UNIVERSIDADE ESTADUAL DE SANTA CRUZ
Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade

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ESTRUTURA DE COMUNIDADE DE SAMAMBAIAS EM UMA FLORESTA MONTANA, BAHIA, BRASIL: diversidade e redes de interação

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Dissertação apresentada à Universidade Estadual de Santa Cruz, para a obtenção de Título de Mestre em Ecologia e Conservação da Biodiversidade.

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RESUMO

ESTRUTURA DE COMUNIDADE DE SAMAMBAIAS EM UMA FLORESTA MONTANA, BAHIA, BRASIL: diversidade e redes de interação

Este trabalho consiste em um estudo de ecologia de comunidade de samambaias em uma floresta ombrófila montana no sul da Bahia, Brasil, seguindo duas abordagens: estrutura filogenética de comunidades e redes de interação. Na primeira abordagem analizamos o comportamento de cada forma de vida: erva epífita, erva hemiepífita, erva terrestre e arborescente em relação a diferentes medidas de diversidade taxonômica e filogenética. Com isso, pudemos inferir sobre os processos evolutivos por trás da diferenciação em formas de vida no grupo. Ainda, analisamos a contribuição do componente epífita na diversidade total da comunidade e obtivemos um ganho significativo em comparação com o esperado pelo acaso. Com isso, evidenciamos não só a importância das epífitas, mas da diferenciação entre as samambaias no solo e sobre forófitos. Seguindo a abordagem de redes de interação, pudemos identificar a especialização da rede samambaia epífita vs. forófito e a estrutura compartimentalizada da rede epífita vs. epífita. As duas redes apresentaram estrurura aleatória em relação a aninhamento, entretanto, as relações de co-ocorrência entre as epífitas são estruturadas em sub-grupos de interação, enquanto a rede epífita-forófito apresenta espécies com poucos links, i.e. especialistas. Detectamos a especialização entre epífitas e forófitos, mas não uma preferência das samambaias epífitas por samambaias arborescentes como forófito. Ao invés, identificamos a importância das árvores mortas na manutenção da riqueza da comunidade epífita. Com isso, esperamos que nossos resultados sirvam para direcionar os esforços de conservação das samambaias em processos e interações, ao invés de seguir abordagens tradicionais de conservação de espécies.

Palavras-chave: diversidade filogenética; partição aditiva; metacomunidade epífita; epífita-forófito

ABSTRACT

FERN COMMUNITY STRUCTURE IN A TROPICAL MONTANE FOREST, BAHIA, BRAZIL: diversity and ecological networks

This work consists of a fern community ecology study in a montane forest in southern Bahia, Brazil, following two approaches: community phylogenetic structure and ecological networks. Following the first approach we analyzed the behavior of each life form: epiphytic herb, hemiepiphytic herb, terrestrial herb an tree fern in relation to different measures of taxonomic and phylogenetic diversity. This allowed us to understand the evolutionary processes behind life forms differentiation in the group. Still, we analyzed the contribution of epiphyte component in total community diversity and found a significant gain than expected by a null model. With this, we highlight not only the epiphyte importance, but the differentiation between the ferns on soil and on phorophytes. Following the approach of ecological networks, we could identify specialization of epiphye vs. phorophyte network and a compartmentalised structure of epiphyte vs. epiphyte network. This shows that relations of co-occurrence between epiphytes are structured into sub-groups of interaction, while the epiphyte-host interactions are specialized. We detected specialization between epiphytes and phorophytes, but not a preference of epiphytic ferns for tree ferns as hosts. Instead, we identified the importance of dead trees in maintaining the richness of the epiphytic community. Thus, we hope that our findings serve to guide fern conservation efforts on the processes and interactions, rather than follow traditional approaches of species conservation.

