 2013; Sperotto et al., 2020; Zotz et al., 2021). However, the distinction between the two groups in nature is not clear and the ontogeny of the species is complex with great variation in germination sites (whether they germinate on the forest soil or on trees) (Bautista-Bello et al., 2021), in addition, current bibliographies do not provide standardized information about the subject. Because of this, we chose to maintain Benzing's classical classification, including as hemiepiphytes those connected to the ground, considering Observed as epiphyte in the study areas and bibliography. To alleviate the problem that could be in the results, we analyzed the data separately: all epiphytes and epiphytes excluding hemiepiphytes.

Sampling protocols for epiphytes suggest that a census of large trees in the forest be carried out and single rope techniques used (Flores-Palacios & García-Franco, 2001; Gradstein et al., 2003). However, as the objective of this research was precisely to analyze the effect of the forest structure on the epiphyte community, we chose to adopt another methodology and, due to the forests being secondary and the occurrence of few emergent trees, the accumulation and rarefaction curves showed up satisfactory (data in the repository). The botanical material was collected with the aid of a telescopic pruning treasure and recorded with a Canon PowerShot SX60 HS camera with superzoom. Identification was based on specific literature, on a study of herborized material, and with the help of specialists. Taxonomic classification and scientific names were verified in Flora and Funga do Brasil (2022). Very young individuals when did not allow accurate identification and clearly accidental epiphytes were not considered in the analyses.

2.3. Data analysis

The variation in diversity was analyzed through species richness and abundance of individuals, as recommended by Hoffmann *et al.* (2019) and Mendieta-Leiva & Zotz (2015), with the aim of providing additional information and support to understand spatio-temporal changes in community structure in future studies. The environmental conditions considered as variables were canopy cover, slope of the area, and tree density, while the morphometric characteristics of the trees were diameter at breast height (DBH), total height, trunk height, depth and crown diameter. The canopy cover was verified using the Canopeo application through the percentage of green cover in the forest canopy (Patrignani and Ochsner, 2015). The means of each sampling unit for the morphometric characteristics of the trees were used, the multicollinearity between the variables was verified, and only those that were not autocorrelated were maintained. The variables were selected according to the relevance that they present in the distribution of plants, especially those that affect luminosity, humidity, and increase in available area for fixation of epiphytes, such as the tree density and their morphometry.

To test hypothesis 1 and answer question (i) of this work, the effect of environmental and morphometric variables of trees on the richness and abundance of epiphytes was verified, considering all sampling units of the five plots together (for landscape scale). To test hypothesis 2 and answer question (ii) we analyzed the sampling units of each plot separately to verify the effect of the variables on the epiphytic community at a local scale (each plot was considered a site). The normality of the data and residuals and the homoscedasticity of the variances were verified using the Shapiro-Wilk test and Levene test, respectively, using the car package (Fox and Weisberg, 2019). Generalized linear (GLM) and mixed (GLMM) models with Poisson Distribution were developed due to the non-normality and homogeneity of the data, even after data transformations, we use packages AID, MASS e lme4 (Asar et al., 2017; Bates et al., 2015; Venables and Ripley, 2002). For the GLMM, the environmental and morphometric conditions of the trees were considered fixed effects and the plots were included as a random effect, in order to assume the spatial dependence and characteristics of each type of vegetation (Bolker et al., 2009). Analysis of variance (ANOVA) was used to test for significant differences between the models, which were compared using the Akaike Information Criterion (AIC), and we selected those models with the best fit with the bbmle package (Bolker and {R Development Core Team}, 2020), including comparisons with null models. The Tukey HSD test was used to verify significant differences in richness and abundance between plots with a multicomp package (Hothorn et al., 2008). Automated Model Selection and Multi-Model Inference with (G)LMs were used with the glmulti package (Burnham and Anderson, 2004; Calcagno and Mazancourt, 2010).

Also to test Hypothesis 1, we verified the variation in composition between the plots through a Principal Coordinate Analysis (PCoA) and Multivariate Homogeneity

Analysis of Group Dispersions - Variances, as well as through similarity index with Bray-Curtis distance (1-dissimilarity). The effect of environmental variables and tree morphometry on the composition was verified with the Canonical Analysis of Principal Coordinates through the function capscale (Anderson and Willis, 2003). We use the variance inflation factor test through the vif.cca function to verify and eliminate the collinearity of the matrix of explanatory variables and select the most suitable model (Gross, 2003). All of these analyses were conducted with the Vegan and BiodiversityR packages (Kindt and Coe, 2005; Oksanen et al., 2020). To verify the effect variables on richness, abundance, and composition on large-scale, data were analyzed with all epiphytes together and later excluding those considered hemiepiphytes, as list shown in Table S7.

In addition, to answer questão (iii) and still testing hypothesis 1, we verify the effects of the environment and trees on the richness and abundance of taxa and epiphyte groups. We separated and evaluated the richest families (Bromeliaceae, Polypodiaceae, Orchidaceae, Araceae and Cactaceae) and we grouped the other species into “other epiphytes” (Gesneriaceae and Piperaceae) and “other ferns” (Dryopteridaceae and Hymenophyllaceae).

All treatments, standardization, and analyses were performed using the program RStudio version 1.3.1093© 2009–2020 (R Core Team, 2020). The graphics were made with the packages ggplot2, RColorBrewer, and ggthemes (Wickham, 2009; Erich, 2014; Arnold, 2021). Each subplot of 100 square meters were considered a sampling unit, as suggested by Mendieta-Leiva & Zotz (2015) for the analyzed scale, and a confidence interval of 95% probability was used in all analyses.

3. RESULTS

3.1. Effect of environmental and tree structure epiphyte diversity in landscape scale

A total of 271 trees were sampled, 71, 60, 42, 44 and 54 in each plot, respectively. We recorded 76 species and 1,735 individuals of epiphytes in 78 subplots. Higher richness and diversity indices were recorded in plot 5, which also recorded the highest abundance of individuals, together with plot 2 (Table 1, Figure 2).

Table 1 Characteristics of the RAPELD plots in Ilha Grande, Rio de Janeiro, Brazil. The vegetation type follows the classification by Veloso et al. (1991) and the Brazilian Institute of Geography and Statistics (IBGE, 2012), the successional stages are in accordance with the National Council for the Environment (BRASIL, 1994), and the other characteristics correspond to the average values of environmental conditions and morphometry of trees with diameter at breast height greater than 15 centimeters (DBH ≥ 15cm). Means of species richness and abundance of individuals followed by the same letter in the columns did not differ by Tukey's test ($p < 0.05$).

Plots and codes	1 – Lowland	2 – Restinga 1	3 – Restinga 2	4 – Submontane 1	5 – Submontane 2
Vegetation	Dense ombrophilous lowland forest	Restinga forest	Restinga forest	Dense ombrophilous submontane forest	Dense ombrophilous submontane forest
Successional stage	Middle	Advanced	Advanced	Middle	Advanced
Number of sample units per plot	10	26	13	13	13
Altitude (m)	10.87 ± 4.49	16.18 ± 3.38	8.08 ± 0.49	142.77 ± 10.98	377.54 ± 13.96
Distance from the ocean (m)	525.62 ± 79.71	119.15 ± 33.47	39.96 ± 9.67	1315 ± 0	1997.3 ± 13.66
Slope (in degrees)	2.48 ± 1.80	3.29 ± 2.62	3.48 ± 2.49	28.46 ± 9.31	27.46 ± 9.34
Canopy cover (in percentage)	57.08 ± 16.33	27.72 ± 11.82	16.53 ± 8.63	33.91 ± 15.32	38.33 ± 16.24
Tree density	3.15 ± 2.38	3.19 ± 2.19	3.31 ± 1.49	3.38 ± 1.33	4.15 ± 1.52

Tree height (m)	15.89 ± 6.47	9.53 ± 1.80	8.05 ± 1.14	20 ± 3.02	24.53 ± 4.93
Tree Diameter at breast height (cm)	29.03 ± 9.50	17.47 ± 2.10	19.05 ± 2.35	22.74 ± 5.15	43.18 ± 10.09
Tree crown diameter (m)	4.74 ± 2.74	4.53 ± 1.28	3.16 ± 1.04	7.18 ± 3.29	7.8 ± 2.13
Mean species richness of epiphytes	4.8 ± 1.81 ab	3.81 ± 2.5 a	6.54 ± 2.03 b	4.77 ± 1.88 ab	9.92 ± 3.95 c
Mean abundance of individuals of epiphytes	19.8 ± 17.37 ab	19.62 ± 16.94 a	34.77 ± 17.20 b	14.08 ± 10.48 a	36.69 ± 17.4 b
Shannon's Diversity Index	1.87	1.96	2.07	2.38	3.54
Simpson's Diversity Index	0.67	0.82	0.83	0.79	0.95

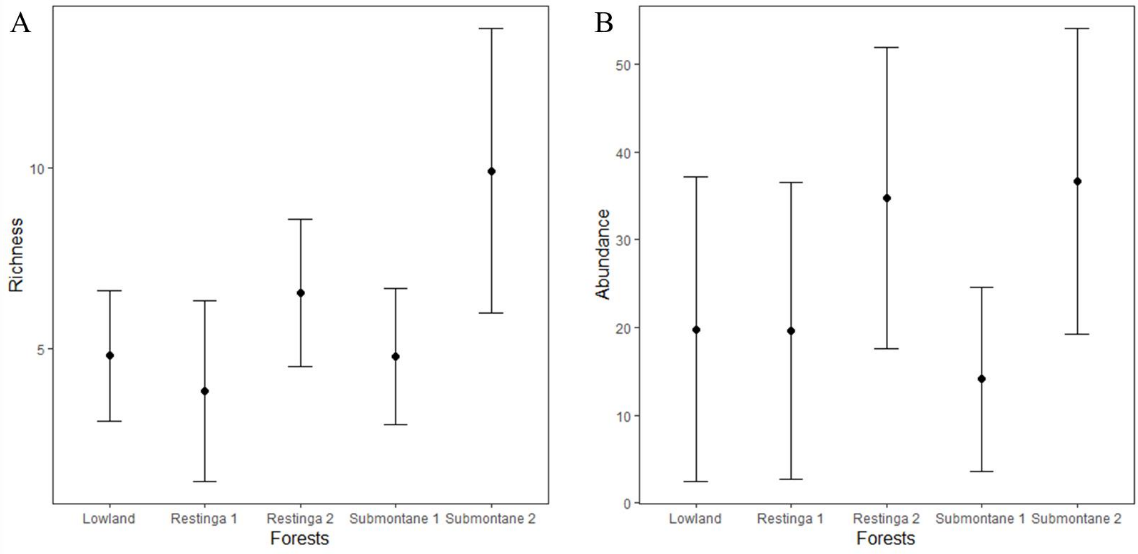


Figure 2 Diversity of vascular epiphytes along plots in different environments of the Brazilian Atlantic Forest. Mean and standard deviation of species richness (a) and abundance of individuals (b).

The GLMM were the best models to explain the effect of the variables on the richness and abundance of epiphytes + hemiepiphytes and on the abundance when only epiphytes. On a large scale, none of the tree morphometric variables had a significant effect on overall epiphyte diversity, however, diameter at breast height had an effect when hemiepiphytes were removed. The environmental conditions of the sampling units were important in both cases. There is a positive effect of the number of trees on species richness and on the abundance of individuals. Canopy cover and abundance of individuals for epiphytes + hemiepiphytes have a negative, albeit weak, relation (see Table S1 and S2, Figures 3 and 4).

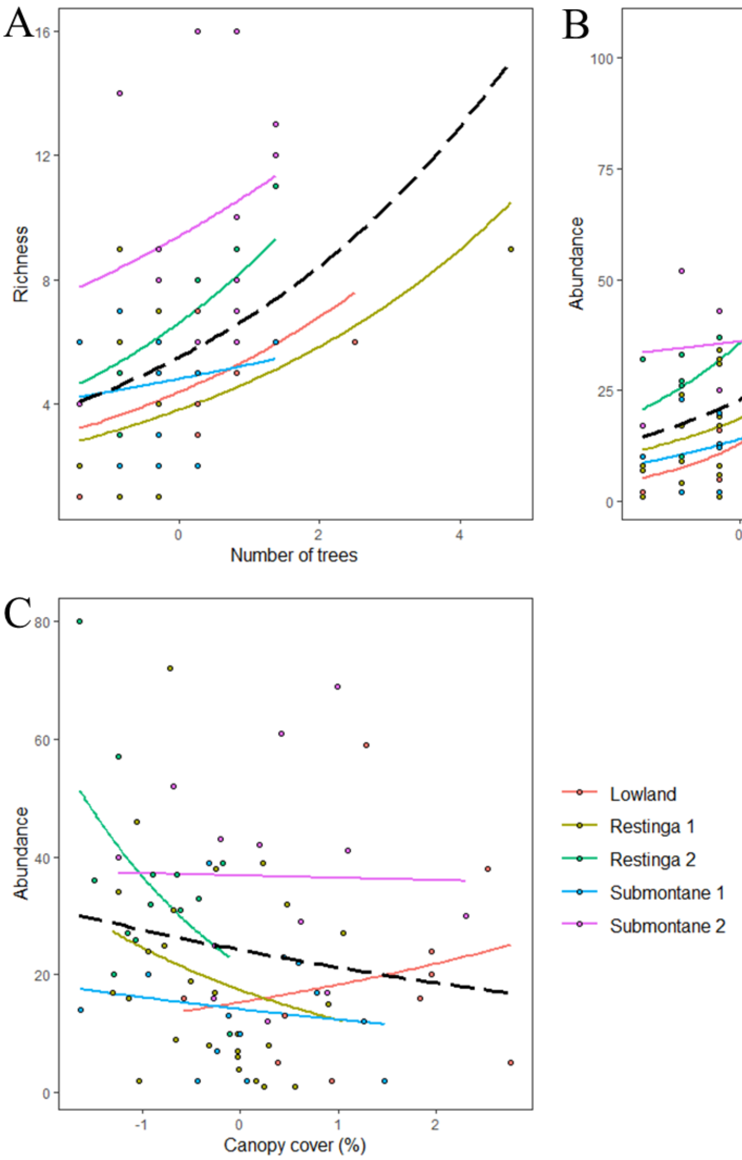


Figure 3 Environmental and structural conditions of the forest that influence the diversity of vascular epiphytes + hemiepiphytes in forests of the Brazilian Atlantic Forest. In (a) the species richness is represented and in (b) the abundance of individuals in relation to the number of trees per sampling unit. In (c) there is a relation between the abundance of individuals and the percentage of canopy cover. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

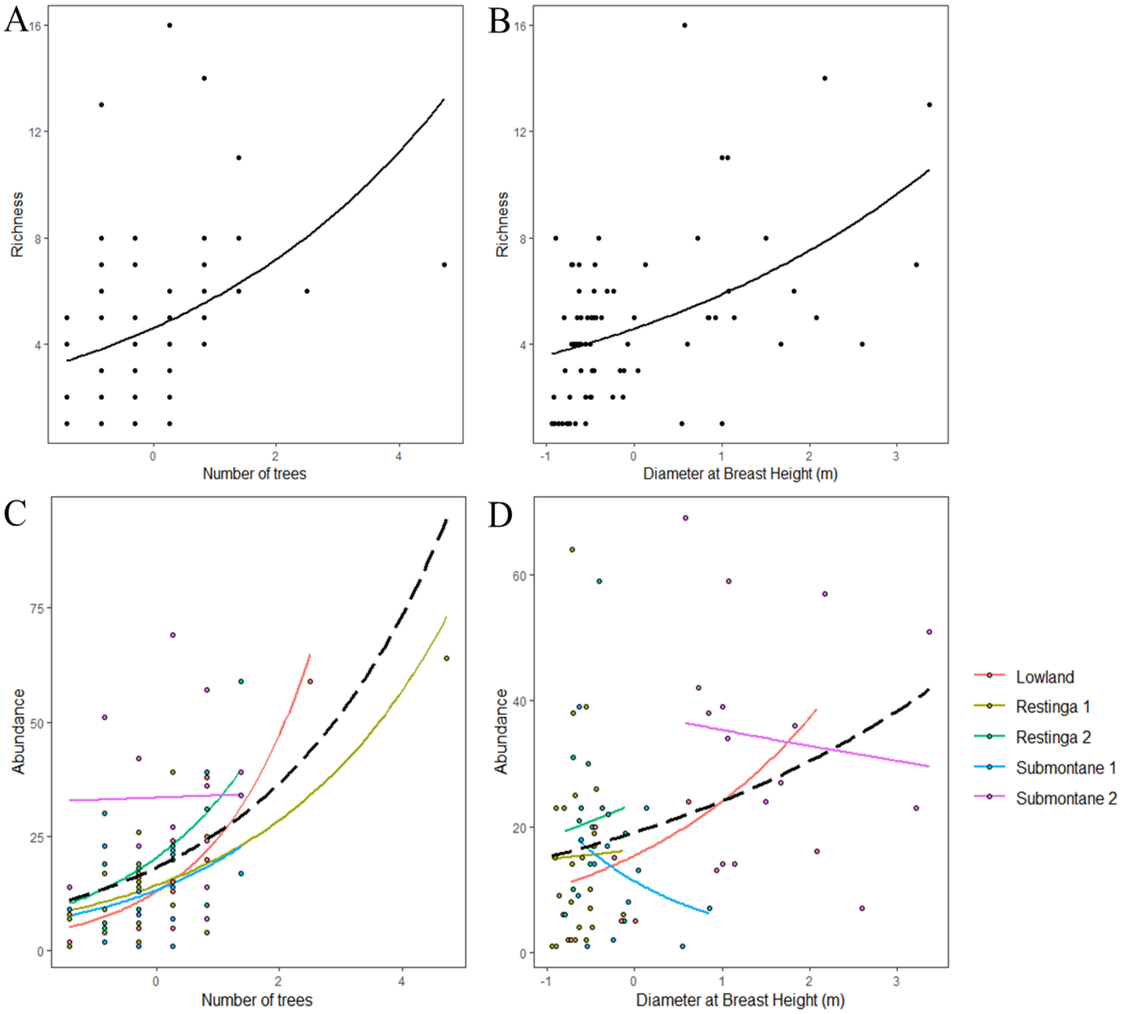


Figure 4 Environmental and structural conditions of the forest that influence the diversity of vascular epiphytes, excluding those considered hemiepiphytes, in forests of the Brazilian Atlantic Forest. In (a) the species richness is represented in relation to the number of trees per sampling unit and in (b) in relation to the diameter at breast height of the trees (DBH, in m). In (c) and (d) the relation between the abundance of individuals with the number of trees per sampling unit and DBH of the trees are represented, respectively. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together. The effects of individual plots are shown just in (c) and (d) because they were important only for the abundance of individuals.

For species composition, the eigenvalues of axes one and two of the PCoA ordination were 19.9% and 17.2%, respectively (Figure 5). Sample units from the same plot are closer and the Multivariate Homogeneity of Groups Dispersions (variances) test indicated that there is a significant difference between the composition of epiphytes in plot 2 in relation to all other plots (F = 6.87, $p < 0.01$, S3). The similarity indices corroborate the PCoA results and indicate that plot 2 has the least similarity with the others. Despite that, the highest similarity value was observed between plots 1 and 2 (Table 2).

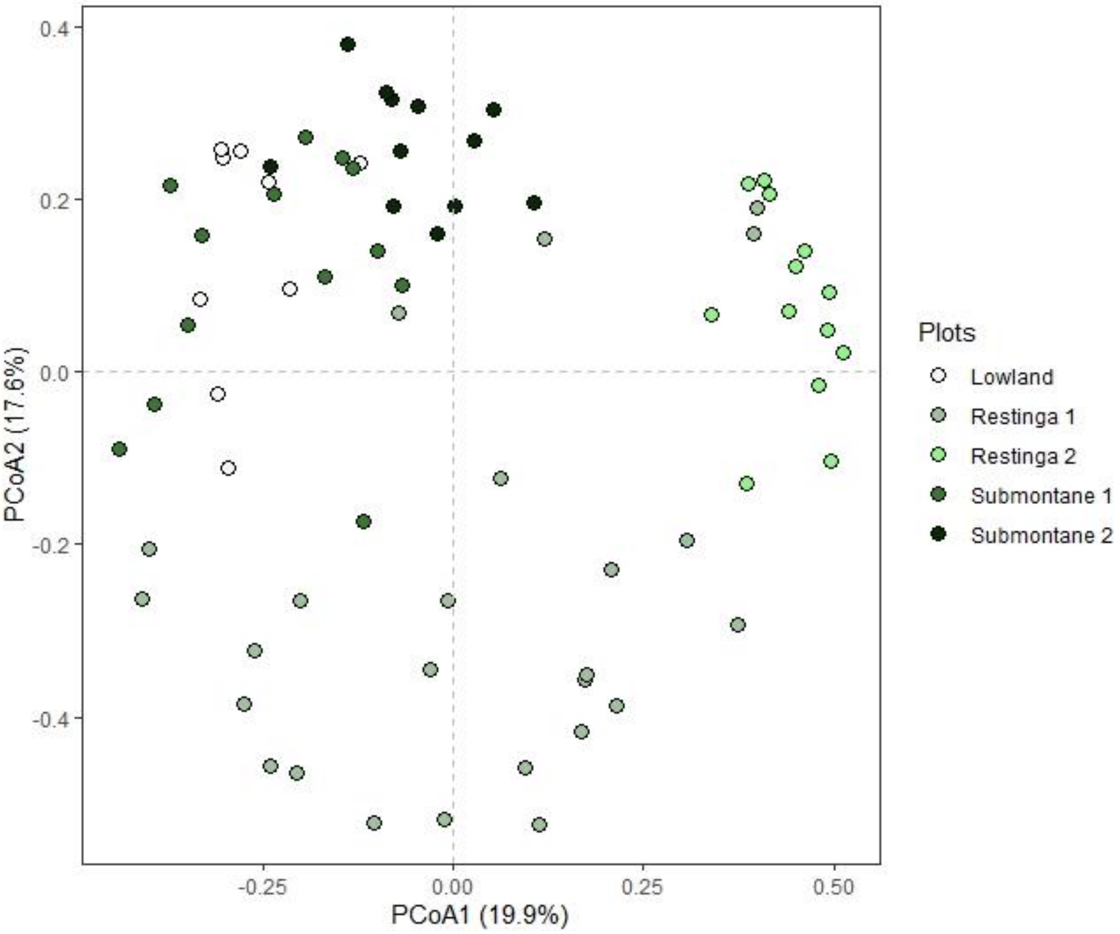


Figure 5 Biplot of Principal Coordinate Analysis for the composition of vascular epiphytes in the Brazilian Atlantic Forest.

Table 2 Paired comparison of the composition of vascular epiphytes in the Brazilian Atlantic Forest through similarity indices with Bray Curtis distance.