Keywords: phylogenetic diversity; additive partitioning; epiphyte metacommunity; epiphyte-phorophyte

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1 INTRODUÇÃO

As tendências em ecologia de comunidades buscam elucidar os processos subjacentes à estrutura e funcionamento de assembléias de espécies (Vellend, 2010). Desde o surgimento da teoria neutra de Hubbel (Hubbell, 2001), a deriva ecológica tornou-se um dos principais processos para explicar padrões de comunidades. Embora não seja a única, nem mesmo totalmente aceita, sua principal contribuição foi fomentar a busca de novos padrões por trás dos processos nesse nível de organização.

Estudos de estrutura de comunidades vegetais são em maior número baseados em espécies de angiospermas, especialmente as arbóreas. No entanto, a utilização de outros grupos de plantas pode ajudar na compreensão dos processos ecológicos e no embasamento de teorias ecológicas. Nesse sentido, as samambaias representam um dos principais grupos de plantas desprovidas de sementes, contribuindo com 80 por cento da diversidade em espécies (Schuettpelz and Pryer, 2009). A diversidade acentuada de samambaias é conseqüência da radiação das Angiospermas no período Cenozóico, proporcionando novos recursos, onde as samambaias puderam diversificar (Schneider et al., 2004).

Com uma estutura de dossel mais desenvolvida, a diferenciação de samambaias herbáceas e epífitas foi acentuada. As samambaias atuais compreendem uma grande variedade de formas de vida, incluindo epífitas, hemiepífitas, ervas terrestres e arborescentes. Com isso, permite uma grande amostra de grupos não arbóreos quando são utilizadas em estudos ecológicos.

Além disso, estudos envolvendo comunidades de samambaias têm contribuído para identificar padrões de distribuição de espécies de plantas vasculares relacionados com as variáveis ambientais, como solo, umidade e luminosidade (Page, 2002). A distribuição do grupo é explicada em parte por vicariância e outra pela dispersão a longa distância (Wolf et al., 2001), sendo as florestas tropicais o centro de diversidade e endemismo do grupo (Tryon, 1972). Além disso, as florestas tropicais montanas funcionam como barreiras para migração, promovendo altos índices de riqueza e endemismo (Moran, 1995). Nesse contexto, as florestas brasileiras contribuem com uma quantidade notável de espécies, cerca de 1200, de uma estimativa de 3000 espécies para a América Tropical (Giulietti et al., 2005).

Neste trabalho a estrutura de uma comunidade de samambaias será discutida

seguindo duas abordagens: diversidade filogenética e redes de interação. No primeiro capítulo medidas de diversidade filogenéticas e taxonômicas são utilizadas para responder qual o efeito filogenético da forma de vida na estrutura filogenética da comunidade, e, também, a relação da comunidade com algumas variáveis ambientais. O segundo capítulo consiste de um estudo da comunidade de samambaias epífitas baseado em redes de interação epífitas-forófitos, bem como redes de co-ocorrência entre as espécies de epífitas. A partir dessas abordagens espera-se testar qual fator, entre competição e facilitação, é mais determinante na estururação da metacomunidade de epífitas, bem como se existe alguma especificidade na rede epífita-forófito.

A estrutura filogenética da comunidade pode ser uma abordagem interessante para entender os processos ecológicos que a mantem (Webb, 2000), pois é baseada na história evolutiva de espécies coexistindo em um determinado ambiente. Por outro lado, o conceito de redes complexas pode esclarecer a interdependência sobre as interações da comunidade (Bascompte et al., 2003), que está diretamente relacionada à especialização e robustez dessas interações (Burns, 2007). Além disso, Estudos envolvendo comunidade de epífitas são de extrema relevância visto que são um dos principais componentes da diversidade em florestas tropicais e a primeira comunidade a entrar em declínio diante de distúrbios (Barthlott et al., 2001).

As abordagens adotadas podem ser úteis para o desenvolvimento de estratégias de conservação e bases conceituais para a ecologia de comunidades de plantas e, com isso, concentrar os esforços de conservação em processos e interações, ao invés de seguir abordagens tradicionais baseadas apenas na conservação de espécies.

Aliando essas abordagens ao conceito de custo efetivo em estudos de conservação (Gardner et al., 2008), espera-se poder reforçar o potencial do grupo em questão, as samambaias, em responder de maneira rápida, efetiva e de baixo custo a perguntas ecológicas, e com isso, servir de subsídio para proposições de manejo e conservação.

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2 REVISÃO BIBLIOGRÁFICA

Diversidade de samambaias

As samambaias e licófitas representam os dois grupos de plantas vasculares desprovidos de sementes, representados por aproximadamente 9.000 espécies (Smith et al., 2006). São grupos bastante diversos e abundantes no Neotrópico, onde se estima a ocorrência de 3.500 espécies (Poulsen and Nielsen, 1995).

O Brasil abriga um dos principais centros de diversidade e endemismo de samambaias e licófitas da região neotropical (Tryon, 1972; Prado and Sylvestre, 2010). Atualmente, são reconhecidas 1176 espécies de samambaias e licófitas no país, das quais 38% são endêmicas (Prado and Sylvestre, 2010). Estimativas anteriores consideravam 600 espécies, sendo 44% de endêmicas (Tryon, 1972).

As samambaias (Monilophyta) e licófitas (Licophyta) foram tradicionalmente classificadas na divisão Pteridophyta, entretanto, segundo estudos recentes, as licófitas representam um grupo à parte das plantas vasculares Monilophyta e Spermatophyta (plantas com sementes), sendo as samambaias mais próximas filogeneticamente das plantas com sementes do que das licófitas (Pryer et al., 2001; Smith et al., 2006). Atualmente, não foi definida uma nomenclatura para o grupo, sendo o termo samambaia, o mais aceito para denominar as Monilophyta.

Apresentam a distribuição determinada em parte pela dispersão, por meio de seus esporos, os quais são capazes de atingir longas distâncias, e, em parte pela vicariância (Wolf et al., 2001). Para as espécies neotropicais a distribuição está relacionada a centros regionais de diversidade e endemismos, sendo o Brasil um deles (Tryon, 1972). Esses centros regionais representam áreas de migração, persistência de espécies e especiação de samambaias e licófitas (Tryon, 1972). No Brasil, consideram-se os limites da Mata Atlântica como o principal centro de endemismo do grupo (Paciencia, 2008; Prado and Sylvestre, 2010).

Observam-se diferenças entre a abundância e riqueza de samambaias entre os diferentes hábitos e estratos de florestas tropicais, havendo uma maior riqueza de formas de vida epifíticas (Dittrich et al., 2005; Watkins Jr et al., 2006). Considerando a comunidade de epífitas vasculares, representam um importante componente desta flora, contribuindo

significativamente na diversidade das florestas (Cardelus et al., 2006).

Dubuisson et al. (2009) e Schuettpelz and Pryer (2009) colocam as adaptações para o epifitismo como sendo o principal motor da diversificação de determinadas famílias de samambaias, como em Hymenophyllaceae e Polypodiaceae. Atualmente, essa diversificação se reflete no fato de que as samambaias são o segundo grupo de plantas vasculares com a maior proporção de epíftas, possuindo 29 por cento das espécies com esse hábito; ocupando o primeiro lugar, estão as monocotiledôneas, com 31 por cento, a maioria representada por Orchidaceae (Dubuisson et al., 2009).

Ecologia de comunidade de samambaias

Os primeiros trabalhos em ecologia envolvendo samambaias surgiram a partir de estudos taxonômicos, como uma forma de compreender aspectos morfológicos do grupo em relação a adaptações ao ambiente onde são encontrados (Mehltreter et al., 2010). Embora as samambaias sejam um grupo negligenciado na maior parte dos estudos ecológicos, nos últimos anos houve um aumento considerável nas publicações em ecologia. Isso resultou na primeira compilação estudos ecológicos em samambaias (Mehltreter et al., 2010), a qual teve, especialmente, o objetivo de reunir as informações geradas até o momento, bem como, a motivação e o direcionamento de novos estudos.