	Lowland	**Restinga 1**	**Restinga 2**	**Submontane 1**
Restinga 1	0.04	**-**	-	-
Restinga 2	0.03	0.69	-	-
Submontane 1	0.20	0.15	0.09	-
Submontane 2	0.14	0.07	0.07	0.15

The Canonical Analysis of Principal Coordinates showed that the three environmental variables analyzed, as well as the diameter at breast height and crown diameter, influence the composition of epiphytes at the landscape scale. Both for epiphytes + hemiepiphytes (ANOVA, F = 2.25, p<0.01), as for only epiphytes (F = 1.95, p<0.01). However, only a small variation in the composition can be explained by these factors (14% and 12.4%, respectively) (Table 3).

Table 3 Results of the Canonical Analysis of Principal Coordinates for the composition of vascular epiphytes in the Brazilian Atlantic Forest with distance from Bray Curtis.

Groups	Variables	Degrees of freedom	Sum of squares	F value	p-value
Epiphytes + hemiepiphytes	Canopy cover	1	1.74	2.80	<0.01
	Slope of the area	1	3.19	3.19	<0.01
	Tree density	1	1.38	1.38	0.04
	Diameter at breast height	1	2.19	2.19	<0.01
	Crown diameter	1	1.66	1.66	0.01
Epiphytes (excluding hemiepiphytes)	Canopy cover	1	1.55	2.22	<0.01
	Slope of the area	1	1.91	2.75	<0.01
	Tree density	1	0.91	1.31	0.04
	Diameter at breast height	1	1.42	2.03	<0.01
	Crown diameter	1	1.03	1.47	0.02

3.2 Effect of environment and tree structure on epiphyte diversity at a local scale

Species richness in plot 1 is negatively affected by canopy cover and positively by a number of trees and crown diameter, while abundance is influenced negatively by canopy cover and positively by number of trees (Figure 6 – a to e). The epiphytes present in plot 3 have their abundance affected only by the number of trees (Figure 6 - f). None of the variables analyzed has a significant effect on the other communities (see Tables S1 e S4).

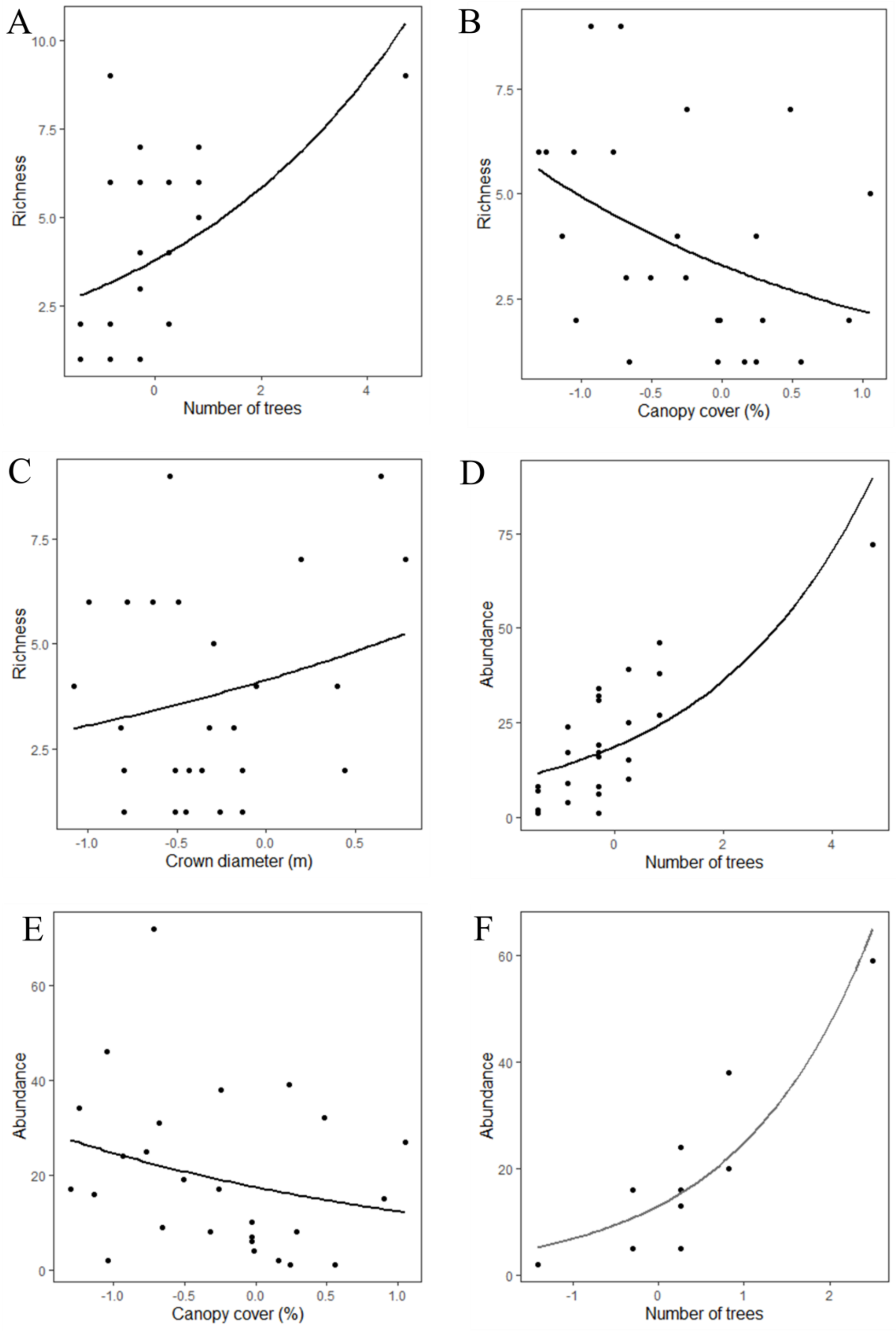

A
Richness
10.0
7.5
5.0
2.5
0
2
4
Number of trees
B
Richness
7.5
5.0
2.5
-1.0
-0.5
0.0
0.5
1.0
Canopy cover (%)
C
Richness
7.5
5.0
2.5
-1.0
-0.5
0.0
0.5
Crown diameter (m)
D
Abundance
75
50
25
0
0
2
4
Number of trees
E
Abundance
60
40
20
0
-1.0
-0.5
0.0
0.5
1.0
Canopy cover (%)
F
Abundance
60
40
20
0
-1
0
1
2
Number of trees

Figura 6 Environmental and structural conditions of the forest that influence the diversity of vascular epiphytes in the Brazilian Atlantic Forest of southeastern. Graphs from (a) to (e) refer to plot 1 located in a restinga forest. The relation between species richness with canopy cover (in percentage), with the number of trees per plot, and with canopy diameter (m) are shown in (a), (b), and (c), respectively. In (d) and (e) the relation between the abundance of individuals with the crown diameter (m) and with canopy cover (in percentage) are presented. Graph (f) refers to plot 3 in a lowland ombrophilous forest and shows the relation between the abundance of individuals and the number of trees per sampling unit.

3.3 Effect of environment and tree structure on different taxonomic groups of epiphytes

The families with the highest number of species in the study area were Bromeliaceae (18), Polypodiaceae (15), Orchidaceae (13), Araceae (10), and Cactaceae (9). The GLM were the best models to explain the effect of variables on the richness of most families, while the GLMM explained abundance. The number of trees influenced the abundance of individuals of all families and groups, however, it only affects the richness of species of Polypodiaceae and orchids. Canopy cover negatively influenced the abundance of Araceae and positively influenced the diversity of “other ferns”. The slope of the terrain had a negative effect on the abundance of Polypodiaceae, but the relationship of this variable was positive on the diversity of “other ferns” and on the richness of orchids. The results are summarized in graphs 7 to 20.

As for the morphometric characteristics of the trees, the height of the trunk positively affected the richness of bromeliads and the abundance of Polypodiaceae, Orchidaceae, and Cactaceae, but there is a negative influence of this variable on the abundance of Araceae and “other epiphytes”. There is a positive relation between crown depth and abundance of Polypodiaceae and Cactaceae, while the relation is negative for orchid richness and abundance of Araceae and “other epiphytes”. The diameter at breast height positively affected the richness of orchids, cacti and "other epiphytes", as well as the abundance of Polypodiaceae, Araceae, and "other epiphytes", but had a negative consequence on the abundance of orchids. The crown diameter positively influences the abundance of Araceae and negatively influences “other epiphytes”. The intensity of the effects of all variables on epiphyte diversity varied greatly (see Tables 4 and S5).

Table 4 Results of Generalized Linear Models (GLM) and Mixed GLM (GLMM) for richness and abundance of the main families and taxonomic groups of vascular epiphytes as a function of environmental conditions and tree morphometry in Brazilian Atlantic Forest forests in Southeastern. Values in bold are significant.

Groups	**Parameter**	**Model type**	**Important variables**	**Estimate**	**z-value**	**p-value**	**Residual deviance**	**Pseudo – R^2 (fixed effects)**	**Pseudo – R^2 (total)**	**Variance (random effects)**	**Deviance (random effects)**
Bromeliaceae	Richness	GLM	Tree density	-0.15	1.57	0.12	59.19	-	-	-	-
			Trunk height	0.22	2.24	**0.03**					
	Abundance	GLMM	Canopy cover	-0.0003	-0.12	0.91	-	0.24	0.63	0.15	780.4
			Slope	0.002	0.301	0.763					
			Tree density	0.30	8.84	<**0.01**					
Polypodiaceae	Richness	GLM	**Depth crown**	0.24	2.06	**0.04**	68.79	-	-	-	-
			Tree density	0.17	2.93	<**0.01**					
	Abundance	GLMM	Canopy cover	0.08	1.18	0.24	-	0.62	0.82	0.207	449.7
			Slope	-0.80	-4.81	<**0.01**					
			Tree density	0.47	13.20	<**0.01**					
			Diameter at breast height	0.23	1.99	**0.04**					
			Trunk height	0.36	3.29	<**0.01**					

			Depth crown	0.28	4.43	**<0.01**					
Orchidaceae	Richness	GLM	**Slope**	0.55	2.65	**<0.01**	48.53	-	-	-	-
			Tree density	0.56	3.62	**<0.01**					
			Diameter at breast height	0.46	2.21	**0.02**					
			Depth crown	-0.68	-2.04	**0.04**					
	Abundance	GLMM	Canopy cover	-0.67	-1.16	0.21	-	0.21	0.72	1.65	261.7
			Slope	-0.19	-0.61	0.54					
			Tree density	0.50	4.90	**<0.01**					
			Diameter at breast height	-0.77	-3.45	**<0.01**					
			Trunk height	0.76	3.84	**<0.01**					
Araceae	Richness	GLMM	Canopy cover	-0.18	-1.41	0.15	-	0.03	0.41	0.35	211.3
	Abundance	GLMM	**Canopy cover**	-0.43	-5.19	**<0.01**	-	0.45	0.84	0.58	482.3
			Slope	0.24	1.67	0.09	-				
			Tree density	0.20	4.33	**<0.01**	-				
			Diameter at breast height	0.37	0.01	**<0.01**	-				
			Trunk height	-0.44	0.02	**<0.01**	-				
			Depth crown	-0.48	-3.42	**<0.01**	-				
			Crown diameter	-0.26	-2.49	**0.01**	-				

Cactaceae	Richness	GLM	**Diameter at breast height**	0.72	5.03	<**0.01**	54.30	-	-	-	-
	Abundance	GLMM	Canopy cover	-0.24	1.27	0.20	-	0.13	0.75	3.54	162.8
			Slope	-0.25	-0.82	0.41					
			Tree density	0.38	2.43	**0.02**					
			Diameter at breast height	-0.44	-1.72	0.09					
			Trunk height	0.94	3.64	<**0.01**					
			Depth crown	0.60	2.45	**0.01**					
			Crown diameter	-0.28	-1.87	0.06					
Other epiphytes	Richness	GLM	**Diameter at breast height**	0.29	2.24	**0.02**	70.48	-	-	-	-
	Abundance	GLMM	Canopy cover	-0.15	-1.38	0.17	-	0.32	0.66	0.50	380.3
			Slope	**0.38**	**2.16**	**0.03**	-				
			Tree density	0.42	7.86	<**0.01**	-				
			Diameter at breast height	0.52	3.45	<**0.01**	-				
			Trunk height	-0.93	-4.57	<**0.01**	-				
			Depth crown	-0.49	-2.83	<**0.01**	-				
			Crown diameter	0.47	3.67	<**0.01**	-				
Other ferns	Richness	GLM	**Canopy cover**	1.33	1.99	**0.05**	10.06				
			Slope	2.38	1.99	**0.05**		-	-	-	-

			Tree density	1.06	1.87	0.06		-	-	-	-
			Diameter at breast height	1.12	1.35	0.18		-	-	-	-
			Trunk height	-2.94	-1.58	0.11		-	-	-	-
			Depth crown	-0.55	-0.90	0.37		-	-	-	-
	Abundance	GLM	**Canopy cover**	1.04	2.19	**0.03**	14.04	-	-	-	-
			Slope	2.39	2.28	**0.02**		-	-	-	-
			Tree density	1.02	2.29	**0.02**		-	-	-	-
			Diameter at breast height	1.24	1.69	0.09		-	-	-	-
			Trunk height	-2.52	-1.66	0.10		-	-	-	-
			Depth crown	0.53	-0.93	0.35		-	-	-	-

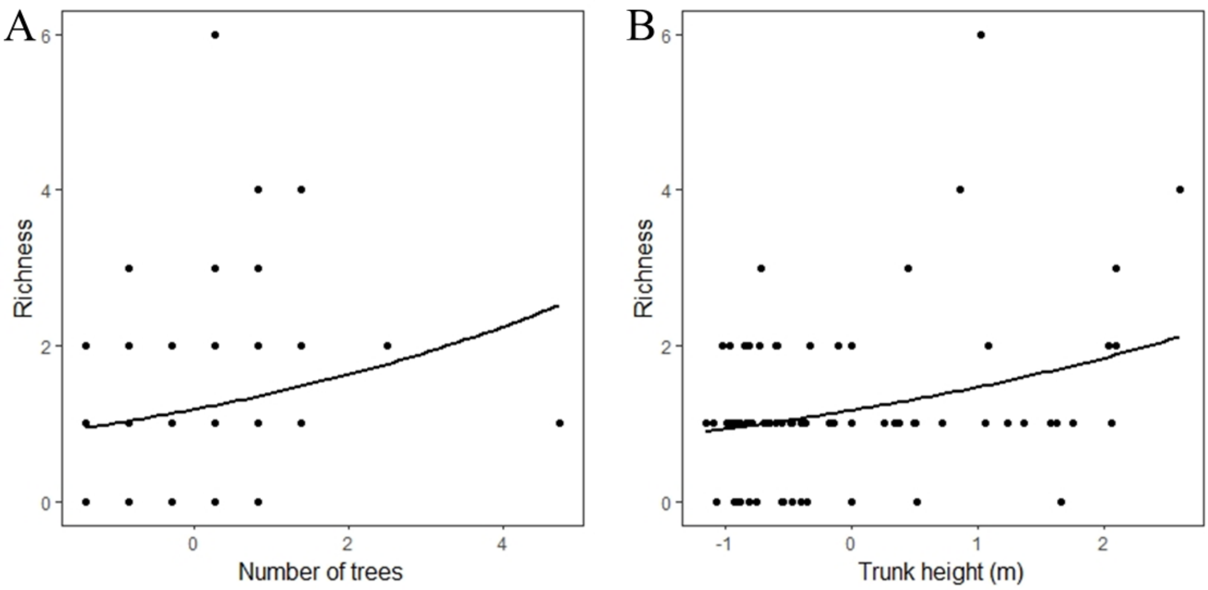


Figure 7 Environmental and structural conditions of the forest that influence the richness of epiphytic bromeliads in the Atlantic Forest of southeastern Brazil. Graph (a) refers to the relation between species richness and number of trees, while graph (b) represents the relation between species richness and trunk height (m).

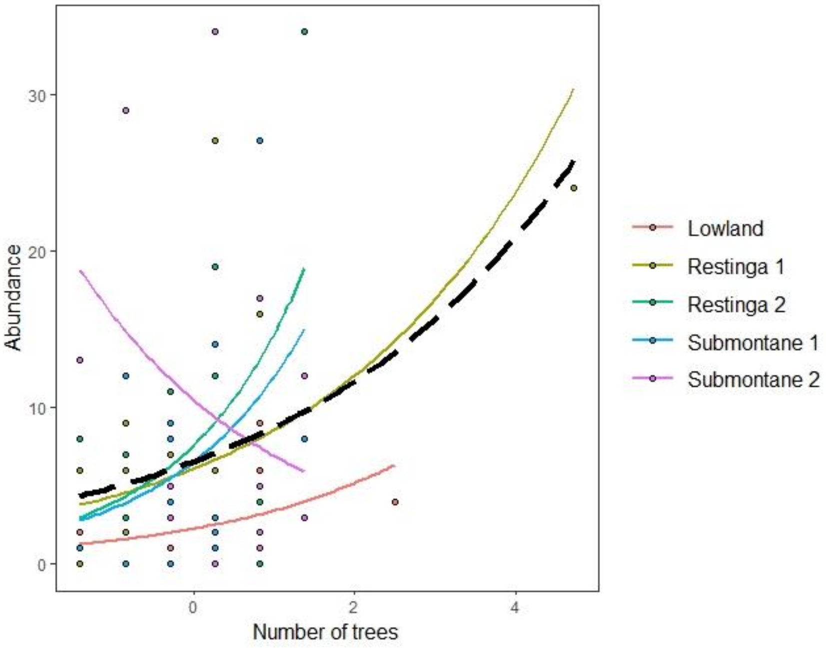


Figure 8 Relation between the abundance of individuals of epiphytic bromeliads and the number of trees in the Atlantic Forest of southeastern Brazil. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

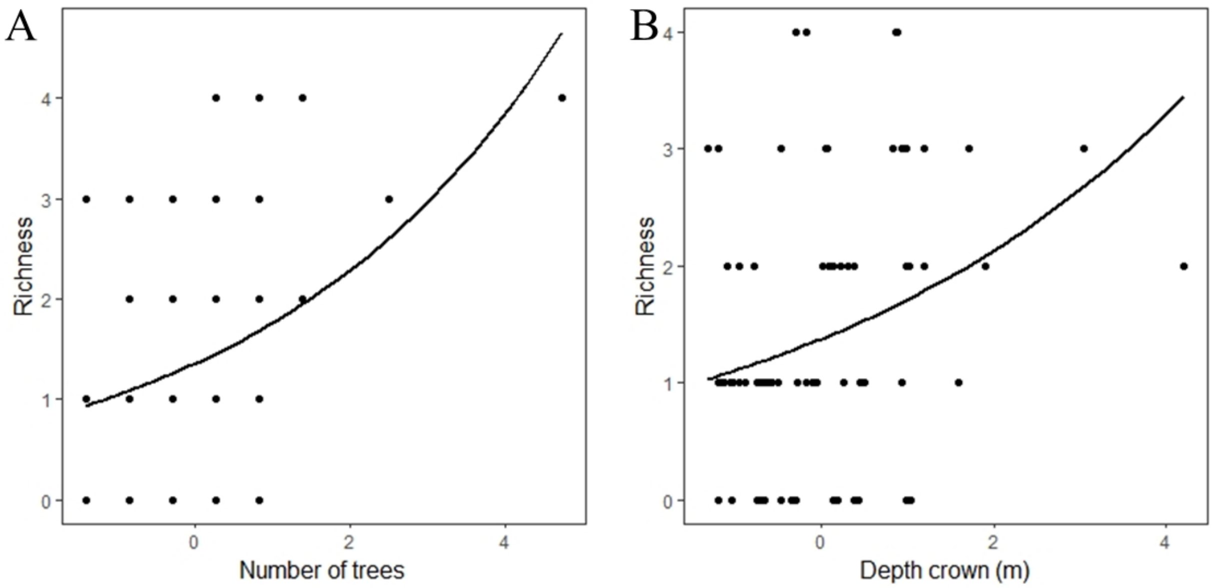
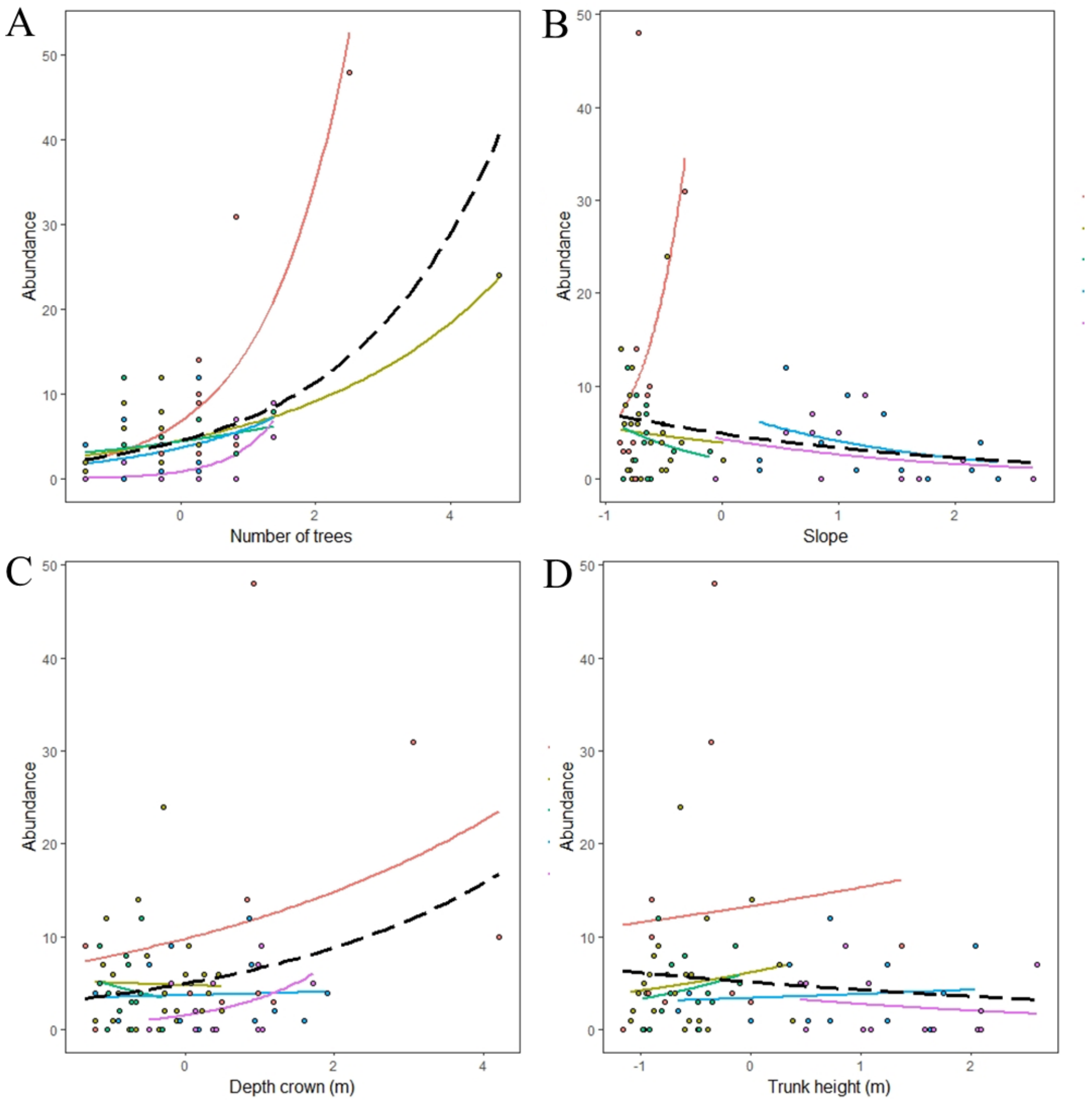


Figure 9 Environmental and structural conditions of the forest that influence the richness of epiphytic Polypodiaceae in the Atlantic Forest of southeastern Brazil. Graph (a) refers to the relation between species richness and number of trees, while graph (b) represents the relation between species richness and tree depth crown (m).


A
Abundance
0
10
20
30
40
50
Number of trees
0
2
4
B
Abundance
0
10
20
30
40
50
Slope
-1
0
1
2
C
Abundance
0
10
20
30
40
50
Depth crown (m)
0
2
4
D
Abundance
0
10
20
30
40
50
Trunk height (m)
-1
0
1
2

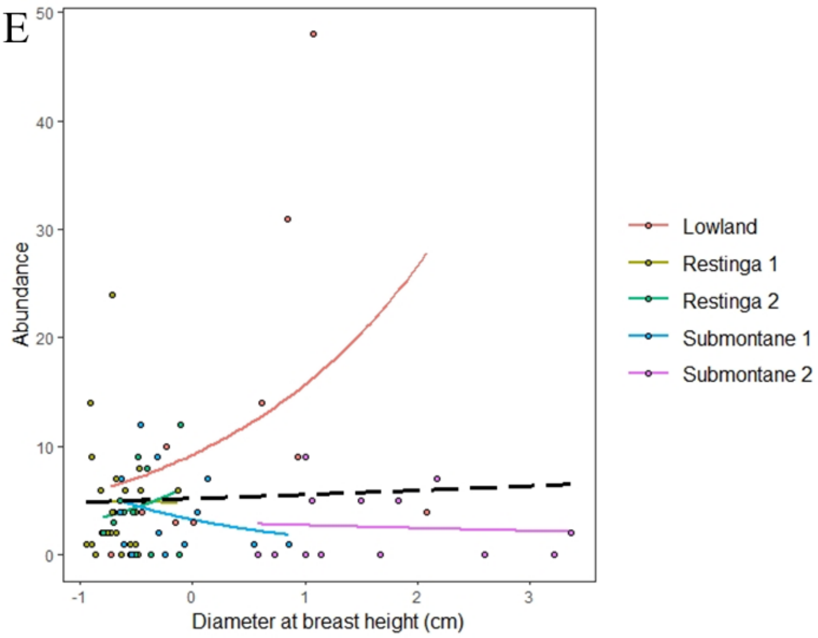


Figure 10 Environmental and structural conditions of the forest that influence the abundance of epiphytic Polypodiaceae in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between the abundance of individuals and the number of trees and the slope of the terrain, respectively. While the graphs from (c) to (e) represent the abundance of individuals and tree crown depth (m), trunk height (m), and diameter at breast height (cm), respectively. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

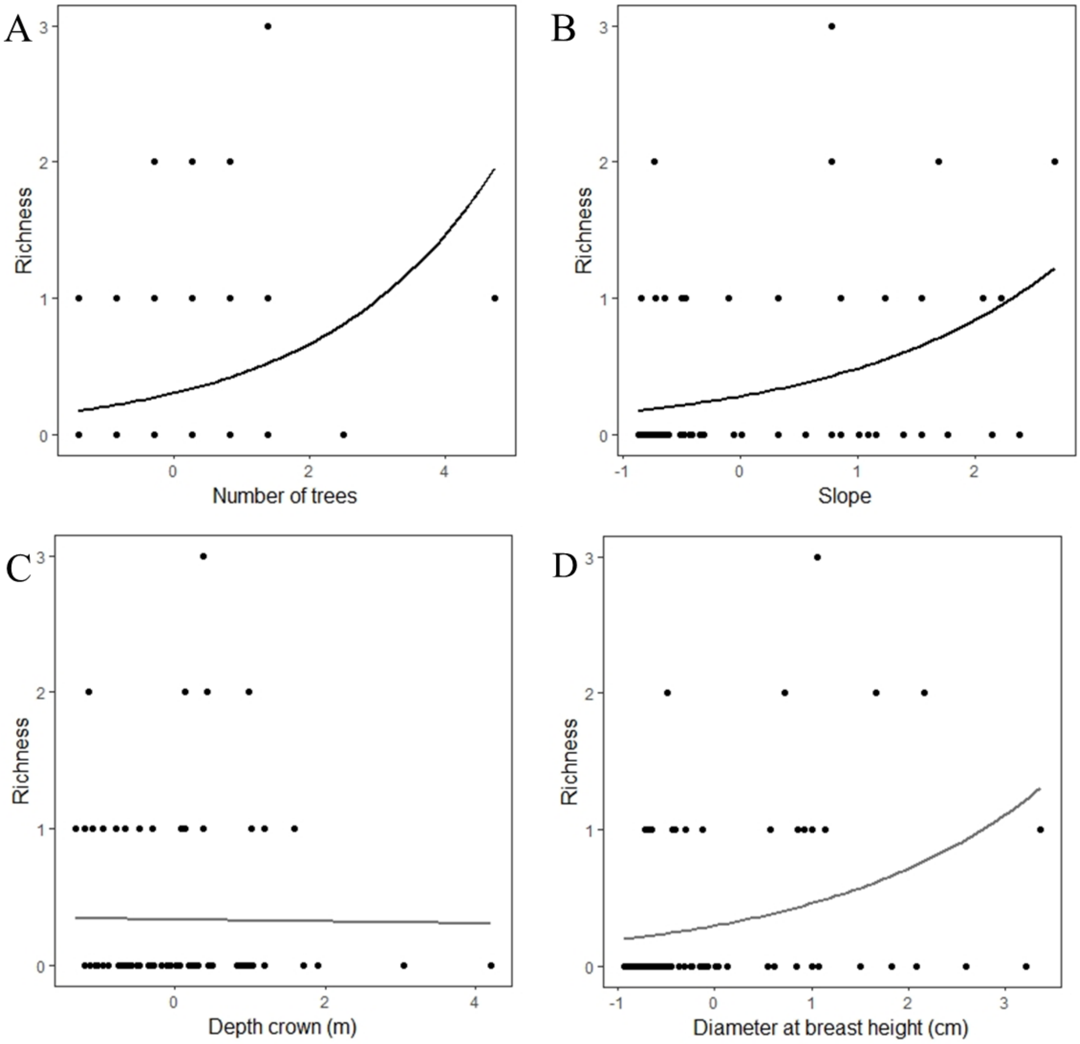


Figure 11 Environmental and structural conditions of the forest that influence the richness of epiphytic orchids in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between species richness and the number of trees and slope, respectively. The graphs of (c) and (d) represent species richness and crown depth (m) and diameter at breast height (cm), respectively.

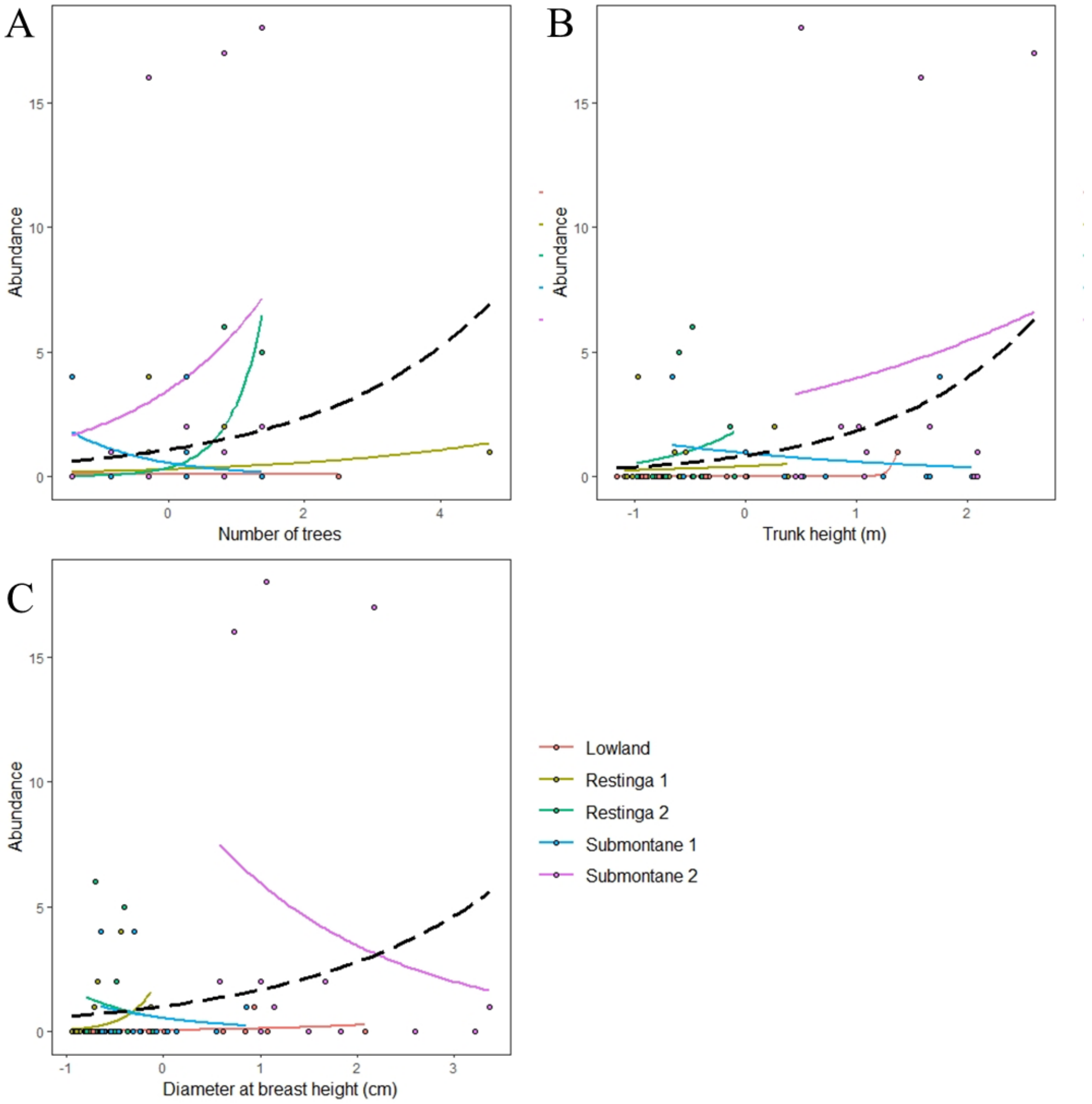


Figure 12 Environmental and structural conditions of the forest that influence the abundance of epiphytic orchids in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between species richness and the number of trees and trunk height (m) respectively. The graphs of (c) represent abundance and diameter at breast height (cm). The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

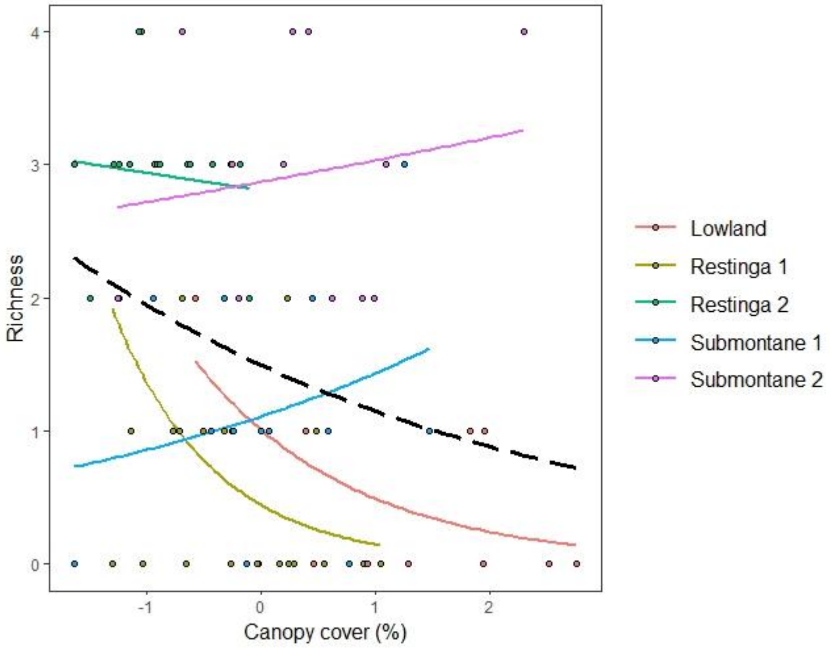
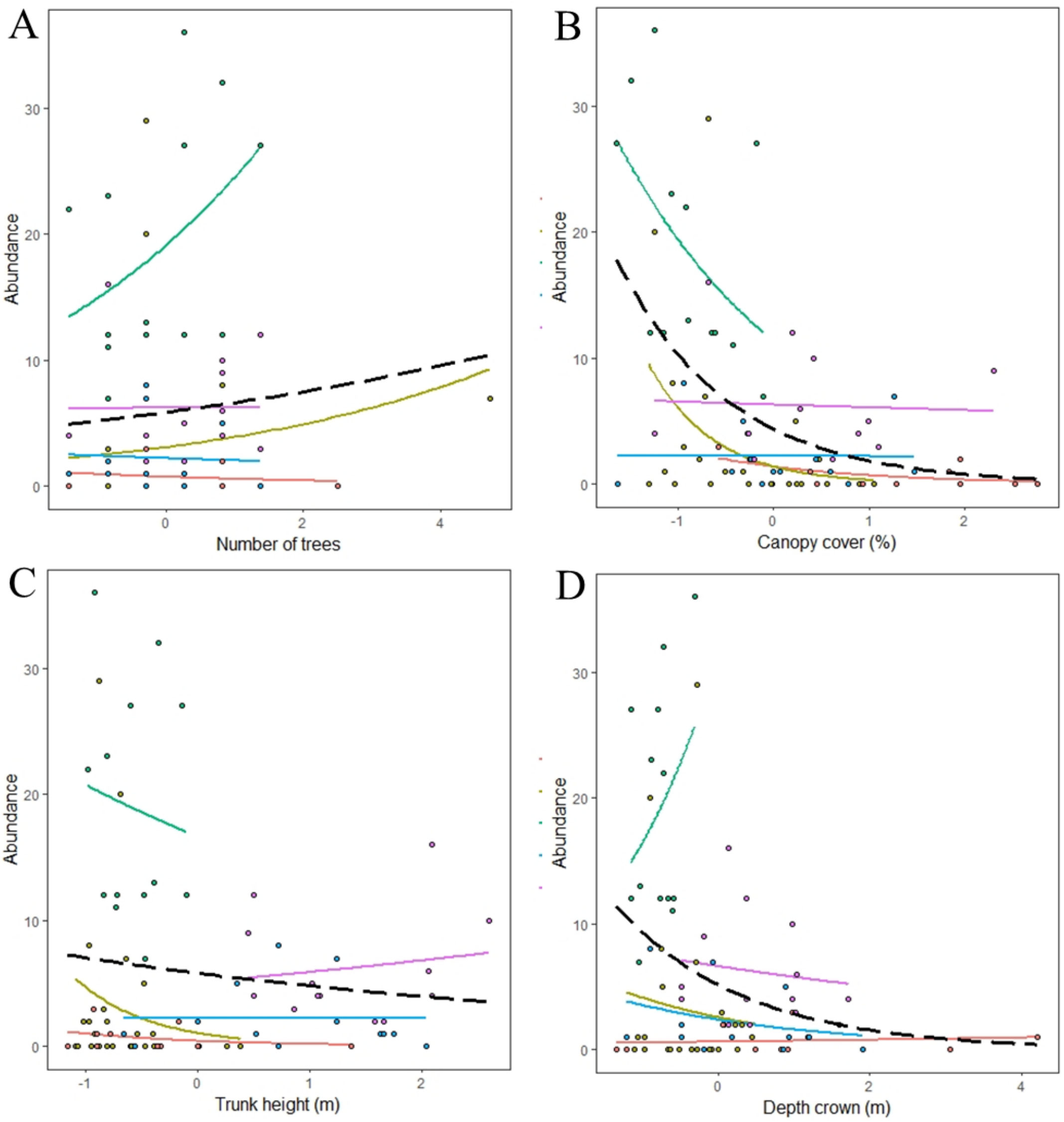


Figure 13 Relation between the richness of species of epiphytic Araceae and the number of trees in the Atlantic Forest of southeastern Brazil. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.


A
Abundance
0
10
20
30
0
2
4
Number of trees
B
Abundance
0
10
20
30
-1
0
1
2
Canopy cover (%)
C
Abundance
0
10
20
30
-1
0
1
2
Trunk height (m)
D
Abundance
0
10
20
30
0
2
4
Depth crown (m)

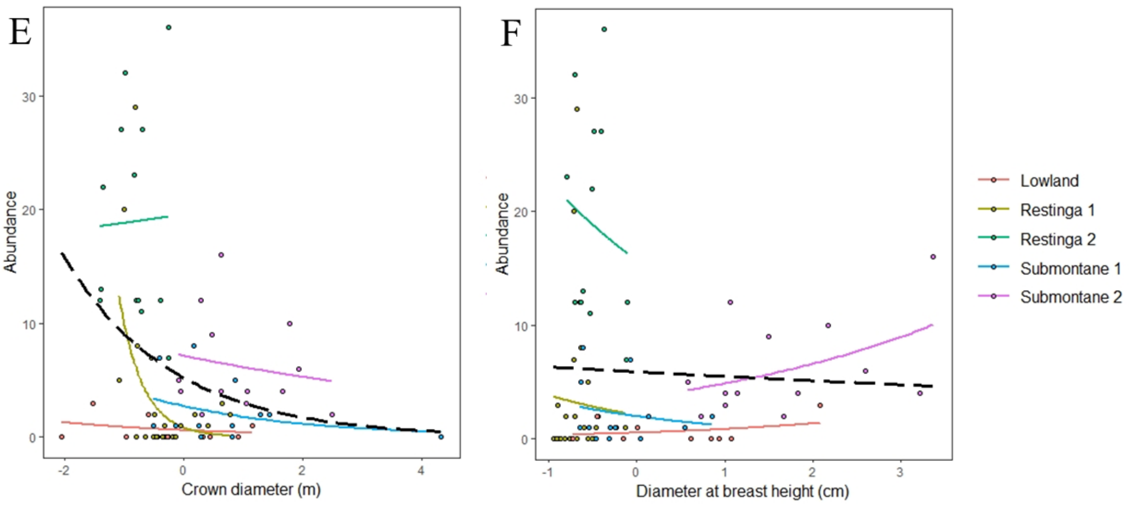


Figure 14 Environmental and structural conditions of the forest that influence the abundance of epiphytic Araceae in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between abundance and the number of trees and canopy cover, respectively. The graphs of (c) to (f) represent abundance and trunk height (m), depth crown (m), diameter crown (m), and diameter at breast height (cm), respectively. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

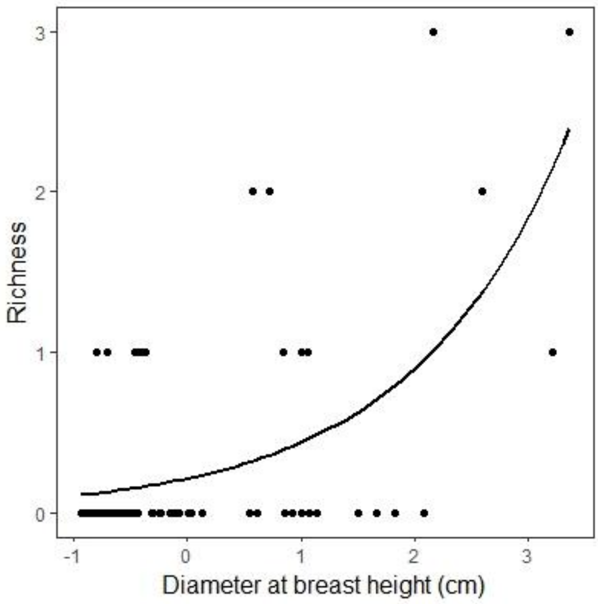


Figure 15 Relation between the richness of species of epiphytic Cactaceae and the diameter at breast height (cm) of trees in the Atlantic Forest of southeastern Brazil.