As bases teóricas dos trabalhos ecológicos com samambaias são fundamentadas especialmente em biogeografia, dinâmica de populações, ciclagem de nutrientes e impactos de espécies invasoras (Mehltreter et al., 2010). Entretanto, na última década houve um crescimento de trabalhos em ecologia de comunidades envolvendo estrutura (Tuomisto et al., 2002; Jones et al., 2006; Zuquim et al., 2009; Kluge and Kessler, 2010), padrões de distribuição espacial (Tuomisto et al., 2003; Kreft et al., 2010) fragmentação (Paciencia and Prado, 2005) e estudos comparativos com outros grupos visando compreender processos gerais em ecologia e conservação da biodiversidade (Faria et al., 2007; Kreft et al., 2010; Mandl et al., 2010).

Diante disso, a ecologia de comunidades de samambaias passou a ser um tópico mais recorrente, entretanto, ainda com poucas repercussões e aplicações em conservação. Em função de alguns conceitos já estabelecidos e de estudos recentes, as samambaias apresentam um potencial para uso em estudos de conservação e manejo de comunidades e paisagem (Mehltreter et al., 2010).

Nesse contexto, uma das discussões emergentes é o papel da diferenciação de nicho vs. neutralidade na estruturação de assembléias de espécies de samambaias. Enquanto alguns autores indicam que diferenciação de nicho é um dos principais determinantes na estruturação de comunidades (Jones et al., 2006), outros apontam a limitação de dispersão aliada a processos estocásticos como fator determinante (Tuomisto et al., 2003). Em contrapartida, uma outra proposta é a de se considerar a influência conjunta da dispersão e do determinismo do ambiente, i.e., uma explicação complementar pelo papel do nicho e da neutralidade, ao invés de idéias controversas (Karst et al., 2005).

De maneira geral, considera-se efeitos de dispersão, competição e estocasticidade na estruturação de assembléias de espécies (Karst et al., 2005). Em menor escala, identifica-se a heterogeneidade ambiental como um importante fator em diferenças florísticas (Jones et al., 2006). Dentre essas variáveis ambientais, destacam-se variações em nutrientes do solo (Tuomisto et al., 2002; Karst et al., 2005), umidade do solo (Karst et al., 2005) e abertura de dossel (Zuquim et al., 2009).

Estudos comparativos de samambaias com outros grupos envolvem tanto plantas vasculares, avasculares, como estudos envolvendo grupos animais distintos. Alguns desses estudos envolveram samambaias vs. plantas avasculares como musgos, líquens e hepáticas. Embora samambaias e plantas avasculares exibam padrões semelhantes de alfa e beta diversidade (Mandl et al., 2010), devido às dificuldades taxonômicas e de amostragem desses grupos, são pouco utilizados em ecologia e conservação (Roberts et al., 2005). Samambaias e licófitas são usualmente tratadas em conjunto devido às relações taxonômicas definidas antes dos trabalhos de Pryer et al. (2001) mas apresentam respostas ecológicas bastante semelhantes Paciencia (2008).

A descoberta de relações evolutivas mais próximas entre samambaias e angiospermas fomentaram perguntas ecológicas envolvendo respostas às variações ambientais, florísticas e estruturais de comunidades vegetais (Schneider et al., 2004). Isso reforçou não só o potencial de estudos comparativos, mas também o papel do grupo na geração de fundamentos teóricos em ecologia de comunidades e conservação.

Nesse contexto de comparações de comunidades de samambaias e de angiospermas, balanço hídrico, luminosidade, solo e relevo são fatores preditores de riqueza para ambos os grupos. Variações edáficas em um continuum são, em parte, suficientes para refletir em variações florísticas dos dois grupos (Tuomisto et al., 2002; Kreft et al., 2010).

Entretanto, para comunidades de samambaias disponibilidade de água no solo aparece como um fator muito mais forte (Kreft et al., 2010). Ainda, as samambaias formam um grupo que responde mais rapidamente a distúrbios e perturbações, podendo ser indicador de perturbações na comunidade vegetal como um todo.