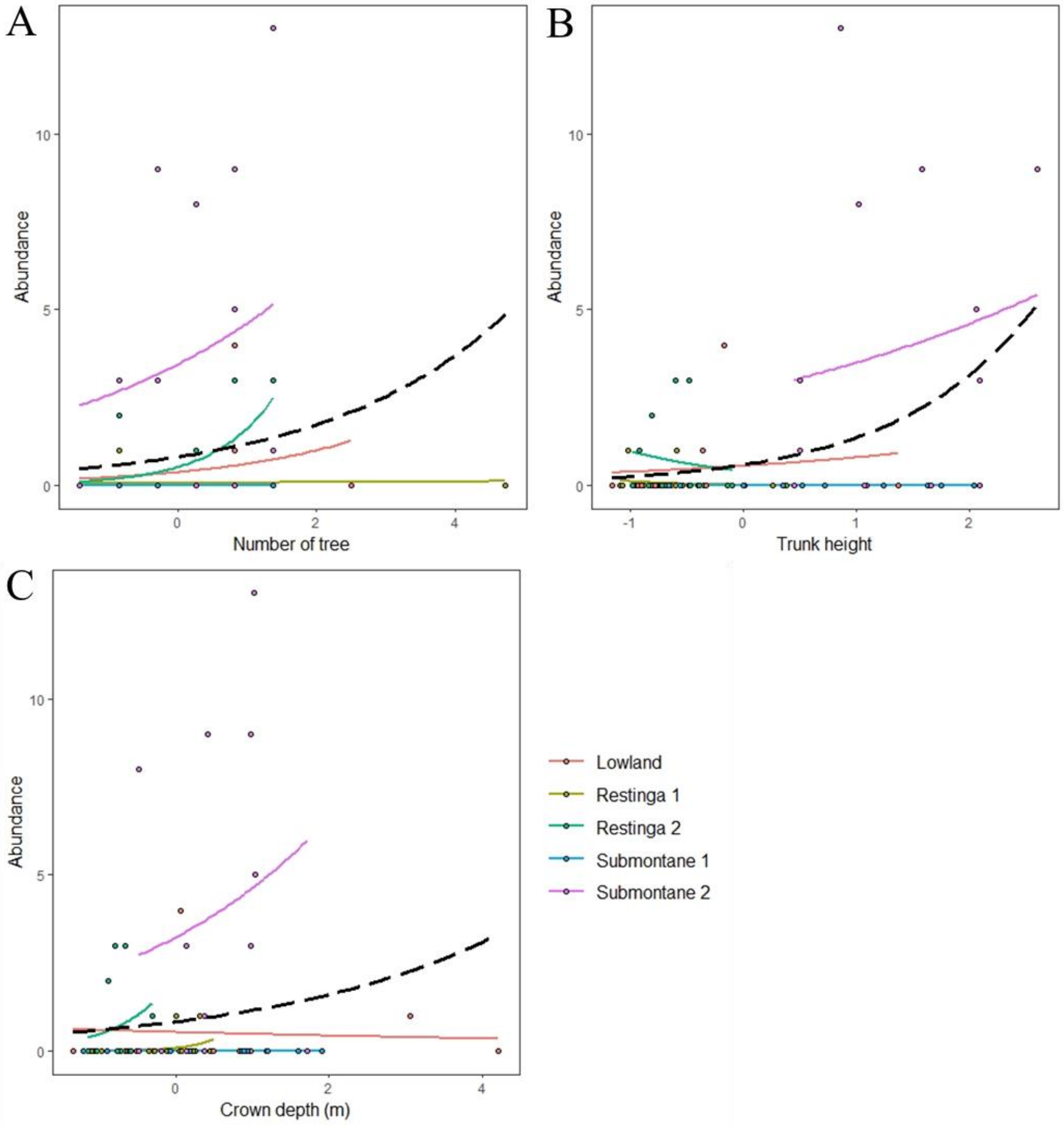


Figure 16 Environmental and structural conditions of the forest that influence the abundance of epiphytic Cactaceae in the Atlantic Forest of southeastern Brazil. Graphs (a), (b) and (c) refer to the relation between abundance and the number of trees, trunk height (m), and crown depth (m), respectively. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

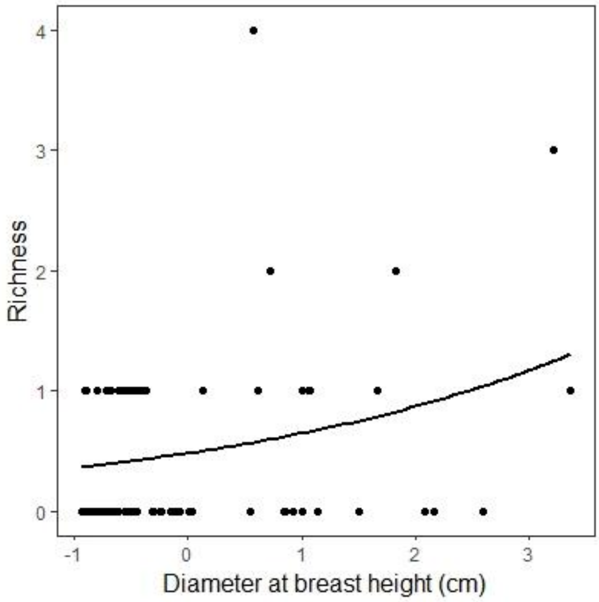
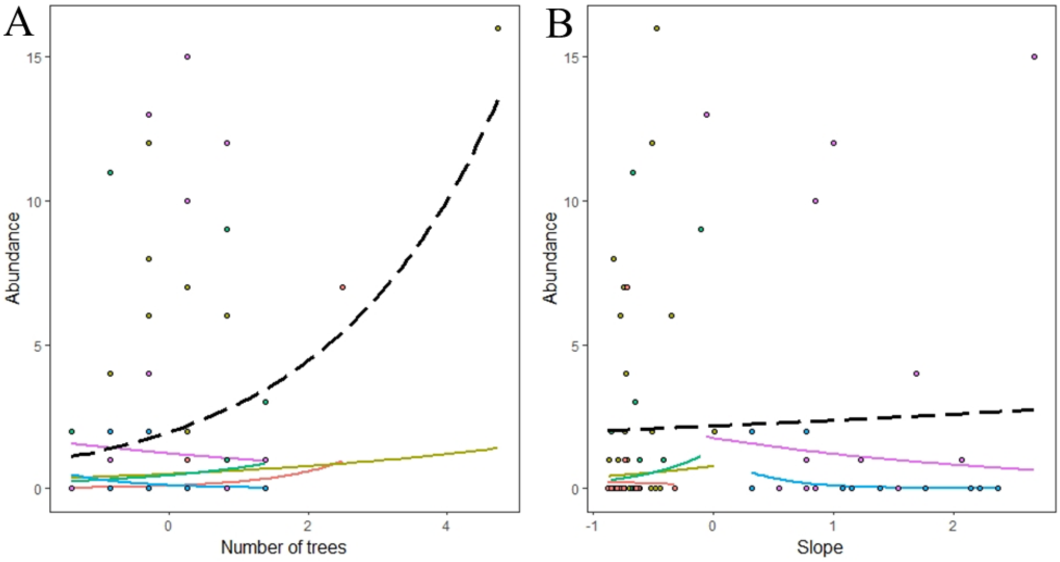


Figure 17 Relation between the richness of species of epiphytic Gesneriaceae and Piperaceae and the diameter at breast height (cm) of trees in the Atlantic Forest of southeastern Brazil.



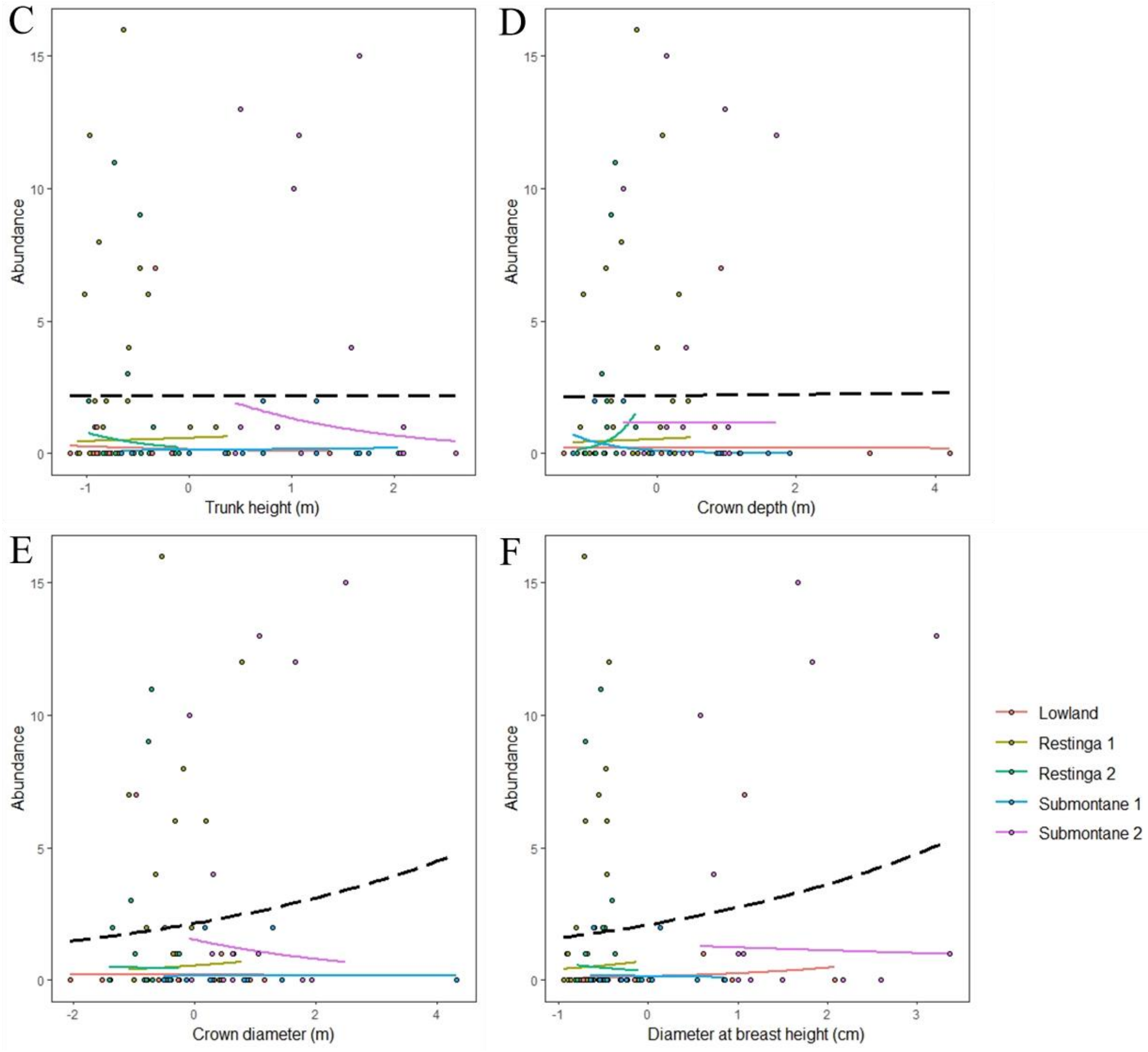


Figure 18 Environmental and structural conditions of the forest that influence the abundance of epiphytic Gesneriaceae and Piperaceae in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between abundance and the number of trees, and slope. Graphs (c) to (f) refer to the relation between abundance and trunk height (m), crown depth (m), crown diameter (m), and diameter at breast height (cm), respectively. The colored dashes correspond to the effect on the epiphytes of each plot separately and the black dashes line is the effect on the epiphytes of all plots together.

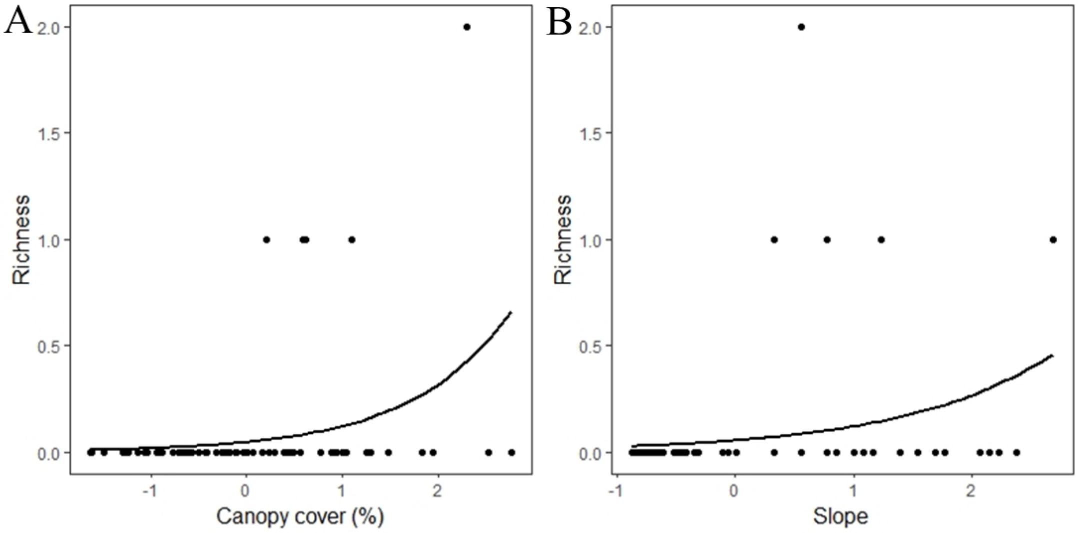


Figure 19 Environmental and structural conditions of the forest that influence the richness of epiphytic Dryopteridaceae and Hymenophyllaceae in the Atlantic Forest of southeastern Brazil. Graphs (a) and (b) refer to the relation between species richness and canopy cover and slope, respectively.

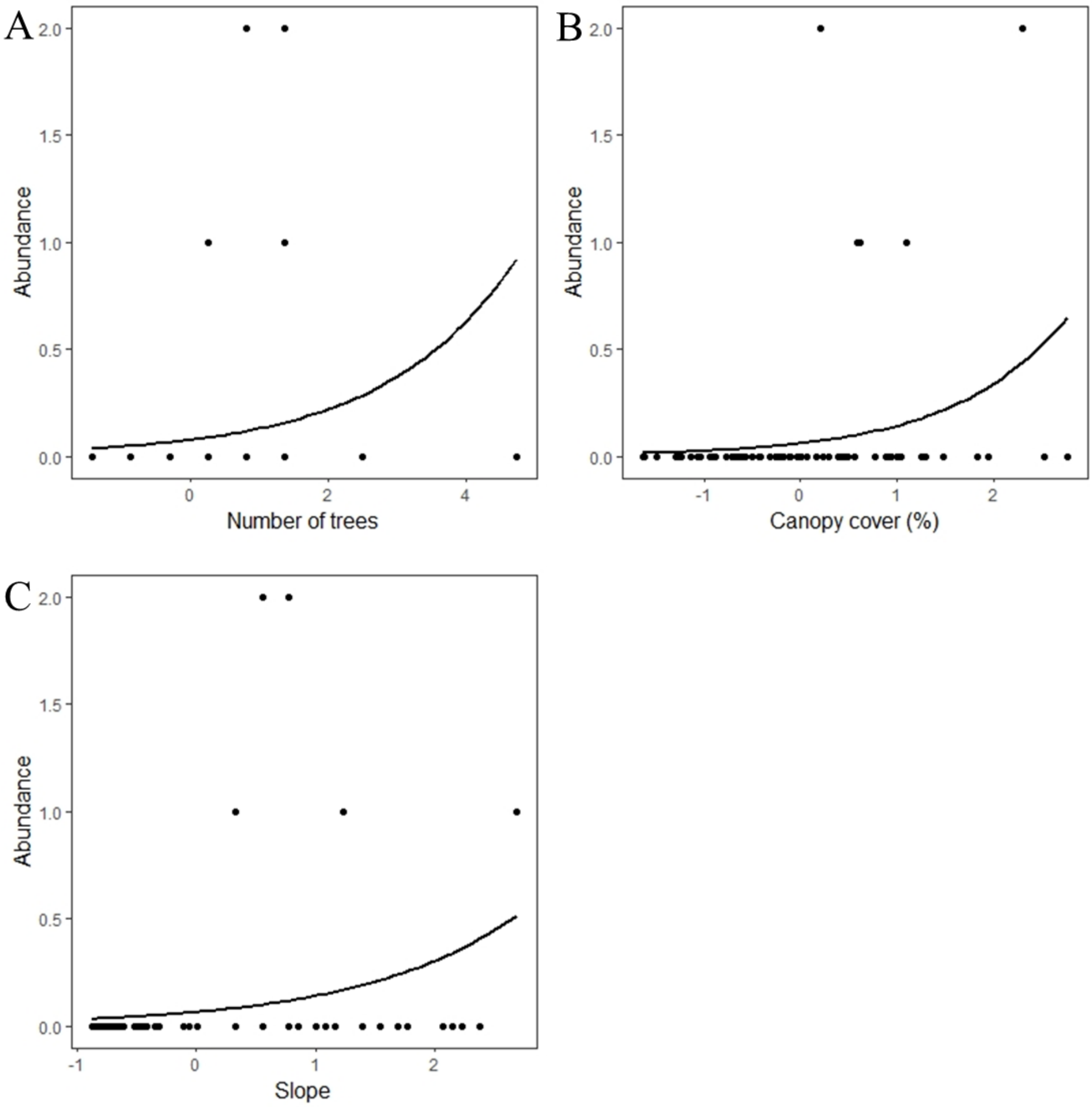


Figure 20 Environmental and structural conditions of the forest that influence the abundance of epiphytic Dryopteridaceae and Hymenophyllaceae in the Atlantic Forest of southeastern Brazil. Graphs (a), (b) and (c) refer to the relation between abundance and the number of trees, canopy cover (%), and slope, respectively.

4. DISCUSSION

4.1. Effect of environment and tree morphometric on epiphyte diversity at different scales

The ombrophilous forest in an advanced successional stage has the greatest diversity, which corroborates hypothesis one of this article, since it has more suitable niches for the establishment of epiphytes, as proposed by Benzing (1990). In addition, each plot presented a different composition, with a greater similarity between the two located in the restinga habitat, which seems to indicate environmental filtering, since not all species can tolerate the abiotic conditions of the various phytophysiognomies (Kraft et al., 2015). These results are in agreement with the ecological niche theory (Chase and Leibold, 2004), because each forest phytophysiognomy has environmental conditions that satisfy the minimum requirements for groups of epiphytic species to survive and reproduce. It is noteworthy that differences in community structure may reflect abiotic but also biotic changes, such as processes related to interaction with pollinators and facilitators (Kraft et al., 2015). In this way, the assembly of communities occurs due to restrictions of several ecological filters, such as the dispersion of species, the environmental factors of each location, and also the biotic interactions between the species (Götzenberger et al., 2012). According to Zotz (2016), epiphytic communities are rarely saturated, so competition is greatly reduced and even ecologically similar species coexist this explains why some sites, such as plot 5, reach such high epiphyte diversity.

Differences between the diversity and composition of epiphytes even in relatively close locations are reported in other studies (Kersten et al., 2009; Freitas & Assis, 2013; Barbosa et al., 2019), as well as the greater richness and abundance found in humid forests and in advanced stages of regeneration (Borgo & Silva, 2003; Dettke et al., 2008; Aguirre et al., 2010; Bataghin et al., 2010; Dislich & Mantovani, 2016; Geraldino et al., 2010; Marcusso & Monteiro, 2016; Padilha et al., 2017; Parra-Sanchez & Banks-Leite, 2020; Adhikari et al., 2021; Furtado & Menini Neto, 2021). Disturbed forests, despite their high conservation value, have greater microclimatic variation, different patterns of structure and composition, as well as changes in biotic relationships, for example, the absence of pollinators such as certain species of bees, butterflies and bats (Barlow et al., 2007). The effect of human disturbances on forests influences epiphytes from the destruction of their substrates through the loss of trees, to changes in microclimatic and biotic dynamics (Zotz & Bader, 2008). Parra-Sanchez

& Banks-Leite (2020) demonstrated that human-modified areas of the Atlantic Forest had low diversity and absence of seedlings and juvenile individuals of epiphytes, a fact that compromises the viability of future populations in these environments and reiterates the importance of well-preserved forests.

Restingas, even if well preserved as in this case, have greater insolation and drier habitats and therefore show less diversity when compared to other Atlantic Forest phytophysiognomies, as indicated by other studies (Waechter, 1998; Mania & Monteiro, 2010; Staudt et al., 2012; Couto et al., 2017; Cruz & Nunes-Freitas, 2019). Despite this, plot 2 presented an abundance similar to or greater than that of ombrophilous forests, which seems to be related to the presence of a large adjacent lagoon. Flores-Palacios & García-Franco (2008) have already observed the positive relationship between the density of epiphytes in low-altitude forests and the proximity of water courses, and thus we reiterate the importance of humidity in the diversity of epiphytes even in admittedly dry environments. On the other hand, the lowland forest, plot 3, despite the proximity of the watercourse, has low diversity due to the history of use of the area and, consequently, to the successional stage of the vegetation. In addition, other studies show that forests in lowlands typically have low density of epiphytes (Laube and Zotz, 2006).

Analysis through GLMM provides the most adequate and flexible approach to investigate the effect of variables on ecological data with non-normal distribution, especially when there is an influence of many random effects derived from different types of environments, as in this case (Bolker et al., 2009). Epiphytes are associated with several external factors that affect the pattern and dynamics of the community, some are intrinsic to the host tree, such as architecture, age, and identity and others are extrinsic that also affect the tree, such as forest disturbance and microclimate (Mendieta-Leiva and Zotz, 2015). Here, the only important factors in landscape-scale epiphyte diversity were tree density and canopy cover. Wolf (2005) reported that the biomass of epiphytes is directly related to the biomass of trees and the lower degree of disturbance, which reinforces the importance of the greater number of trees in colonization by epiphytes. Host density increases the number of available substrates, as predicted by the Island Biogeography Theory (MacArthur and Wilson, 1967). In addition, the greater number of trees provides better quality habitats and facilitates colonization through clonal growth and anemochoric dispersal, predominantly in epiphytes (Benzing, 1990), and also explains the high similarity between the composition of nearby trees (Wolf, 2005).

The inverse relationship of diversity with canopy cover contradicts our hypothesis one since we expected that more shady environments would register more epiphytes. Canham et al. (1990) showed that there is a significant spatial variation of light around the trees, which is related to the total penetration of the canopy and the formation of gaps. For epiphytes, the greatest limitations of growth and distribution are influenced by their water, nutritional and photosynthesis relationships (Zotz & Hietz, 2001; Nunes-Freitas & Rocha, 2007), and according to Padilha et al. (2017), humidity and light incidence are the most important environmental factors associated with species preference for habitat. Our results differ from those found by Kartzinel et al. (2013) and Batke & Kelly (2015), who reported that richness and abundance were negatively correlated with open canopies. We believe that the greater diversity associated with canopies that are more open is due to the high humidity present in the forests of the island, which allows the establishment of a large number of hygrophilous species even in brighter environments.

The size of the trees affected the richness and abundance of epiphytes at the landscape scale, only when hemiepiphytes were excluded, which reinforces the need to analyze this last group separately, as suggested by several authors (Moffett, 2000; Sperotto et al., 2020; Zotz, 2013; Bautista-Bello et al., 2021; Zotz et al., 2021), since their ecological needs differ from those of true epiphytes that do not connect to the soil at any point in their life cycle (Zotz, 2013; Bautista-Bello et al., 2021). Regardless of the exclusion of hemiepiphytes, the size of the trees affected the species composition. Large trees offer greater microclimatic variation and allow the establishment of more demanding groups in relation to habitat, as observed by Zotz & Vollrath (2003) and Dislich & Mantovani (2016). Larger trees allow the formation of an environmental and resource gradient that favor particular sets of species (Woods et al., 2015). In addition to canopy cover and tree size, the composition is also influenced by terrain slope, which may be related to limitations in species dispersion, despite the fact that most epiphytes are anemochoric. Janzen et al. (2020) observed that flat areas have greater limitation in the dispersion of epiphytes. Diaspores of orchids, bromeliads and ferns show a lower dispersion over long distances than expected, which may explain the effect of slope on composition, as well as the more clustered distribution of species (Bullock & Clarke, 2000; Winkler et al., 2009; Burns & Zotz, 2010; Sáyago et al., 2013; Janzen et al., 2020).

The variables analyzed did not affect the diversity of epiphytes in most forests at a local scale, which contradicts our hypothesis two. We expected that different factors would be significant in each plot and that communities would respond in different ways to varying environmental conditions and tree morphometry. For Götzenberger et al. (2012), on a small scale communities are predominantly assembled by biotic processes with intra and interspecific interactions potentially driving this structuring. However, as for epiphytes competition does not seem to be a problem, the internal patterns of the community may be generated by the limitation of species dispersion since close sampling units are more similar. One of the restinga forests has a significant influence on canopy cover, tree density, and canopy diameter, which reiterates the crucial role of luminosity and adequate substrate available for epiphyte diversity in drier environments. According to Götzenberger et al. (2012), environments with high microclimatic variability can present abiotic filtering even on small scales. Studies that evaluate processes that interact at cross-scales and reveal scale-dependent effects allow a more precise and objective perspective of complex ecological systems (Talley, 2007), and the results found in this research emphasize the importance of this approach in understanding the assembly of epiphytic communities, as already suggested by Mendieta-Leiva & Zotz (2015).