Além disso, dentro do próprio grupo existem variações em formas de vida e adaptações entre os diferentes taxons. Destacam-se, especialmente as diferenças funcionais na ecologia de plantas epífitas e terrestres (Watkins and Cardelus, 2009). Assembléias de plantas desses grupos respondem diferentemente em relação à variação de solo, luminosidade e disponibilidade hídrica. Samambaias epífitas parecem ser mais sensíveis à luminosidade e umidade do ar, enquanto para samambaias terrestres variações edáficas são mais influentes (Watkins and Cardelus, 2009).

De maneira geral, as samambaias epífitas apresentam um arcabouço teórico mais desenvolvido, com algumas contribuições para teorias mais gerais em ecologia de comunidades, como o "mid-domain effect", por exemplo. Cardelus et al. (2006) utilizaram as samambaias como grupo modelo para explicar as variações de riqueza ao longo de um gradiente altitudinal, evidenciando um pico de riqueza em elevações médias (i.e. "mid-domain effect"), e, ainda, apontando a efetividade do grupo em responder a estas variações (Cardelus et al., 2006; Paciencia, 2008; Kluge and Kessler, 2010).

Um outro aspecto relevante quanto às samambaias é sua elevada representatividade em áreas tropicais montanas, principalmente em função de suas necessidades hídricas e de limitação de dispersão, promovendo altos valores de diversidade (Moran, 1995; Mehltreter et al., 2010). Embora o Brasil seja um dos centros de diversidade do grupo, especialmente nas cadeias de montanhas, os estudos ainda são mais desenvolvidos nas áreas de florestas baixas na Amazônia. No sul da Bahia, por exemplo, existe apenas um trabalho que reporta sobre comunidades de samambaias, sendo desenvolvido em áreas de floresta ombrófila densa de terras baixas (Paciencia and Prado, 2005).

Em suma, quando o grupo é foco de estudos ecológicos resulta em conclusões inovadoras e inusitadas (Mehltreter et al., 2010). Diante disso, mesmo com trabalhos em ecologia de samambaias em ascensão, ainda existem potencialidades para o desenvolvimento de estudos mais propositivos em relação à conservação da biodiversidade, inseridos em um contexto de fragmentação e mudanças na paisagem.

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3 CAPÍTULO 1

Phylogenetic differentiation among life forms on a fern community in a tropical montane forest, Bahia, Brazil[1]

Sara R. Mortara, Daniela C. Talora, André M. Amorim

ABSTRACT

We studied fern community structure based on phylogenetic and taxonomic characters, as well as life form differentiation effect on community complexity. Survey plots were placed in a tropical montane forest, in Southern Bahia, Brazil. We found 78 fern species belonging to epiphyte and hemiepiphyte herbs, terrestrial herb, rupestrial herb and tree fern life forms. We considered two subscales on our sample: ferns on phorophytes and ferns on soil so as to identify epiphyte contribution to community diversity. Fern community was significantly related with canopy openness, but in inverse relationships between species (Shannon index) and taxonomic distinctness, driving conclusions about process generating the community in general. Among life forms, epiphyte and tree fern communities presented phylogenetic aggregation, others were phylogenetically random. When contrasting soil and phorophyte ferns we found beta-diversity significantly higher than expected of a random model between these scales. We expect that conservation strategies on tropical forests directed to fern communities consider complexity of life forms and sensitivity to light disturbances. Also, we suggest that fern community should be adopted for studies leading to conservation strategies due to their cost-effectiveness aspects.

Keywords: additive partitioning; epiphyte ferns; canopy openness; taxonomic diversity.

3.1 Introduction

Diversity and richness measures are generally used to characterize ecological communities. These community descriptors are directly related to their structure and functioning and yet they will determine ecological models and conservation strategies. Al-

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though simple diversity measures are frequently used, they supply incomplete information about community structure and functioning, and about the process that generate species diversity variation as well (Kluge and Kessler, 2010). Hence, it is advisable to combine other parameters with conventional species measures to act as a background for conservation strategies. As each species contributes on its own way to the diversity of a community, given its genetic and morphological characters, these issues should be considered when selecting high priority conservation areas (Allen et al., 2009).