4.2. Effect of environment and tree structure on different taxonomic groups of epiphytes

The results of taxonomic groups support hypothesis one of this article, as each taxon and group of epiphytes had their diversity influenced in different ways by the abiotic factors evaluated on a large scale. We also emphasize that the joint analysis of all epiphytes can mask particular patterns. This is due to the high taxonomic diversity of the community, which allows epiphytes to have varied adaptations to different canopy microhabitats. The density of trees was a significant factor in the diversity of all groups, highlighting how the availability of habitats is crucial for the occurrence of epiphytes. The increase in tree size expands the available microhabitats and favors the establishment of a greater diversity of all epiphytic taxa, with the exception of the group of “other ferns”. Larger and older trees offer better humidity conditions due to the presence of mosses and lichens, in addition to greater humus accumulation (Laube and Zotz, 2006; Winkler et al., 2009; Woods et al., 2019). We emphasize that the positive effect of increasing DBH is notable in most groups, while the total height, trunk or crown depth varies according to taxon specificities. DBH size is directly related to the age of the trees, that is, those with higher DBH are available to receive propagules for a longer time, which favors the establishment of more and more demanding taxa (Nieder et al., 2001; Richards et al., 2020; Zotz & Schultz, 2008; Zotz & Vollrath, 2003). Longer trunks and crowns can occur regardless of the age of the trees, as in fast-growing species.

The highest diversity of bromeliads is associated only with trunk height and number of trees. The results are justified because, according to Cruz et al. (2022), the highest diversity of bromeliads in the study area occurs on the trunk and inner canopy of the trees. Richards et al. (2020), when analyzing the colonization process by epiphytes, he noticed that bromeliads are the first recorded in small trees and trunk, while all "other epiphytes" appear in trees with higher DBH and crown. An inverse relationship between canopy cover and bromeliad diversity was expected due to the functional characteristics of the species. Adaptations to xeromorphic environments are morphological, such as the formation of tanks (Benzing et al., 2000; Gobara et al., 2020), reduced size and small leaf area in atmospheric species, and also physiological, such as CAM photosynthesis (Crayn et al., 2015; Hietz et al., 2022) and a strong reduction in transpiration rate and osmotic adjustment (Gobara et al., 2020). Despite this, although some species have reached high densities in restinga forests, for example *Billbergia amoena* (Lodd.) Lindl., the greatest richness of bromeliads occurred in the well-shaded forest in an advanced successional stage (twelve of the eighteen species). Silva et al. (2021) demonstrated that canopy cover and luminosity do not affect the abundance of epiphytic bromeliads, but there is a relationship with DBH, texture, and branching aspect of the tree trunk. Our results contradict those of Nunes-Freitas & Rocha (2007) and Rocha et al. (2022) in which *Canistropsis microps* (E.Morren ex Mez) Leme have their distribution limited by the availability of light in forests. This difference may indicate that other epiphytic bromeliad species have different needs and habitat availability becomes a more important factor for the family as a whole. Leitman et al. (2015) showed that for bromeliads the effect of space is more important than the environmental conditions of the sites and reinforces the importance of the limitations of dispersion in the distribution of this family.

The richness and abundance of Polypodiaceae are strongly influenced by the size of the trees, which may also be related to the greater accumulation of moisture and organic matter, since its species have very branched roots that maximize uptake (Andrade and Nobel, 1997; Mehltreter et al., 2010). As for composition, we highlight that some genera were widely distributed in all phytophysiognomies, such as *Microgramma*, *Pleopeltis*, and *Serpocaulon*. In addition, some species had high abundances in certain locations, for example, *Microgramma crispata* (Fée) R.M.Tryon & A.F.Tryon in the restinga plots and *Pleopeltis pleopeltifolia* (Raddi) Alston in the lowland forest. Ferns, especially Polypodiaceae, have several traits that favor their occurrence in xeromorphic environments, which can be the canopy itself or drier environments, such as sandbanks and forests in early or intermediate stages of succession. According to Mehltreter et al. (2010), many species have a thick and extensive rhizome to allow water storage and trichomes with different functions (reflecting light, decreasing leaf temperature, reducing transpiration, and influencing other gas exchange). In addition, there is strong tolerance to desiccation and poikilohydry (Andrade & Nobel, 1997; Mehltreter et al., 2010; Hietz et al., 2022). The reduction of water in tissues causes changes in cell shape, solute concentration, and hydration states of membranes and macromolecules, which occurs especially in *Microgramma*, *Pleopeltis*, and *Polypodium* (Mehltreter et al., 2010). In addition to the influence of tree size and type of phytophysiognomy, terrain slope is a relevant factor for ferns, just like it is for orchids, which seems to be related to species dispersion (Winkler et al., 2009; Burns & Zotz, 2010; Janzen et al., 2020).

The results for Orchidaceae regarding canopy cover contradict our expectation since Kartzinel et al. (2013) reported that older trees with more closed crowns support higher germination rates. More open environments affect the germination of species due to exposure to wind, sun, or drought (Kartzinel et al., 2013). Our results show a strong positive relation between orchids with luminosity and with trees with lower DBH. This may be related to the greater abundance of heliophilous species in the study area, such as *Epidendrum filicaule* Lindl., as well as the high humidity of the forest in an advanced successional state, as it recorded the greatest richness and abundance of orchids. The forests of the study area showed a low richness of orchids compared to other research carried out in the Atlantic Forest, where the family is usually the most representative (see Kersten, 2010; Ramos et al., 2019). The results are probably related to the secondary character of the analyzed forests that lead to changes in the taxonomic pattern of the epiphyte community. Barthlott et al. (2001) states that the composition of epiphytes in areas of secondary or disturbed forests is composed of a smaller proportion of ferns and orchids, but presents many more species of bromeliads, as we observed in the present research and in other works carried out in this area of study (Cruz et al., 2021; Cruz and Nunes-Freitas, 2019). Adhikari et al. (2012), when comparing epiphytic orchids in environments with different intensities of land use, identified that larger and older trees with rough bark, low pH, and in areas of lower human impact showed greater diversity, which explains the difference in epiphytic composition in relation to the secondary forests.

Environments that are more open have more aroids, while those with trees with larger trunks and canopies have fewer aroids, probably due to shading. However, the variables affect the abundance but not the richness of Araceae, which may be due to the hemiepiphytic habit, common in *Philodendron* and *Monstera*, which is much more affected by large differences between habitats (Nieder et al., 2001). We point out that most of the aroid species occurred in the submontane forest in an advanced stage of succession (eight of the ten species), although the abundance of these species is low. The highest abundance values occurred in the restinga plots, an environment with greater luminosity, where three heliophilous species reached high densities, *Monstera adansoni* Schott, *Philodendron cordatum* Kunth ex Schott, and *Philodendron crassinervium* Lindl. Hemiepiphytism strongly diverges from the ecology of true epiphytes, those that do not connect to the ground at any point in their life cycle (Janzen et al., 2020; Zotz, 2013; Zotz et al., 2021). Epiphytes are limited by canopy water stress, nutrient scarcity, and anemochoric dispersal, while hemiepiphytes have other demands, including those related to zoochory (Nieder et al., 2001), and they can remain connected to the soil indefinitely (Bautista-Bello et al., 2021). Recent studies show that the ontogeny of climbing aroids is quite complex and variable, and they can germinate in the soil and climb trees, breaking or not the connections with the soil, but the same species can also germinate in trees, therefore, it is not possible to draw conclusions with punctual Observed as epiphyte in the study areas (Bautista-Bello et al., 2021). For this reason, many authors suggest that hemiepiphytes (mainly the secondary, also called nomadic vines) should not be included in ecological studies regarding epiphytes (Moffett, 2000; Zotz, 2013; Sperotto et al., 2020; Bautista-Bello et al., 2021; Zotz et al., 2021) and our results reinforce this.

Cactus have several functional traits related to xeromorphism, such as CAM photosynthesis and succulent structures, although they preferentially occur in the shaded areas of the trunk and inner canopy of trees, as already demonstrated by some authors (Andrade & Nobel, 1997; Cruz et al., 2022). This is due to the accumulation of organic matter in these microenvironments, which favors the absorption of nutrients and explains the positive effect of trunk height and canopy depth on Cactaceae. According to Benzing (1990), cactus does not occur in places with high exposure to radiation, which was corroborated by Chaves et al. (2022). These authors demonstrated that the epiphytic species *Epiphyllum phyllanthus* (L.) Haw. has a high mortality rate in full sun and that the best fitness occurs in shading (Chaves et al., 2022). Our results support this information, since the submontane forest in an advanced state of succession, with high values of canopy cover, harbored most of the species (seven of the nine species).

For “other epiphytes”, the number and size of host trees are relevant factors. Environments with many trees and older and larger trees, with greater DBH, create a differentiated microclimate, in addition to greater area and time available for colonization, as already mentioned. According to Richards et al. (2020), epiphytes from families where epiphytism is less pronounced colonize trees over time as conditions become more favorable. The smallest and youngest trees mostly have the most common species (Richards et al., 2020). Piperaceae has its diversity strongly influenced by environmental conditions, as already demonstrated in another study (Leitman et al., 2015), which also seems to be true for Gesneriaceae, which occurred preferentially in well-preserved forests. Begoniaceae, despite not being included in the analysis because the species occurred outside the subplots, was also recorded only in the most conserved forest. The "other ferns" have their diversity directly related to canopy cover and terrain slope, possibly due to shading, greater moisture entry, and retention, since they are hygrophilous and ciophilous species. Although many ferns have adaptations to xeric environments, as in Polypodiaceae, few outside this family perform CAM photosynthesis and water storage in tissues is rare (Hietz et al., 2022). Hymenophyllaceae, in particular, is a family whose distribution is strongly guided by microclimatic factors and is restricted to humid environments, especially those adjacent to permanent or temporary streams (Zotz & Büche, 2000), as observed in the study area. This is because the species are poikilohydric and the lack of water control leads to lower water use efficiency (Hietz et al., 2022).

5. CONCLUSIONS

This is one of the first studies to evaluate the effect of forest structure, environmental variables and tree morphometric on the assembly of vascular epiphyte communities in a multiscale approach in the Atlantic Forest. Our main conclusions are: a) forests with different types and vegetation structures present different epiphyte diversities and the submontane rainforest in an advanced state of regeneration is the one with the greatest species richness; b) There was an effect of tree morphometry on the diversity of epiphytes at the landscape scale only when hemiepiphytes were removed from the analysis, but there was a positive effect of the number of trees and a negative effect of canopy cover with and without hemiepiphytes; c) the variables analyzed do not influence the diversity of epiphytes in most forests at a local scale; d) families and groups of epiphytes are not affected in the same way by environmental conditions and tree morphometric, but the number of trees positively influences all of them.

Although our models are simplified given the complexity of ecosystems, we recognize the value of generalizations and reinforce with our results the importance of analyzing individual taxa or groups of epiphytes separately, especially without the hemiepiphytes, in ecological studies, as well as the multiscale approach to understanding patterns of biodiversity. Other studies should take this into account.

Conservation efforts must be made to maintain or increase the number of species and, with regard to the implications of our results, we reiterate that forests in a better state of conservation and with a greater number of trees present greater diversity of vascular epiphytes and should be prioritized. However, there is low floristic similarity even between nearby areas and, therefore, each environment has a unique pool of species and any human disturbance, especially the selective cutting of trees, even in habitats with lower richness, can lead to the loss of diversity in this group, as there is little overlap of species between forests.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at:
< https://github.com/AnaCruzUFRJ/Assembly-of-the-vascular-epiphyte-community-of-Ilha-Grande-Brazil.git >.

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SUPPORTING INFORMATION

Table 1 Results of Generalized Linear Models (GLM) and GLM Mixed (GLMM) for richness and abundance of vascular epiphyte species under environmental conditions and arboreal morphometry in Atlantic Forest forests in Southeast Brazil. Values in bold are significant. The information criteria (AIC) for the GLMM, GLM and the null model and the p values referring to the analysis of variance (ANOVA) for the comparison of two models are presented. Values in bold are significant.

Plots	**Parameters**	**GLM**			**GLMM**		
		Variables selected in the model	**AIC**	**AIC null model**	**Variables selected in the model**	**AIC**	**p-value compared to GLMM X GLM**
All environments together	Richness	Canopy cover, density tree, and diameter at breast height	353.5	399.73	Canopy cover, slope, and density tree	348.0	<**0.01**
	Abundance	Canopy cover, density tree, diameter at breast height, and canopy diameter	969.7	1354	Canopy cover, slope, and density tree	871.41	<**0.01**
All environments together - excluding hemiepiphytes	Richness	density tree and diameter at breast height	337.62	379.24	Canopy cover, slope, density tree, and diameter at breast height	340.9	**0.44**
	Abundance	density tree and diameter at breast height	922.59	1267.7	Canopy cover, slope, density tree, and diameter at breast height	892.8	<**0.01**

1	Richness	Canopy cover, density tree, and canopy diameter	105.95	120.92	-	-	-
	Abundance	Canopy cover and density tree	292.95	467.79			
2	Richness	Density tree	42.62	42.91	-	-	-
	Abundance	Slope, density tree, and trunk height	59.42	163.4			
3	Richness	Density tree	42.62	42.91	-	-	-
	Abundance	Density tree	81.45	173.24			
4	Richness	none	55.49	42.91	-	-	-
	Abundance	none	152.08	152.08			
5	Richness	none	74.03	74.03	-	-	-
	Abundance	none	173.22	173.22	-	-	-

Table 2 Results of Generalized Linear Models (GLM) and Mixed GLM (GLMM) for the richness and abundance of vascular epiphyte species as a function of environmental conditions and tree morphometry in Atlantic Forest in Southeastern Brazil. Values in bold are significant.

	Parameter	**Model type**	**Selected variables**	**Estimate**	**z-value**	**p-value**	**Residual deviance**	**Pseudo – R^2 (fixed effects)**	**Pseudo – R^2 (total)**	**Variance (random effects)**	**Deviance (random effects)**
All epiphytes	Richness	GLMM	Canopy cover	-0.07	-1.15	0.25	-	0.14	0.44	0.08	0.29
			Slope	0.02	0.21	0.83					
			Tree density	**0.20**	**4.50**	**<0.01**					
	Abundance	GLMM	**Canopy cover**	**-0.01**	**-3.32**	**<0.01**	-	0.43	0.84	0.11	0.33
			Slope	-0.02	-0.40	0.69					
			Tree density	**0.33**	**18.10**	**<0.01**					
Epiphytes, excluding hemiepiphytes	Richness	GLM	**Tree density**	**0.21**	**4.46**	**<0.01**	89.20	-	-	-	-
			Diameter at breast height	**0.23**	**0.05**	**<0.01**		-	-	-	-
	Abundance	GLMM	Canopy cover	-0.02	-0.55	0.58	-	0.60	0.79	0.05	0.21
			Slope	0.02	0.36	0.72					
			Density tree	**0.35**	**17.17**	**<0.01**					
			Diameter at breast height	**0.10**	**2.14**	**0.03**					

Table 3 Pairwise comparisons of test Multivariate homogeneity of groups dispersions (variances) for the composition of vascular epiphytes in trees of different plots of RAPELD in the Brazilian Atlantic Forest. Observed p-value below diagonal, permuted p-value above diagonal. Values in bold are significant.

	Plot 1	**Plot 2**	**Plot 3**	**Plot 4**	**Plot 5**
Plot 1	**-**	**<0.01**	**0.66**	**0.66**	**0.16**
Plot 2	**<0.01**	**-**	**<0.01**	**<0.01**	**<0.01**
Plot 3	**0.63**	**<0.01**	**-**	**0.42**	**0.07**
Plot 4	**0.66**	**<0.01**	**0.44**	**-**	**0.39**
Plot 5	**0.18**	**<0.01**	**0.07**	**0.38**	**-**

Table 4 Results of Generalized Linear Models (GLM) for the richness and abundance of vascular epiphyte species as a function of environmental conditions and tree morphometry in different phytophysiognomies of the Brazilian Atlantic Forest in Southeast. Values in bold are significant.

Plots	Parameter	Model type	Selected variables	Estimate	z-value	p-value	Residual deviance	Pseudo – R^2 (fixed effects)	Pseudo – R^2 (total)	Variance (random effects)	Deviance (random effects)
1	Richness	GLM	**Canopy cover**	**-0.41**	**-2.44**	**0.01**	19.66	- -	- -	- -	- -
			Tree density	**0.23**	**3.78**	**<0.01**					
			Crown diameter	**0.49**	**2.37**	**<0.01**					
	Abundance	GLM	**Canopy cover**	**-0.25**	**-3.45**	**<0.01**	173.62	-	-	-	-
			Tree density	**0.32**	**14.16**	**<0.01**		-	-	-	-
2	Richness	GLM	Tree density	0.25	1.87	0.06	3.98	-	-	-	-
	Abundance	GLM	Slope	-0.16	-0.23	0.81	3.34	- -	- -	- -	- -
			Tree density	0.30	1.88	0.06					
			Trunk height	-0.32	-0.72	0.47					
3	Richness	GLM	Tree density	0.22	1.55	0.12	5.17	-	-	-	-
	Abundance	GLM	**Tree density**	**0.64**	**10.12**	**<0.01**	32.95	-	-	-	-
4	Richness	GLM	None of the variables -	1.56	12.3	0.00	9.97	-	-	-	-

			(Intercept)								
	Abundance	GLM	None of the variables - (Intercept)	2.64	35.77	0.00	96.08	-	-	-	-
5	Richness	GLM	None of the variables - (Intercept)	2.29	26.07	0.00	19.07	-	-	-	-
	Abundance	GLM	None of the variables - (Intercept)	3.19	136.8	0.00	1001.8	-	-	-	-

Table 5 Results of Generalized Linear Models (GLM) and GLM Mixed (GLMM) for richness and abundance of the main families and groups of vascular epiphytes in function of environmental conditions and tree morphometry in the forests of the Atlantic Forest in Southeast Brazil. Values in bold are significant. The information criteria (AIC) for the GLMM, GLM and the null model and the p values referring to the analysis of variance (ANOVA) for the comparison of two models are presented. Values in bold are significant.

		GLM			**GLMM**		
Groups	**Parameters**	**Variables selected in the model**	**AIC**	**AIC null model**	**Variables selected in the model**	**AIC**	**p-value compared to GLMM X GLM**
Bromeliaceae	Richness	Density tree and trunk height	200.34	203.83	Canopy cover	203.70	3.36
	Abundance	Density tree	816.70	875.45	Canopy cover, Slope, and density tree	790.38	**<0.01**
Polypodiaceae	Richness	Density tree and depth crown	215.35	224.91	Canopy cover, slope, and density tree	218.81	0.76
	Abundance	Slope, density tree, and depth crown	485.56	724.88	Canopy cover, slope, density tree, DBH, trunk height, and depth crown	465.7	**<0.01**
Orchidaceae	Richness	Slope, density	99.98	116.06	Canopy cover, slope, and	106.0	**0**

		tree, DBH, and depth crown			density tree		
	Abundance	Density tree and trunk height	312.10	399.06	Canopy cover, slope, density tree, DBH, and trunk height	275.7	**<0.01**
Araceae	Richness	Canopy cover, DBH, and depth crown	228.25	247.71	Canopy cover	217.25	**0**
	Abundance	Canopy cover, density tree, and depth crown	664.14	930.82	Canopy cover, slope, density tree, DBH, trunk height, profundidade, and diâmetro da copa	500.3	**<0.01**
Cactaceae	Richness	DBH	94.13	113.70	Canopy cover	98.50	**0**
	Abundance	DBH and trunk height	234.93	300.29	Canopy cover, slope, density tree, DBH, trunk height, depth and crown diameter	180.77	
Other epiphytes	Richness	DBH	139.97	142.38	Canopy cover	139.97	0.36
	Abundance	Density tree, DBH, trunk height, depth and crown diameter	415.61	512.63	Canopy cover, slope, DBH, trunk height, depth and crown diameter	398.3	**<0.01**
Other ferns	Richness	Canopy cover, slope, density tree,	34.67	45.70	Canopy cover, slope, and density tree	36.7	0.07

		DBH, trunk height, and depth crown					
	Abundance	Canopy cover, slope, density tree, DBH, trunk height, depth and crown	39.26	51.97	Canopy cover, slope, and density tree	41.9	0.06

Table 6 List of epiphyte and hemiepiphyte species collected in RAPELD - Ilha Grande plots, in different types of Atlantic Forest vegetation, with their respective ecological categories and bibliography used to classify the category.

Taxons	**Species**	**Ecological categories**	**Source of information**
Araceae	*Anthurium intermedium* Kunth	Epiphyte	Observed as epiphyte in the study area
Araceae	*Anthurium minarum* Sakur. & Mayo	Epiphyte	Observed as epiphyte in the study area
Araceae	*Anthurium pentaphyllum* (Aubl.) G.Don	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Coelho, M.A.N.; Temponi, L.G.; Camelo, M.C.; Mayo, S.J.; Pimenta, K.M.; Pontes, T.A.; Andrade, I.M. *Anthurium* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB4965>. Acesso em: 22 abr. 2022
Araceae	*Anthurium urvilleanum* Schott	Epiphyte	Observed as epiphyte in the study area
Araceae	*Anthurium* sp1	Epiphyte	Observed as epiphyte in the study area
Araceae	*Monstera adansonii* Schott	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Mayo, S.J.; Andrade, I.M. *Monstera* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB5010>. Acesso em: 22 abr. 2022
Araceae	*Philodendron cordatum* Kunth ex Schott	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Sakuragui, C.M.; Calazans, L.S.B.; Soares, M.L.; Mayo, S.J.; Ferreira, J.B. *Philodendron* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em:

			<https://floradobrasil.jbrj.gov.br/FB5029>. Acesso em: 22 abr. 2022
Araceae	*Philodendron crassinervium* Lindl.	Epiphyte	Observed as epiphyte in the study area
Araceae	*Philodendron martianum* Engl.	Epiphyte	Observed as hemiepiphyte in the study area and according to Sakuragui, C.M.; Calazans, L.S.B.; Soares, M.L.; Mayo, S.J.; Ferreira, J.B. *Philodendron* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB5046>. Acesso em: 22 abr. 2022
Araceae	*Philodendron* sp1	Hemiepiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea gracilis* Lindm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea nudicaulis* Griseb.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea* sp1	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea* sp2	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia amoena* (Lodd.) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia pyramidalis* (Sims) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Canistropsis microps* (E.Morren ex Mez) Leme	Epiphyte	Observed as epiphyte in the study area

Bromeliaceae	*Neoregelia johannis* (Carrière) L.B.Sm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia dura* Baker	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia stricta* Sol.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia geminiflora* Brongn.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia tenuifolia* L.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia* sp1	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia* sp2	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea procera* (Mart. ex Schult. & Schult.f.) Wittm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea vagans* (L.B.Sm.) L.B.Sm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea* sp1	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Selenicereus setaceus* (Salm-Dyck) Berg	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis clavata* F.A.C.Weber	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis teres* (Vell.) Steud.	Epiphyte	Observed as epiphyte in the study area

Cactaceae	*Rhipsalis crispata* (Haw.) Pfeiff.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis elliptica* G.Lindb. ex K.Schum.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis pachyptera* Pfeiff.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis* sp1	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis* sp2	Epiphyte	Observed as epiphyte in the study area
Dryopteridaceae	*Ctenitis* sp1	Epiphyte	Observed as epiphyte in the study area
Gesneriaceae	*Codonanthe devosiana* Lem.	Epiphyte	Observed as epiphyte in the study area
Gesneriaceae	*Nemathanthus* sp1	Epiphyte	Observed as epiphyte in the study area
Hymenophyllaceae	*Didymoglossum* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Epidendrum filicaule* Lindl.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp2	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp3	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Eurystyles* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Lankesterella ceracifolia* (Barb.Rodr.) Mansf.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Masdevallia infracta*	Epiphyte	Observed as epiphyte in the study area

	Lindl.		
Orchidaceae	*Maxillaria* sp	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Miltonia spectabilis*	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Scaphyglottis modesta* (Rchb.f.) Schltr.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Vanilla chamissonis* Klotzsch	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to *Vanilla* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro.Disponível em: <https://floradobrasil.jbrj.gov.br/FB12351>. Acesso em: 22 abr. 2022
Orchidaceae	*Polystachia* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	Orchidaceae sp1	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia rotundifolia* (L.) Kunth	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia elongata* Kunth	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp1	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp2	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp3	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp4	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum atlanticum* R.C. Moran & Labiak	Epiphyte	Observed as epiphyte in the study area

Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum rigidum* Sm.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum* sp1	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma crispata* (Fée) R.M.Tryon & A.F.Tryon	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma geminata* (Schrad.) R.M.Tryon & A.F.Tryon	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma tecta* (Kaulf.) Alston	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pecluma sicca* (Lindm.) M.G. Price	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pecluma* sp1	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pleopeltis astrolepis*	Epiphyte	Observed as epiphyte in the study area

	(Liebm.) E.Fourn.		
Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pleopeltis pleopeltifolia* (Raddi) Alston	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Serpocaulon menisciifolium* (Langsd. & Fisch.) A.R.Sm.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Serpocaulon triseriale* (Sw.) A. R. Sm.	Epiphyte	Observed as epiphyte in the study area

CAPÍTULO III

Importance of the vertical gradient in the variation of epiphyte community structure in the Brazilian Atlantic Forest

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ABSTRACT

Epiphytes are strongly affected by the microclimate of the forest canopy. Therefore, understanding how microclimatic changes are related to the functional characteristics of taxa and the patterns of communities is essential. Our objective was to examine the stratification of the epiphyte community along the vertical gradient of the forests and to investigate whether the pattern of species distribution in the canopy height zones is similar among forests with different characteristics and between the families of epiphytic plants. The study was carried out in the Atlantic Forest of Ilha Grande, in southeastern Brazil, where we recorded 76 species. The highest richness and abundance were found on tree trunks. The high crown had less diversity and a characteristic set of species. The vertical stratification pattern was similar across forests with different phytophysiognomies. The main epiphytic families exhibited different patterns of diversity along the canopy. The highest richness of Araceae occurred in the trunk zones, while Polypodiaceae, Bromeliaceae, and Orchidaceae were more diverse in the trunk and inner crown, and Cactaceae were more diverse in the inner crown. Tree height zones select epiphytic taxa with distinct characteristics according to the fundamental conditions for their survival and, therefore, we suggest that the ecological niche theory is adequate to explain the assembly of epiphytic communities at a local scale.

Keywords: bromeliads, community assembly, drought adaptations, ecological niche, environmental filtering, ferns.

1. INTRODUCTION

The architecture of treetops, branches and leaves, the presence of climbing plants and epiphytes, and other abiotic factors determine the creation and control of microclimates in forest ecosystems (Hallé et al., 1978). A vertical gradient with marked microlimatic variation is especially typical of tropical forests (Richards, 1996). It is known that towards the highest parts of the canopy moisture decreases while luminosity and temperature increase (Anhuf and Rollenbeck, 2001; Fauset et al., 2017; Hallé et al., 1978; Murakami et al., 2022; Stark et al., 2012). In addition to microclimatic variation, there is vertical stratification of other environmental conditions and resources, including humus and nutrient availability (Catling and Lefkovitch, 1989; Sillett and Van Pelt, 2007; Woods et al., 2015) and, consequently, the plant and animal communities that inhabit parts of trees (Smith, 1973; Stan et al., 2020). According to Moffett (2000), small vertical distances in the canopy are equivalent to much larger horizontal extensions and this explains the high alpha diversity of tropical forests as ecosystems become more structurally complex.

Vascular epiphytes, non-parasitic plants that are structurally dependent on other plants, have a prominently tropical distribution (Benzing, 1990; Gentry and Dodson, 1987) and contribute about 40% of the vascular flora in neotropical forests (Taylor et al., 2021). Epiphytes are strongly influenced by the vertical gradient of a forest and the three-dimensional structure of tree crowns (Benzing, 1990) and, according to Taylor et al. (2021), the high diversity of tropical forests is precisely due to niche partition in the communities, since the many species of epiphytes present an exceptional variety of functional traits within diverse taxonomic groups. Classical studies have already shown that epiphytes do not have a random distribution along tree height zones (Benzing, 1990; 1995; Catling and Lefkovitch, 1989; Gentry and Dodson, 1987; Johansson, 1974; Kelly, 1985; Schimper, 1888). Recent research has detected preferential spatial patterns for specific groups of epiphytes in the canopy (Krömer et al., 2007; Martínez-Meléndez et al., 2008; Nieder et al., 2000; Wagner et al., 2013; Woods et al. 2015, 2019) and this is related to the functional characteristics of the species (Graham and Andrade, 2004; Guzmán-Jacob et al., 2022; Miranda et al., 2020; Petter et al., 2016; Rascher et al., 2012; Zotz, 2004).

Hygrophilous epiphytes dominate the lower zones of tree trunks, which include some fern families (for example, Hymenophyllaceae and Aspleniaceae) and Araceae (Zotz, 2007). Many species of this last family may have adventitious roots that connect the plant to the soil at some stage of life, making it impossible to classify them as true epiphytes (Bautista-Bello et al., 2021; Gerhard Zotz et al., 2021; Zotz, 2013). The inner and middle crowns of the trees are the habitat where there is generally larger diversity, and the families Orchidaceae, Bromeliaceae, and Polypodiaceae are predominant (Woods et al., 2015). In this zone, there are plants with adaptations to drought, such as pseudobulbs, succulent leaves, or arrangement in rosettes forming tanks that accumulate water, and desiccation tolerance strategies (Hietz et al., 2022; Krömer et al., 2007). In the outer crown, diversity is lower and only heliophilous species, such as many polypodioid ferns (e.g. *Pleopeltis* and *Microgramma*), some orchids, and atmospheric bromeliads occur (Krömer et al., 2007). Small and linear leaves, smaller specific leaf area, and photosynthesis through Crassulaceae acid metabolism (CAM) are important morphophysicological adaptations for life in the high canopy (Crayn et al., 2015; Guzmán-Jacob et al., 2022; Zotz, 2004; Zotz and Hietz, 2001; Zotz and Ziegler, 1997). In addition, high crown species have very specialized trichomes with different functions, occurring mainly in bromeliads and ferns (Benzing, 2000; Benzing et al., 1976; Zotz, 2016). Learning about the specificity of epiphytes for tree height zones is important because it contributes to understanding how stratification is related to the functional characteristics of taxa and allows us to predict how microclimatic and land use changes can affect species distribution and cause changes in community patterns.

Although the number of studies on the vertical distribution of epiphytes in tropical forests in Brazil has grown in recent years, few approaches contemplate how each epiphyte family responds to the vertical gradient in different Atlantic Forest ecosystems (Bataghin et al., 2012; 2017; Bonnet and Queiroz, 2006; Fraga et al., 2008; Kersten et al., 2009; Pos and Sleegers, 2010; Santana et al., 2017). Therefore, there is a lack of studies about the patterns and processes that govern the assembly of epiphyte communities, especially in southeastern Brazil, an exceptionally biodiverse area with respect to this group of plants (Furtado and Menini Neto, 2021; Leitman et al., 2015; Ramos et al., 2019b). To contribute to knowledge in this area, the purpose of this research was to investigate how the vascular epiphyte community structure varies along the vertical gradient and whether the stratification pattern is similar among forests with distinct characteristics and among the main families. We tested two hypotheses. The first hypothesis is that microhabitats with higher humidity and more available substrates along the tree height zones, such as trunk and inner canopy, have larger diversity and characteristic composition, even in forests with different conditions, corroborating the ecological niche theory (Chase and Leibold, 2004; Hutchinson, 1957). The second hypothesis is that different families present different patterns of stratification and, therefore, environmental conditions and available nutritional resources along the vertical gradient of the forest operate together by selecting species, as proposed by Johansson (1974). Our null hypothesis was that there is a homogeneous distribution of all vascular epiphytes along the tree height zones. More specifically, we aimed to answer the following questions:

(a) What is the structure of the vascular epiphyte community along the tree height zones, in terms of richness, abundance and composition?

(b) How does the vertical stratification of epiphytes change in forests with different environmental conditions?

(c) Which species are associated with each height zone?

(d) How do the richness and abundance of the main taxonomic groups vary along the vertical gradient?

2. MATERIAL AND METHODS

2.1. Study site

Ilha Grande is located in the municipality of Angra dos Reis, on the southern coast of the state of Rio de Janeiro, Brazil, and has an area of 65,258 hectares (23º09'26.77" S, 44º13'53.72" W) (Bastos and Callado, 2009) (Figure S1). The island is home to two strict protection conservation units, Ilha Grande State Park and Praia do Sul State Biological Reserve, and is one of the largest preserved areas of Atlantic Forest in southeastern Brazil (Alho et al., 2002). Ilha Grande is part of one of the coastal mountains of Serra do Mar, it has a mountainous relief oriented in the northeast-southwest direction and most of the territory is located below 500 meters altitude (Bastos and Callado, 2009). The highest points are Pedra Dágua, 1,031 m, and Pico do Papagaio, 735 m. The climate is tropical, with an average annual temperature of 23.2ºC and average relative humidity of 82%, without significant variations throughout the year (Bastos and Callado, 2009). Precipitation on the island is uneven due to the rugged terrain and can reach up to 4,500 mm of rain in some regions (Oliveira and Neto, 2000). On average, annual rainfall is 1,977 mm, with the summer months being the rainiest (above 240 mm monthly) and, despite not having a dry season, rainfall is lower in July (Bastos and Callado, 2009). The vegetation has ecosystems associated with the Atlantic

Forest Domain, including rainforests in different successional stages, *restinga* and marshy forests, and mangroves (Bastos and Callado, 2009; Oliveira and Neto, 2000). Research indicates that the region has a high richness of vascular plants, especially epiphytes (Callado et al., 2009; Cruz et al., 2021; Cruz and Nunes-Freitas, 2019; Nunes-Freitas et al., 2009, 2006; Rocha et al., 2022).

Data were collected from RAPELD plots, whose acronym unites the two scales covered by the method: rapid inventories (RAP) and long-term ecological projects (PELD) (Magnusson et al., 2005). Five plots were used for sampling, all in secondary vegetation in a good state of conservation, two in *restinga* forest, one in dense lowland rainforest and two in dense submontane rainforest, following the classification of Veloso et al. (1991) and the Brazilian Institute of Geography and Statistics (IBGE, 2012) (see details about the plots in Figure S1 and in Table S1).

2.2. Data collection

We established 78 subplots measuring 10 meters by 10 meters in the long, narrow plots of RAPELD (see plot structures in Magnusson et al. 2005). The subplots were 10 meters apart. All trees with a diameter at breast height (DBH) larger than or equal to 15 centimeters were sampled in the subplots. All species of epiphytes were considered, including holoepiphytes and hemiepiphytes according to the classification by Benzing (1990). We opted for this simple form of categorization due to the difficulty of identifying the hemiepiphytes during fieldwork and even in the bibliography. Recent studies recommend that primary and secondary hemiepiphytes be classified as hemiepiphytes (*only*) and nomadic vines, respectively (Moffett, 2000; Sperotto et al., 2020; Gerhard Zotz et al., 2021). However, the ontogeny of these species is very complex and some show large variations in the germination substrate (whether the life cycle starts on the forest soil or in the tree), therefore we cannot draw conclusions based on specific observations from the field work (Bautista-Bello et al., 2021). We used the classic method of tree division by Johansson (1974) to facilitate comparisons with other works: Z1 – trunk base to 1 meter high; Z2 – trunk (up to the first bifurcation); Z3 – inner crown; Z4 – medium crown; Z5 – outer crown (Figure 1 - A). Protocols for sampling epiphyte diversity recommend the use of single rope techniques and the census of large trees (Flores-Palacios and García-Franco, 2001; Gradstein et al., 2003). Because of the methodological difficulties in accessing the RAPELD plots and the objective of evaluating the effect of the forest structure on the epiphyte community, we chose to use the sampling of all trees with DBH larger than or equal to 45 cm in the subplots at from the ground and observation through superzoom camera. Since the forests had few emergent trees with dense canopy, the diversity was satisfactorily recorded as shown by the rarefaction curves, although this methodological bias needs to be considered. Seedlings, very young individuals, or that could not be accurately identified through visualization were not considered in the analyses. We identified the species based on specific literature, a study of herbarium material and by consulting specialists. The taxonomic classification and scientific names were checked against The International Plant Names Index.

2.3. Data analyses

The diversity was analyzed through species richness and abundance of individuals in order to provide additional information about the community, as recommended by Hoffmann et al. (2019). To answer questions (a) and (b), the plots were analyzed together and independently to verify if the pattern is maintained in different types of forests. To test hypothesis 1, data were compared across the five tree height zones for all epiphytes. To test hypothesis 2 and to answer the research question (d), families with the highest number of species were tested separately. The normality of the data and residuals and the homoscedasticity of the variances were verified using the Shapiro-Wilk test and Levene test, respectively, using the car package (Fox and Weisberg, 2019). Generalized linear (GLM) and Mixed GLM (GLMM) models with Poisson distribution were developed due to non-normality and homogeneity, even after data transformations with the AID, MASS and lme4 packages (Asar et al., 2017; Bates et al., 2015; Venables and Ripley, 2002). For the GLMM, the height zones were considered fixed effects and the different plots were included as a random effect, assuming the spatial dependence of the samples and assessing their individual differences (Bolker et al., 2009). An analysis of variance (ANOVA) was used to test significant differences between the models, which were then compared using the Akaike information criterion (AIC), and those with the best fit were selected with the bbmle package (Bolker and R Development Core Team, 2020). The Tukey HSD test was used to verify significant differences in richness and abundance between height zone pairs with a multcomp package (Hothorn et al., 2008).

Also to test hypothesis 1 and answer question (a), the variation in species composition was verified through a principal coordinate analysis (PCoA) and multivariate homogeneity analysis of group dispersions - variances, as well as through indices similarity with Bray-Curtis distance (1 - dissimilarity); all of these analyses were conducted with the Vegan and BiodiversityR packages (Kindt and Coe, 2005; Oksanen et al., 2020). To answer question (c), indicator species were identified with the indicspecies package, which associated species with tree height zones based on occurrence and abundance (Cáceres and Legendre, 2009; Dufrene and Legendre, 1997). Component A corresponds to the species specificity at that location and component B is the fidelity or sensitivity of the species as an indicator of the target location

(Cáceres and Legendre, 2009; Dufrene and Legendre, 1997). The statistical significance of the relationships was tested using the permutation test (Dufrene and Legendre, 1997).

Richness and abundance analyzes were previously performed with holoepiphytes and hemiepiphytes and then excluding hemiepiphytes. Since the results were very similar, we chose to present only data that considered all epiphytes together (Table S2).

All standardizations and analyzes were performed using the program R version 4.10 (R Core Team, 2020). The graphics were made with the packages ggplot2, RColorBrewer, and ggthemes (Arnold, 2021; Erich, 2014; Wickham, 2009). Each tree was considered a sampling unit and a confidence interval of 95% probability was used in all analyses.

3. RESULTS

3.1. Vertical community patterns

We recorded 76 species of epiphytes in 271 trees (Table S3). Mean richness and abundance were larger in zone 2 and smallest in zone 5 with high data variation. There was a significant difference between the number of species and epiphyte individuals for all tree height zones, except between zones 1 and 3 for richness and 1, 3, and 4 for abundance that have intermediate mean values (Table S2 and Figure 1). The mixed models had a better fit for both richness and abundance, assuming that there is variation in the vertical partition between the different plots (Tables S4, S5, and S6).

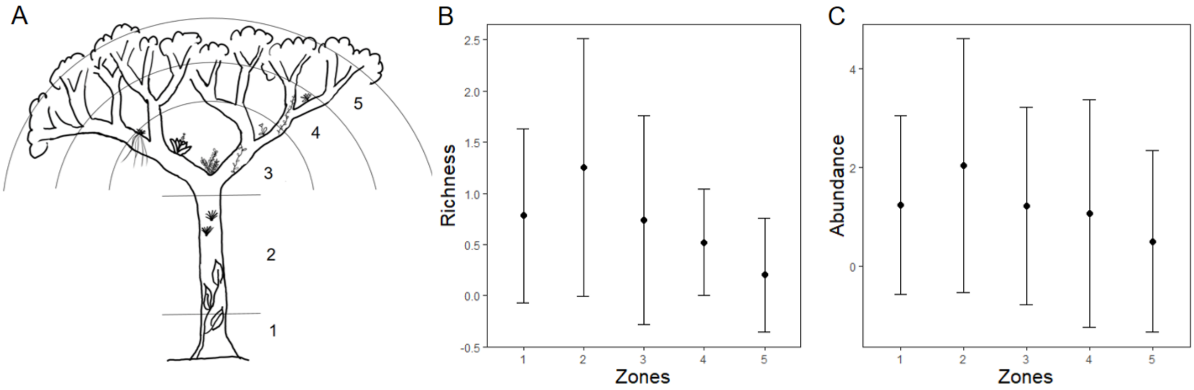

Figure 10 Diversity of vascular epiphytes along height zones, according to Johansson (1974) (a), in trees in Ilha Grande, Brazilian Atlantic Forest. Mean and standard deviation of species richness (b) and abundance of individuals (c).

Regarding species composition, the eigenvalues of axes one and two of the PCOA ordination were 17.7% and 13.7%, respectively (Figure 2). Zones 4 and 5 clustered on the right side of the ordering, while zones 1, 2, and 3 clustered on the left side. The Permutation Test for Homogeneity of Multivariate Dispersions indicated that there was a significant difference between zone 5 in relation to all others ($F = 17.77$, $p < 0.01$). We found the highest floristic similarities in adjacent height zones, Z3 and Z4, followed by Z2 and Z3, and Z1 and Z2, and the smallest similarities were observed in Z5 when compared to all others (Table 1).

Table 2 Similarity matrix based on the Bray-Curtis index for the abundance of vascular epiphytes along height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest.

	Zone 1	**Zone 2**	**Zone 3**	**Zone 4**
Zone 2	0.60			
Zone 3	0.41	0.64		
Zone 4	0.31	0.50	0.70	
Zone 5	0.18	0.26	0.35	0.48

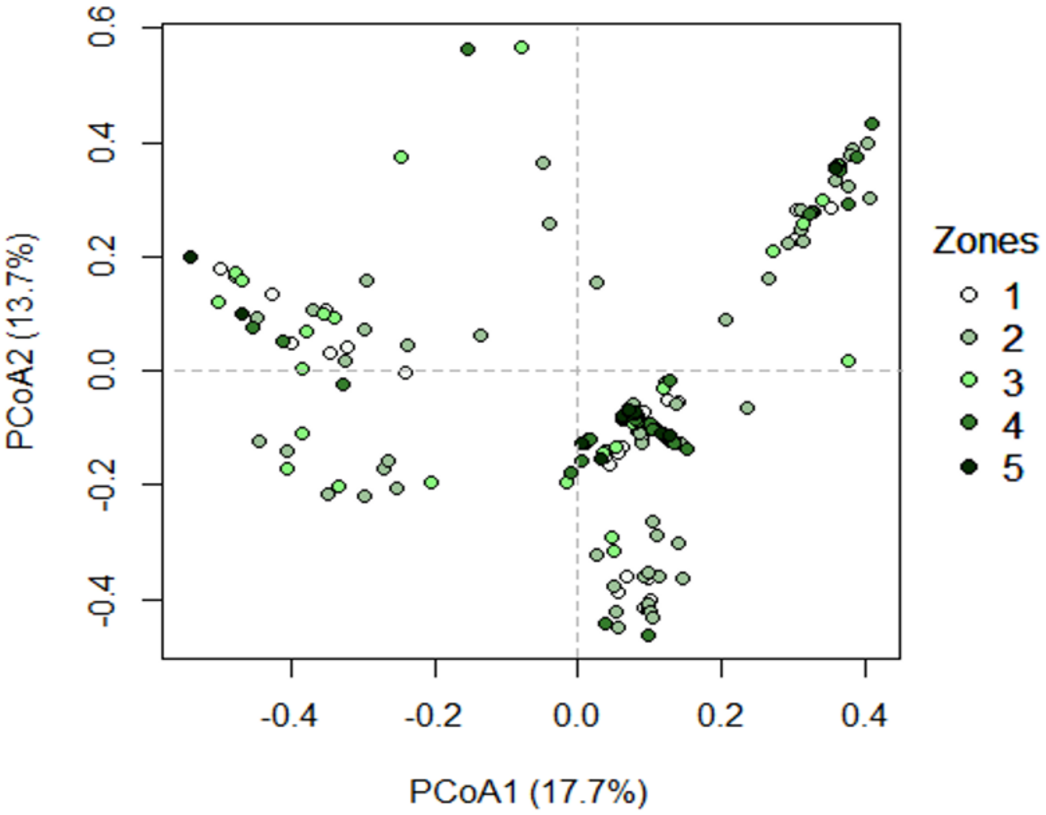

Figure 2 Biplot of Principal Coordinate Analysis for the composition of vascular epiphytes along height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest.

All plots showed differences between richness and abundance by height zone when analyzed separately (Table S7). In all forest types, the highest richness and abundance were recorded in zone 2 and the lowest values were recorded in zone 5, except for plot 5 where there was no difference between the average richness in this zone compared to the others and the highest mean abundance was in zones 2 and 5 (Table 2).

Table 2 Minimum, maximum, average and standard deviation richness and abundance of vascular epiphytes along tree height zones, according to Johansson (1974), in the Brazilian Atlantic Forest, for the RAPELD plots in Ilha Grande, RJ. Means followed by the same letter in the columns do not differ by Tukey's test (p < 0.05).

Plots	**Zones**	**Richness**		**Abundance**	
		Minimum and maximum value	**Average and standard deviation**	**Minimum and maximum value**	**Average and standard deviation**
1	1	0-3	0.89 ± 0.82 a	0-11	1.70 ± 2.21 a
	2	0-7	1.45 ± 1.14 b	0-11	2.49 ± 2.67 b
	3	0-3	0.59 ± 0.75 a	0-6	0.93 ± 1.52 c
	4	0-2	0.30 ± 57 c	0-5	0.44 ± 0.98 d
	5	0-1	0.01 ± 0.12 d	0-4	0.06 ± 0.47 e
2	1	0-5	1.32 ± 1.00 a	0-11	2.25 ± 2.22 a
	2	0-5	1.91 ± 1.15 a	0-11	2.79 ± 2.00 a
	3	0-6	1.68 ± 1.27a	0-14	2.40 ± 2.51 a
	4	0-4	1.32 ± 0.87a	0-11	2.08 ± 1.81 a
	5	0-2	0.66 ± 0.62 b	0-5	0.96 ± 1.16 b
3	1	0-2	0.29 ± 0.51 ac	0-2	0.26 ± 0.50 a
	2	0-3	0.74 ± 0.50 b	0-9	1.55 ± 2.24 b
	3	0-4	0.62 ± 0.94 bc	0-7	1.17 ± 1.97 b
	4	0-2	0.36 ± 0.62 bc	0-15	1.29 ± 3.00 b
	5	0-1	0.02 ± 0.15 a	0-6	0.14 ± 0.93 a
4	1	0-3	0.68 ± 074 ab	0-6	0.95 ± 1.31 a

	2	0-6	1.09 ± 1.57 b	0-17	1.86 ± 3.4 b
	3	0-3	0.41 ± 0.82 a	0-9	1.00 ± 2.24 a
	4	0-4	0.30 ± 0.82 ac	0-12	0.59 ± 2.05 a
	5	0-1	0.02 ± 0.15 c	0-5	0.11 ± 0.75 c
5	1	0-2	0.56 ± 0.69 ab	0-4	0.65 ± 0.91 a
	2	0-6	0.85 ± 1.16 a	0-11	1.22 ± 2.07 b
	3	0-2	0.39 ± 38 b	0-16	0.69 ± 1.31 a
	4	0-3	0.31 ± 0.67 b	0-5	1.13 ± 3.15 ab
	5	0-5	0.30 ± 0.90 b	0-16	1.22 ± 3.57 b

3.2. Indicator species

The indicator species analysis showed one species associated with zone 1, one species for zone 4, three species for zone 5, two species related to the trunk (Z1 + Z2), and three species associated with the crown of trees (Z3, Z4, and Z5) (Table 3).

Table 3 Significant results of multilevel pattern analysis for vascular epiphyte species indicative of clustering along the height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest, considering p values < 0.05. Component A corresponds to species specificity at that location and component B is species fidelity as an indicator.

Family	**Species associated**	**Zones**	**A**	**B**	**p**
Polypodiaceae	*Serpocaulon triseriale* (Sw.) A.R.Sm.	1	1.00	0.02	0.03
Orchidaceae	*Acianthera* sp.	4	1.00	0.03	<0.01
Bromeliaceae	*Tillandsia dura* Baker	5	0.63	0.09	<0.01
Piperaceae	*Peperomia rotundifolia* (L.) Kunth	5	0.59	0.09	<0.01
Orchidaceae	*Epidendrum filicaule* Lindl.	5	0.57	0.05	0.03
Bromeliaceae	*Billbergia amoena* (Lodd.) Lindl.	1 + 2	0.93	0.14	<0.01
Araceae	*Philodendron* sp.	1 + 2	1.00	0.06	<0.01
Araceae	*Philodendron cordatum* Kunth ex Schott	3 + 4 + 5	0.81	0.33	<0.01
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	3 + 4 + 5	0.88	0.16	<0.01
Bromeliaceae	*Neoregelia johannis* (Carrière) L.B.Sm.	3 + 4 + 5	0.92	0.05	0.03

3.3. Taxon variation along the vertical gradient

The families with the highest number of species in the study area were Bromeliaceae (18), Polypodiaceae (15), Orchidaceae (13), Araceae (10), and Cactaceae (9), and there was a statistical difference in the standard stratification for each taxon (Table S3). Bromeliaceae and Orchidaceae do not differ in richness between height zones, but there was a difference in abundance, with zone 5 having the lowest averages for bromeliads and the highest averages for orchids. For Polypodiaceae, the highest diversity occurred in zones 2, 3, and 4. For Araceae, the highest means for richness occurred in zones 1 and 2, and the highest abundances occurred in zones 2 and 5. For Cactaceae, the highest diversity occurred in zones 3 and 4 (Table 4).

Table 4 Minimum, maximum, average, and standard deviation richness and abundance of the main vascular epiphyte families along tree height zones, according to Johansson (1974), in trees in the Brazilian Atlantic Forest, for the RAPELD plots in Ilha Grande, RJ. Means followed by the same letter in the columns do not differ by Tukey's test (p < 0.05).

Family of epiphytes	**Zones**	**Richness**		**Abundance**	
		Minimum and maximum value	**Average and standard deviation**	**Minimum and maximum value**	**Average and standard deviation**
Bromeliaceae	Z1	0-2	0.40 ± 0.52 a	0-7	0.94 ± 1.64 a
	Z2	0-3	0.48 ± 0.64 a	0-12	1.12 ± 2.08 a
	Z3	0-1	0.37 ± 0.48 a	0-8	0.76 ± 1.42 a
	Z4	0-2	0.41 ± 0.53 a	0-15	0.95 ± 2.19 a
	Z5	0-1	0.16 ± 0.37 a	0-2	0.18 ± 0.45 b
Polypodiaceae	Z1	0-3	0.25 ± 0.53 a	0-3	0.26 ± 0.54 a
	Z2	0-3	0.55 ± 0.65 b	0-6	0.74 ± 1.11 b
	Z3	0-3	0.57 ± 0.60 b	0-7	0.91 ± 1.34 bc
	Z4	0-3	0.50 ± 57 b	0-15	1.08 ± 2.12 c
	Z5	0-2	0.27 ± 0.54 ab	0-8	0.57 ± 1.56 c
Orchidaceae	Z1	0-1	0.02 ± 0.14 a	0-1	0.02 ± 0.14 a
	Z2	0-2	0.06 ± 0.26 a	0-6	0.14 ± 0.69 b
	Z3	0-1	0.04 ± 0.19 a	0-3	0.06 ± 0.35 ab
	Z4	0-1	0.06 ± 0.23 a	0-2	0.08 ± 0.33 ab
	Z5	0-1	0.09 ± 0.29 a	0-15	0.47 ± 2.32 c

Araceae	Z1	0-3	0.72 ± 0.73 ab	0-5	0.84 ± 0.97 ab
	Z2	0-3	0.73 ± 0.79 a	0-6	0.92 ± 1.11 a
	Z3	0-3	0.55 ± 0.69 b	0-4	0.82 ± 1.12 abc
	Z4	0-2	0.41 ± 0.55 bc	0-4	0.64 ± 1.00 c
	Z5	0-2	0.64 ± 0.53 c	0-4	1.09 ± 1.14 bc
Cactaceae	Z1	0-1	0.01 ± 0.11 a	0-1	0,01 ± 0,11 a
	Z2	0-1	0.04 ± 0.2 ab	0-3	0,06 ± 0,35 a
	Z3	0-2	0.11 ± 0.34 b	0-5	0,17 ± 0,61 b
	Z4	0-1	0.09 ± 0.29 ab	0-5	0,20 ± 0,75 b
	Z5	0-1	0.02 ± 0.15 ab	0-1	0,02 ± 0,15 ab

4. DISCUSSION

4.1. Vertical community pattern

The results point out the heterogeneous distribution of vascular epiphyte diversity with specific taxa occurring in certain height zones of the trees, which indicates that niche theory, proposed by Hutchinson (1957), appears to apply to the assembly of these communities at a local scale, which corroborates the first hypothesis of our research. An ecological niche can be defined as a set of environmental conditions and resources that allow species to satisfy their minimum population growth requirements (Chase and Leibold, 2004). Competition between epiphytes is reduced because communities are rarely saturated, this fact allows many ecologically similar species to coexist in the same tree height zone, which increases diversity in environments (Catling and Lefkovitch, 1989; Zotz 2016).

The highest values of richness and abundance occurred in zone 2, which corresponds to the trunk of the tree (up to the first bifurcation). Our results were similar to those found by Adhikari et al. (2021) and by Acebey and Krömer (2001). The cited studies were developed in subtropical forests of Nepal with different types of management and higher altitudes and in the well-preserved submontane forest of Bolivia at intermediate altitude, respectively. The highest diversity in the trunk of the tree partially corroborates our hypothesis one, since we also expected high diversity in the inner canopy. Ambients with larger areas have more habitats available for colonization, as demonstrated by Richards et al. (2020) in a study on the process of colonization by epiphytes in forest fragments in Nicaragua. In addition to the larger area, the trunk may provide adequate conditions for the establishment of epiphytes, since in some large trees the trunks may have rougher bark that can accumulate organic matter (Adhikari et al., 2021; Freiberg, 1996). Additionally to larger area and time available for colonization, there is highest coverage of lichens and bryophytes on the trunk which increases the moisture and nutrients available to vascular epiphytes (Gehrig-Downie et al., 2011). Because of the location of the trunk in the forest understory, this provides a more humid and stable microclimate than the high canopy, as well as adequate luminosity for species that can occur there and in the inner canopy of the trees (Krömer et al., 2007).

Different methods of dividing the host tree have been used to analyze the vertical stratification of epiphytes, the most common are those by Johansson (1974), ter Steege and Cornelissen (1989), and for the Atlantic Forest, also Kersten and Silva (2002). In general, the tree is divided into trunk and crown zones. Unlike our results, where highest diversity and richness were found in the trunk, most studies show that the highest diversity of epiphytes occurs in zones located in the canopy of the trees, regardless of the tree partition method used. This is due to the combination of the crown architecture with the arrangement of the branches, providing places for the establishment and accumulation of humus, in addition to intermediate light (Bataghin et al., 2012; Kersten et al. 2009; Krömer et al., 2007; Nieder et al., 2000; Nieder et al., 2001; Pos and Sleegers, 2010; Santana et al., 2017; Woods et al., 2015). The difference in our result, when compared to other surveys, seems to be related to the successional stages of the forests and the sampling method. The areas sampled by us represent secondary vegetation with a high density of trees and many young trees, which were also sampled. According to Richards et al. (2020), the trunk is where colonization by epiphytes begins and, therefore, only older trees will harbor many epiphytes in the crown. Our study did not only sample large trees, unlike what is suggested in the main protocols (Flores-Palacios and García-Franco, 2001; Gradstein et al., 2003). Most surveys follow these protocols and only sample larger and older trees, which may explain the higher values of diversity in the crown zones.

The species composition of the outer canopy is different from all other zones because this microhabitat has larger microclimatic variability, higher temperatures and insolation, and low air humidity compared to the lower zones (Anhuf and Rollenbeck, 2001; Fauset et al., 2017; Miranda et al., 2020; Murakami et al., 2022; Nunes-Freitas and Rocha, 2007; Stark et al., 2012). Furthermore, the smaller stable area and larger exposure to strong winds and rain explain the differentiated composition and low richness found by several authors in Z5 (Cabral et al., 2015; Nadkarni, 1984; Nieder et al., 2001; Woods et al., 2015; Zotz, 2007) and corroborated in this research. The composition of the upper canopy is subject to selection due to microclimatic variation and the restriction of moisture and nutrients, as well as substrate instability. The outer crown species have adaptations to resist drought and larger vapor pressure deficits, of which we highlight as functional traits the CAM metabolism, smaller average sizes, and smaller specific leaf area (Hietz et al., 2022; Petter et al., 2016; Zotz, 2004). Adjacent zones have larger floristic similarity because of similar environmental conditions, since the zonation scheme is an abstraction of the actual complexity of trees, and distinct but close zones can have homogeneous conditions (Zotz, 2007). The result was similar to that observed by Pos and Sleegers (2010) in the Amazon rainforest, where trunk zones were more similar to each other than when compared to canopy zones.

The pattern of vertical stratification with larger diversity in the trunk and less diversity in the outer canopy was similar in all forest types in the study area, as predicted in hypothesis 1. This indicates that the variation of conditions and resources in the vertical gradient is similar in all environments analyzed. Specifically, on the microclimate, studies in the Atlantic Forest show that light slowly decreases from the upper to lower canopy zones, regardless of the successional stage (Fauset et al., 2017; Miranda et al., 2020; Nunes-Freitas and Rocha, 2007). In addition, there is a positive relation between the highest canopy zones and temperature, as well as a negative relation with relative humidity (Murakami et al., 2022).

However, trees in larger stands may suffer buffering from neighboring trees and show less microclimatic variation (Murakami et al., 2022). This explains the high abundance and similar richness to other height zones in the outer canopy of the submontane forest in an advanced stage of regeneration, which may also be related to the high humidity of the forest and the larger variation in the height and composition of the trees. Due to this, the crowns of the understory trees are shaded and colonized by epiphytes with diverse functional traits and not just those tolerant to high canopy microclimatic stress, as observed in other tropical forests (Krömer et al., 2007).

4.2. Indicator species

Although there were differences in diversity and composition between height zones, few species showed high specificity and were associated with height zones of specific trees. We expected to find a larger number of indicator species due to ecological niche differentiation, however, previous studies show that really few taxa are restricted to specific height zones (Zotz, 2007). Additionally, IndVal did not indicate any indicator species for Z2 and Z3, which suggests that the compositions of these zones are subsets of the others. This is possible because these zones have intermediate environmental conditions, allowing a larger number of species, usually generalists, to occupy these strata. These generalist habitat species are more ecologically flexible and can establish themselves in various tree height zones (Krömer et al., 2007). The results differed from those found by Pos and Sleegers (2010) in their study in the Amazon rainforest, in which most of the specialist species occurred at the base of the trunk, inner and middle crown.

In general, indicator species have morphological, anatomical, and behavioral adaptations that explain their classification habitats. For Z1, the indicator species was

Serpocaulon triseriale (Sw.) A.R.Sm., which is a facultative epiphyte that can also occur in soil or on rocks. Possibly, its occurrence in this zone is because the base of the trunk is rougher and there is more humus and moisture, ensuring the necessary conditions for its establishment. However, this same species occurred exclusively as an epiphyte in lowland ombrophilous forest in Mexico in the study of Acebey et al. (2017), this difference is probably due to differences in humidity between the study areas. As for Z5, three species were classified as indicators, all with adaptations for larger microclimatic variability and lower humidity. *Epidendrum filicaule* Lindl. is a heliophilous orchid with a caespitose, graminoid, pendently curved habit, and extremely branched stems (Forster and Souza, 2013). *Tillandsia dura* Baker has linear, erect, and highly scaled leaves and has been recorded in the upper canopy in another work (Lima and Wanderley, 2007). *Peperomia rotundifolia* (L.) Kunth has prostrate growth with succulent leaves and, as opposed to our results, was recorded as dominant at the base of the trunk in a shaded environment by Bataghin et al. (2017). This may have occurred because of the shading in the high canopy of many trees, especially in the submontane forest in an advanced stage of regeneration, where the species was more abundant.

The IndVal pointed out two species as trunk epiphytes (Z1 + Z2) and three as canopy epiphytes (Z3 + Z4 + Z5), all with high specificity. *Billbergia amoena* (Lodd.) Lindl. is a facultative epiphyte that can occur as an epiphytic, terrestrial, or rupicolous plant in the understory of the study area, while *Philodendron* sp. was recorded linked to the forest floor, this indicates that it is a hemiepiphyte and may or may not break its connections with the soil and establish itself on the tree only. The canopy epiphytes noted here are heliophilic plants with adaptations to the water stress provided by life in the canopy, except *Philodendron cordatum* Kunth ex Schott. This species are a fast-growing hemiepiphyte most frequently found in *restinga* forests almost exclusively attached to the soil. On the other hand

Microgramma vaccinifolia (Langsd. and Fisch.) Copel. presents a highly branched rhizome and with many adpressed scales (Almeida, 2020), and *Neoregelia johannis* (Carrière) L.B.Sm. is a bromeliad with a tank that can accumulate water and nutrients (Benzing, 1990; 2000).

4.3. Taxon variation along the vertical gradient

The results corroborate hypothesis two of this research, since different families with epiphytic species showed different patterns along the vertical gradient, as we expected. Taxa have different strategies to avoid or tolerate water stress and this explains the non-random distribution in the forest canopy (Woods et al., 2015). Our results also endorse those of Johansson (1974) and Benzing (1998), since they indicated that the diversity of epiphytes is related to the specific abiotic conditions of each microenvironment.

There was a high richness and abundance of Araceae in Z1 and Z2 due to the hemiepiphytic habit predominant in *Philodendron* and *Monstera*. A similar pattern was observed by Pos and Sleegers (2010), Krömer et al. (2007) and Nieder et al. (2000), the latter two associated this fact with the direct contact with the soil that occurs in these genera. Secondary hemiepiphytes, currently classified as nomadic vines, are climbing plants that germinate in or near the ground and may lose the proximal portion of the stem during ontogeny (Moffett, 2000). For this reason, the classification and inclusion of hemiepiphytes in studies such as this one causes a lot of uncertainty, since the adventitious roots can keep them connected to the soil and they are never really epiphytes throughout their life cycle (Bautista-Bello et al., 2021; Zotz, 2013). Some researchers recommend that classification into secondary hemiepiphytes should avoided because it confuses plants with different life cycle strategies, as these plants can supplement their water needs by the supply of adventitious roots that are connected to the soil and not exclusively dependent on the canopy (Moffett, 2000;

Gerhard Zotz et al., 2021; Zotz, 2013). We chose to maintain the classic classification (Benzing, 1990) since we performed the analysis with and without hemipiphytes and there was no change in the general pattern of the community. The high abundance of Araceae in Z5 may be related to *Philodendron cordatum* Kunth ex Schott and *Monstera adansoni* Schott, since they are heliophilic species that reach high densities in the crowns of some trees in the study area, however, it is essential to consider that these species occurred mainly linked to the forest soil.

Ferns and bromeliads were dominant on the trunk and in the inner and middle crown, while orchids were more diverse in the outer crown, corroborating the results of other authors (Bonnet and Queiroz, 2006; Krömer et al., 2007; Pos and Sleegers, 2010; Santana et al., 2017; Woods et al., 2015). The epiphytes that occur in the high canopy have adaptations that allow them to survive in this environment with functional traits that enable them to be more efficient in water use. We can point for example reduced specific leaf area and CAM photosynthesis (Guzmán-Jacob et al., 2022), pseudobulbs and succulent structures for water storage (as in orchids), and poikiloydria, in the case of many ferns (Hietz et al., 2022; Krömer et al., 2007). Regarding bromeliads, Miranda et al. (2020) and Bonnet and Queiroz (2006) reported that *Tillandsia* species tend to be more diverse at intermediate height zones and Nunes-Freitas and Rocha (2007) found a similar pattern for the abundance of *Canistropsis microps* (E. Morren ex Mez) Leme. For Bonnet and Queiroz (2006) there was a difference in the distribution of types of bromeliads, since atmospheric species preferentially occur in the highest canopies with larger luminosity and tank bromeliads occur in more humid and shady environments. This is supported by our research, because *Tillandsia* species were more abundant in the canopy zones, while *Canistropsis*, *Billbergia* and *Aechmea* occurred preferentially in the trunk. This information reinforces that bromeliads are heterogeneously distributed along the vertical gradient. The pattern is related to the functional characteristics of bromeliads. In the higher canopy zones, for example, there is an increase in the proportion of species with CAM metabolism because of the more intense luminosity that performs the selection of these species (Zotz & Hietz 2001). According to Crayn et al. (2015), in the subfamily Tillandsioideae, in which all clades are epiphytes, the high dominance of CAM metabolism is related to extreme xeromorphy, since *Tillandsia* species are overwhelmingly atmospheric. In the lower zones, tank formers species occur, as they depend on the accumulation of water and humus to supply nutrients, although there are also many CAM species (Benzing 1976).

Woods et al. (2015) observed that inner canopies have high humidity, humus availability, and intermediate luminosity due to self-shading, which prevents species from experiencing extremely dry conditions in the canopy. This explains the high diversity of bromeliads and ferns in these environments and not just of heliophilous species. According to Hallé et al. (1978), tree transpiration creates a microclimate at the highest parts of the trunk and in the inner crown, and some groups of epiphytes are adapted to these regions. Cactaceae, for example despite having many xeromorphic characteristics (such as succulence and CAM photosynthesis), occurred predominantly in the inner and middle canopy. According to Benzing (1990), epiphytic cacti do not colonize areas with thin branches and direct exposure to the sun, but rather microhabitats with a higher concentration of humus. The study of Andrade and Nobel (1997) partially corroborates this because they recorded a larger abundance of epiphytic cactus in deciduous trees, with larger exposure to radiation than in evergreen trees in lowland forests in Panama. However, the species were distributed mainly in the trunk crevices, the crotches, and primary branches, which, for the authors, reinforces the importance of water interception and the accumulation of organic matter in these environments, endorsed by the fact that the species have long roots growing towards the canopy humus (Andrade and Nobel, 1997).

5. CONCLUSIONS

Although the relevance of variation in light and moisture levels is widely known in ecology, few studies have a more refined approach to how epiphytic taxa respond to this vertical gradient. Here we present one of the first works for the Atlantic Forest of southeastern Brazil that addresses the community as a whole, but also evaluates taxa separately, performing pattern comparison and testing hypotheses. Our conclusions can be summarized as follows: 1) the forests analyzed have highest diversity in the trunk and in the intermediate zones and the lowest values in the outer crown, where there was also a unique composition; 2) the stratification pattern is quite similar in different types of forests; 3) some species are associated with certain microhabitats, suggesting that there is high specificity for these epiphytes; and 4) the main epiphytic families exhibit different patterns of diversity along the vertical gradient, which seems is related to their adaptive strategies to deal with canopy conditions.

Although the present research does not perform microclimate measurements, our descriptive results and the two tested hypotheses contribute to understanding the microhabitat requirements of vascular epiphytes and the organization of plant communities as a whole, as well as reinforcing the need to evaluate families separately in ecological studies. Furthermore, it provides evidence of the importance of microclimatic variability for the high diversity of tropical forests. Finally, we also show that secondary forests have different patterns from what is commonly found in primary vegetation and that the analysis of trees of different sizes, and not just large ones, is important to understand the effect of forest structure on the vertical distribution of the community. Future studies should perform empirical tests involving microclimate variables of the vertical gradient relating them to patterns of epiphyte diversity in forests of different successional stages within the Atlantic Forest and other morphoclimatic domains.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at: <https://github.com/AnaCruzUFRJ/Ilha-Grande-epiphyte-stratification-dataset-and-scripts.git>.

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SUPPORTING INFORMATION

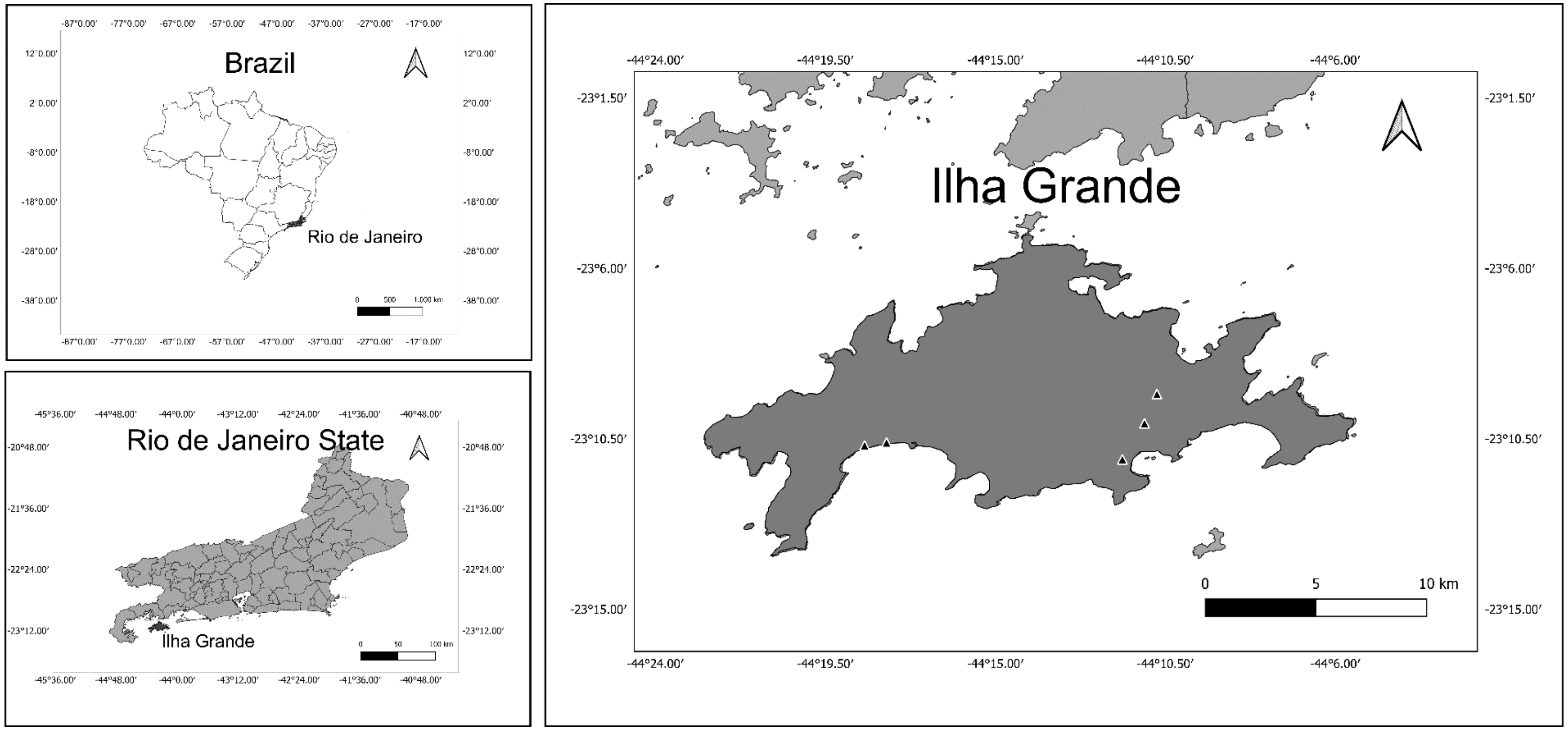

Figure 1 Location of Ilha Grande, municipality of Angra dos Reis, state of Rio de Janeiro, Brazil. Filled triangles correspond to RAPELD plots.

Table 1 Characteristics of RAPELD plots in Ilha Grande, RJ. The vegetation type follows the classification by Veloso et al. (1991) e Brazilian Institute of Geography and Statistics (IBGE, 2012), successional stages are in accordance with the National Council for the Environment (Brasil 1994) and the other characteristics correspond to the average values of each plot followed by the standard deviation in meters (m) and centimeters (cm).

Plots	**Vegetation**	**Successional stage**	**Altitude (m)**	**Distance from the ocean (m)**	**Tree height (m)**	**Tree diameter at breast height (cm)**	**Tree crown diameter (m)**
1	Restinga forest	Advanced	16.18 ± 3.38	119.15 ± 33.47	9.53 ± 1.80	17.47 ± 2.10	4.53 ± 1.28
2	Restinga forest	Advanced	8.08 ± 0.49	39.96 ± 9.67	8.05 ± 1.14	19.05 ± 2.35	3.16 ± 1.04
3	Dense ombrophilous lowland forest	Middle	10.87 ± 4.49	525.62 ± 79.71	15.89 ± 6.47	29.03 ± 9.50	4.74 ± 2.74
4	Dense ombrophilous submontane forest	Middle	142.77 ± 10.98	1315 ± 0	20 ± 3.02	22.74 ± 5.15	7.18 ± 3.29
5	Dense ombrophilous submontane forest	Advanced	377.54 ± 13.96	1997.3 ± 13.66	24.53 ± 4.93	43.18 ± 10.09	7.8 ± 2.13

Table 2 Richness and abundance minimum, maximum, average, and standard deviation of vascular epiphytes along the height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest. Means followed by the same letter in the columns do not differ by Tukey's test ($p < 0.05$).

Zones	**Richness**		**Abundance**	
	Minimum and maximum value	**Average and standard deviation**	**Minimum and maximum value**	**Average and standard deviation**
Holoepiphytes + hemiepiphytes				
Z1	0-5	0.78 ± 0.85 a	0-11	1.24 ± 1.81 a
Z2	0-7	1.25 ± 1.26 b	0-17	2.04 ± 2.57 b
Z3	0-6	0.74 ± 1.02 a	0-14	1.22 ± 2.00 a
Z4	0-4	0.52 ± 0.81 c	0-16	1.07 ± 2.31 a
Z5	0-5	0.02 ± 0.56 d	0-16	0.50 ± 1.84 c
Only holoepiphytes				
Z1	0-5	0.59 ± 0.79 a	0-11	0.95 ± 1.72 a
Z2	0-7	1.02 ± 1.22 b	0-17	1.67 ± 2.79 b
Z3	0-6	0.67 ± 0.95 a	0-13	1.05 ± 1.9 a
Z4	0-4	0.5 ± 0.8 a	0-16	0.95 ± 2.28 a
Z5	0-5	0.2 ± 0.55 c	0-16	0.43 ± 1.78 c

Table 3 List of epiphyte and hemiepiphyte species collected in RAPELD - Ilha Grande plots, in different types of Atlantic Forest vegetation, with their respective ecological categories and bibliography used to classify the category.

Taxons	**Species**	**Ecological categories**	**Source of information**
Araceae	*Anthurium intermedium* Kunth	Epiphyte	Observed as epiphyte in the study area
Araceae	*Anthurium minarum* Sakur. & Mayo	Epiphyte	Observed as epiphyte in the study area
Araceae	*Anthurium pentaphyllum* (Aubl.) G.Don	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Coelho, M.A.N.; Temponi, L.G.; Camelo, M.C.; Mayo, S.J.; Pimenta, K.M.; Pontes, T.A.; Andrade, I.M. *Anthurium* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB4965>. Acesso em: 22 abr. 2022
Araceae	*Anthurium urvilleanum* Schott	Epiphyte	Observed as epiphyte in the study area

Araceae	*Anthurium* sp1	Epiphyte	Observed as epiphyte in the study area
Araceae	*Monstera adansonii* Schott	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Mayo, S.J.; Andrade, I.M. *Monstera* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB5010>. Acesso em: 22 abr. 2022
Araceae	*Philodendron cordatum* Kunth ex Schott	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to Sakuragui, C.M.; Calazans, L.S.B.; Soares, M.L.; Mayo, S.J.; Ferreira, J.B. *Philodendron* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB5029>. Acesso em: 22 abr. 2022
Araceae	*Philodendron crassinervium* Lindl.	Epiphyte	Observed as epiphyte in the study area
Araceae	*Philodendron martianum* Engl.	Epiphyte	Observed as hemiepiphyte in the study area and according to Sakuragui, C.M.; Calazans, L.S.B.; Soares, M.L.; Mayo, S.J.; Ferreira, J.B. *Philodendron* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <https://floradobrasil.jbrj.gov.br/FB5046>. Acesso em: 22 abr. 2022
Araceae	*Philodendron* sp1	Hemiepiphyte	Observed as epiphyte in the study area

Bromeliaceae	*Aechmea gracilis* Lindm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea nudicaulis* Griseb.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea* sp1	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Aechmea* sp2	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia amoena* (Lodd.) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia pyramidalis* (Sims) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Billbergia zebrina* (Herb.) Lindl.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Canistropsis microps* (E.Morren ex Mez) Leme	Epiphyte	Observed as epiphyte in the study area

Bromeliaceae	*Neoregelia johannis* (Carrière) L.B.Sm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia dura* Baker	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia stricta* Sol.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia geminiflora* Brongn.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia tenuifolia* L.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia* sp1	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Tillandsia* sp2	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea procera* (Mart. ex Schult. & Schult.f.) Wittm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea vagans* (L.B.Sm.) L.B.Sm.	Epiphyte	Observed as epiphyte in the study area
Bromeliaceae	*Vriesea* sp1	Epiphyte	Observed as epiphyte in the study area

Cactaceae	*Selenicereus setaceus* (Salm-Dyck) Berg	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Lepismium cruciforme* (Vell.) Miq.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis clavata* F.A.C.Weber	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis teres* (Vell.) Steud.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis crispata* (Haw.) Pfeiff.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis elliptica* G.Lindb. ex K.Schum.	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis pachyptera* Pfeiff.	Epiphyte	Observed as epiphyte in the study area

Cactaceae	*Rhipsalis* sp1	Epiphyte	Observed as epiphyte in the study area
Cactaceae	*Rhipsalis* sp2	Epiphyte	Observed as epiphyte in the study area
Dryopteridaceae	*Ctenitis* sp1	Epiphyte	Observed as epiphyte in the study area
Gesneriaceae	*Codonanthe devosiana* Lem.	Epiphyte	Observed as epiphyte in the study area
Gesneriaceae	*Nemathanthus* sp1	Epiphyte	Observed as epiphyte in the study area
Hymenophyllaceae	*Didymoglossum* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Epidendrum filicaule* Lindl.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp2	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Acianthera* sp3	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Eurystyles* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Lankesterella ceracifolia* (Barb.Rodr.) Mansf.	Epiphyte	Observed as epiphyte in the study area

Orchidaceae	*Masdevallia infracta* Lindl.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Maxillaria* sp	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Miltonia spectabilis*	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Scaphyglottis modesta* (Rchb.f.) Schltr.	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	*Vanilla chamissonis* Klotzsch	Hemiepiphyte	Observed as hemiepiphyte in the study area and according to *Vanilla* in Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro.Disponível em: <https://floradobrasil.jbrj.gov.br/FB12351>. Acesso em: 22 abr. 2022
Orchidaceae	*Polystachia* sp1	Epiphyte	Observed as epiphyte in the study area
Orchidaceae	Orchidaceae sp1	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia rotundifolia* (L.) Kunth	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia elongata*	Epiphyte	Observed as epiphyte in the study area

	Kunth		
Piperaceae	*Peperomia urocarpa* Fisch. & C.A.Mey.	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp1	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp2	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp3	Epiphyte	Observed as epiphyte in the study area
Piperaceae	*Peperomia* sp4	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum atlanticum* R.C. Moran & Labiak	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum nitidum* (Kaulf.) C.Presl	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum rigidum* Sm.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Campyloneurum* sp1	Epiphyte	Observed as epiphyte in the study area

Polypodiaceae	*Microgramma crispata* (Fée) R.M.Tryon & A.F.Tryon	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma geminata* (Schrad.) R.M.Tryon & A.F.Tryon	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma tecta* (Kaulf.) Alston	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.	Epiphyte	Observed as epiphyte in the study area

Polypodiaceae	*Pecluma sicca* (Lindm.) M.G. Price	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pecluma* sp1	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pleopeltis astrolepis* (Liebm.) E.Fourn.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Pleopeltis pleopeltifolia* (Raddi) Alston	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Serpocaulon menisciifolium* (Langsd. & Fisch.) A.R.Sm.	Epiphyte	Observed as epiphyte in the study area
Polypodiaceae	*Serpocaulon*	Epiphyte	Observed as epiphyte in the study area

	triseriale (Sw.) A. R. Sm.

Table 4 Results of Mixed Generalized Linear Models (GLMM) for vascular epiphyte species richness and abundance as a function of height zones, according to Johansson (1974), in trees in Ilha Grande, Brazilian Atlantic Forest. The information criteria (AIC) for the GLMM, GLM and the null model and the p values referring to the analysis of variance (ANOVA) of the comparison of the models are presented. Values in bold are significant.

Groups	**Parameters**	**Pseudo – R^2 (fixed effects)**	**Pseudo – R^2 (total)**	**Variance (radom effects)**	**Deviance (radom effects)**	**AIC - GLMM**	**AIC – GLM**	**AIC – null model**	**p-value compared to GLM *versus* GLMM**	**p-value compared to GLM *versus* null model**
Epiphytes in general	Richness	0.24	0.36	0.18	0.43	2680.3	2858.3	3087.1	<**0.01**	<**0.01**
	Abundance	0.22	0.33	0.10	0.32	4764.6	4934.8	5196.9	<**0.01**	<**0.01**
Bromeliaceae	Richness	0.01	0.22	0.36	0.60	905.8	998.9	1002.3	<**0.01**	**0.02**
	Abundance	0.10	0.30	0.23	0.47	1949.3	2065.1	2108	<**0.01**	<**0.01**
Polypodiaceae	Richness	0.06	0.36	0.57	0.75	966.4	1057.7	1077.8	<**0.01**	<**0.01**
	Abundance	0.19	0.57	0.66	0.81	1321.1	1569.2	1060.5	<**0.01**	<**0.01**
Orchidaceae	Richness	0.08	0.09	0.03	0.16	250.0	248.0		0.84	0.17

								246.3		
	Abundance	0.20	0.38	0.73	0.86	448.4	485.4	528.6	<**0.01**	<**0.01**
Araceae	Richness	0.04	0.53	1.47	1.21	1077.6	1277.4	1285.3	<**0.01**	<**0.01**
	Abundance	0.02	0.54	1.38	1.16	1327.8	1629.5	1631.3	<**0.01**	<**0.01**
Cactaceae	Richness	0.14	0.36	1.16	1.08	252.0	271.7	281.9	<**0.001**	<**0.001**
	Abundance	0.19	0.50	1.97	1.40	339.8	409.6	281.9	<**0.001**	<**0.001**

Table 5 Result of the paired comparison of the mixed generalized linear model for the richness of the height zones in trees in Ilha Grande, Brazilian Atlantic Forest, according to Johansson (1974).

Compared zones	**Standard deviation**	**z-score**	**p-value**
Z1-Z2	0.05	-5.32	<0.01
Z1-Z3	0.10	0.45	0.99
Z1-Z4	0.16	3.71	<0.01
Z1-Z5	0.58	8.73	<0.01
Z2-Z3	0.15	5.75	<0.01
Z2-Z4	0.25	8.68	<0.01
Z2-Z5	0.89	12.32	<0.01
Z3-Z4	0.16	3.28	<0.01
Z3-Z5	0.56	8.40	<0.01
Z4-Z5	0.40	5.75	<0.01

Table 6 Result of the paired comparison of the mixed generalized linear model for the abundance of the height zones in trees in Ilha Grande, Brazilian Atlantic Forest, according to Johansson (1974).

Compared zones	**Standard deviation**	**z-score**	**p-value**
Z1-Z2	0.05	-5.32	<0.01
Z1-Z3	0.10	0.45	0.99
Z1-Z4	0.17	3.71	0.34
Z1-Z5	0.58	8.73	<0.01
Z2-Z3	0.15	5.75	<0.01
Z2-Z4	0.25	8.68	<0.01
Z2-Z5	0.90	12.32	<0.01
Z3-Z4	0.16	3.28	0.45
Z3-Z5	0.56	8.40	<0.01
Z4-Z5	0.40	5.75	<0.01

Table 7 Results of the Generalized Linear Models for vascular epiphyte species richness and abundance as a function of the height zones in trees in Ilha Grande, Brazilian Atlantic Forest, according to Johansson (1974). Plots located in RAPELD da Ilha Grande, Rio de Janeiro, two in restinga vegetation, one in dense lowland rainforest and two in dense submontane rainforest, respectively in that order in the table.

Plots	**Parameters**	**p-value**	**Pseudo – R^2 (Cragg-Uhler)**	**AIC**	**AIC – null model**	**p-value compared to null model**
1	Richness	<0.01	0.40	635.4	784.7	**<0.001**
	Abundance	<0.01	0.55	1043.6	1310.6	**<0.001**
2	Richness	<0.01	0.14	726.8	756.5	**<0.001**
	Abundance	<0.01	0.19	1018.3	1064.7	**<0.001**
3	Richness	<0.01	0.22	329.8	363.1	**<0.001**
	Abundance	<0.01	0.37	660.5	745.3	**<0.001**
4	Richness	<0.01	0.30	402.5	460.7	**<0.001**
	Abundance	<0.01	0.34	738.2	819.0	**<0.001**
5	Richness	<0.01	0.09	514.3	528.2	**<0.001**
	Abundance	<0.01	0.07	1059.9	1071.1	**<0.001**

CONSIDERAÇÕES FINAIS

A alta diversidade de epífitas nas florestas da Mata Atlântica é amplamente reconhecida e é corroborada nesta pesquisa. A Ilha Grande se destaca como uma das áreas com maior riqueza de epífitas no estado do Rio de Janeiro. Apesar da maior parte das espécies terem sido levantadas a partir de trabalhos publicados e herbários online, a amostragem de campo em apenas cinco parcelas do RAPELD registrou uma riqueza elevada, cuja curva de rarefação mostra crescimento contínuo. A maioria das espécies possui estado de conservação desconhecido, mas foram registradas espécies consideradas como vulneráveis e outras ameaçadas de extinção. Os resultados do capítulo 1 evidenciam a necessidade de maiores esforços de coleta em áreas pouco amostradas da ilha e a importância da realização de estudos que investiguem a dinâmica das populações e comunidades de plantas epífitas na área de estudo para verificar que fatores que regem a montagem dessas comunidades e que possam subsidiar a elaboração de estratégias efetivas para a preservação desta flora.

Os capítulos 2 e 3 correspondem a alguns dos primeiros trabalhos a analisar o efeito das variáveis ambientais e morfométricas das árvores em uma abordagem multiescalas em florestas da Mata Atlântica onde testa-se a hipótese de que habitats, ou microhabitats, com maior umidade e substratos disponíveis possuem maior diversidade de epífitas vasculares e composição de espécies diferenciada. As principais conclusões estão resumidas a seguir:

i. florestas com diferentes fitofisionomias apresentam riqueza, abundância e composição únicas, ressaltando que a floresta submontana em estado avançado de regeneração é a que apresenta maior riqueza de espécies;

ii. a análise em macroescala mostrou que não há efeito da morfometria arbórea sobre a diversidade de epífitas, mas há efeito positivo do número de árvores e efeito negativo da cobertura do dossel; quando as hemiepífitas foram removidas, houve efeito do diâmetro à altura do peito na riqueza e na abundância.

iii. em mesoescala, as variáveis analisadas não influenciam a diversidade de epífitas na maioria das florestas, apenas em uma das florestas de restinga e na floresta de terras baixas;

iv. em microescala, a maior diversidade de epífitas ocorre no tronco das árvores e os menores valores ocorrem na copa externa, onde também há uma composição única; o padrão de estratificação vertical se mantém quando as florestas são analisadas separadamente;

v. a análise das famílias epifíticas com maior riqueza mostrou que elas não são afetadas da mesma forma pelas condições ambientais e morfométricas das árvores, bem como apresentam diferentes padrões de diversidade ao longo do gradiente vertical da floresta.

As conclusões mostram como a heterogeneidade espacial das florestas da Ilha Grande afeta a diversidade de epífitas de distintas formas nas diferentes escalas. Os padrões observados corroboram a hipótese central da tese e vão de encontro com a teoria do nicho ecológico, uma vez que habitats mais úmidos e bem conservados, com mais árvores, árvores de grande porte ou áreas com maior superfície ao longo das árvores, como o tronco, foram os ambientes, ou microambientes, que se destacaram com maior diversidade de epífitas. Além disso, há influência destes fatores na composição florística e os táxons responderam de formas diferentes às variações ambientais. Por isso, sugere-se que as condições abióticas das florestas e das zonas de altura das árvores atuam selecionando táxons e grupos de epífitas de acordo com as características funcionais direcionando a montagem das comunidades nesses ambientes.

Entretanto, aspectos relacionados a dispersão das espécies não podem ser descartados, pois a disponibilidade de habitats foi um importante fator em todas as escalas e o principal em escala de paisagem (número de árvores por unidade amostral), tendo sido o único significativo para todas as famílias. Além disso, estudos futuros devem incluir outras variáveis ambientais nas análises, pois, apesar das variáveis aqui analisadas terem efeito significativo, as intensidades dos efeitos foram fracas em quase todos os casos, indicando que outros fatores são importantes na estruturação das comunidades. Podem ser incluídos: gradiente de altitude, outras fitofisionomias e estágios sucessionais, identidade das árvores hospedeiras, rugosidade e química da casca, mensuração de luminosidade, umidade e temperatura ao longo do gradiente vertical, relações bióticas de competição ou facilitação e outros reconhecidamente relevantes na distribuição das epífitas. Além disso, os resultados apontam a necessidade da análise individual dos táxons epifíticos e daquelas consideradas hemiepífitas ou videiras nômades (que se conectam ao solo em algum estágio da vida), pois as estratégias adaptativas de determinados táxons e grupos podem mascarar padrões gerais da comunidade.

Por fim, reiteramos que florestas bem conservadas, com maior número de árvores, em especial aquelas de maior porte, devem ser priorizadas para a proteção de um maior número de espécies de epífitas. Entretanto, demonstramos que há baixa similaridade florística entre as fitofisionomias, com baixa redundância na composição de espécies, com cada floresta possuindo uma composição singular, o que indica que mesmo aquelas com menor riqueza também devem ser consideradas nas estratégias de conservação. Além disso, alterações antrópicas nas florestas da ilha devem ser cuidadosamente fiscalizadas, especialmente o corte seletivo de árvores, pois leva à redução dos substratos disponíveis e mudanças microclimáticas, fatores que afetam a riqueza e a composição das epífitas acarretando a perda desta parcela da biodiversidade.