Phylogenetic structure analysis of a community provides information about the process that generates it (Webb, 2000). It can be very useful to understand ecological relationships between species and also predict extinction scenarios, both fundamental for conservation strategies. Since they became widespread, phylogenetic and taxonomic measures were adopted for describing plant community structure, its relation with environment, phylogenetic traits and for indicating conservation actions. They were used specially for angiosperm communities, but were recently adopted for fern assemblages (Kluge and Kessler, 2010).

Ferns represent well diversified taxa in tropical forests, and despite being absent in most of the vegetation community studies, they seemed to elucidate relevant issues in plant ecology (Tuomisto et al., 2003; Karst et al., 2005; Cardelus et al., 2006; Zuquim et al., 2009). In terms of morphology, taxonomy and phylogeny, there is a well defined theory, although, subtle questions about ecology and adaptations of these groups remain unsolved (Page, 2002).

Moreover, ferns present a wide range of life forms, such as herbs (epiphyte, hemiepiphyte and terrestrial) and tree ferns, occupying different *stracta* in a tropical forest. Among these life forms, epiphyte herbs can occupy more extreme habitats due to a wider distribution as compared to the terrestrial ones and seem to present higher community diversity (Watkins Jr et al., 2006).

Living groups of ferns are represented by recent diversified species on Cenozoic, due to more complex canopies dominated by Angiosperms (Schneider et al., 2004). Among all fern taxa, the Polypodiales Order, represented specially by epiphytic life form, is considered the most recent diversified fern phylogenetic group (Schuettpelz and Pryer, 2009). Although epiphytic ferns are, in general, supported by phylogeny, other life forms do not seem to be directly related with the group evolutive history (Schuettpelz and Pryer,

2009).

Ferns are well diversified on the tropics and seem to reflect the complexity of the community where they occur. Ecological studies involving these groups need to be correlated with the community as a whole, as well as the individual species niche (Page, 2002). As a consequence of the fern spore dispersion, they hold a wide distribution, which is balanced by habitat restrictions and generates regional diversity and endemism centers for these groups (Tryon, 1972).

In Brazil, the diversity sites correspond, in general, to the Atlantic Forest boundaries, specially southeastern mountain ranges as Serra do Mar (Tryon, 1972). Even though ferns can disperse through wide distances, mountain ranges constitute ecological limits for migration, resulting on high richness and endemism taxa (Tryon, 1972; Moran, 1995). The high levels of alpha diversity can be partially explained by habitat heterogeneity, result of different elevations, soil, geological origin and microclimate; and in part by the random walk model, derived from the neutral theory (Tuomisto et al., 2003).

Montane forests on southern Bahia present characteristics similar to Serra do Mar mountain ranges, but there are few studies of fern communities in these areas. Despite some works with edge effect and multi-taxa fragmentation studies (Paciencia and Prado, 2005; Faria et al., 2007) all on lower forests, there is an information gap in southern Bahia fern montane communities. A floristic study evidenced a high diversity area for ferns on southern Bahia, harboring 178 fern species in a single 2.000 ha locality (Matos et al., 2010). Previous work with species assembly of ferns along elevational gradients reported that terrestrial and epiphytic ferns present random phylogenetic structure, also that only epiphytes presented phylogenetic trait variation along it, being overdispersed on mid-elevations and clustered on extremes (Kluge and Kessler, 2010).

On our work we analyzed which diversity measurements we should adopt for quantify fern community structure and the role of canopy openness influencing diversity. We also investigated questions concerning the phylogeny effect in structuring fern life forms and tested if the epiphyte community represents the major component of community diversity. Our predictions are that measures that incorporate phylogenetic information may be more suitable to translate aspects of community structure. Additionally, due to fern recent diversification the community phylogenetic structure would be, in general, aggregated and as epiphyte ferns are even more recent, they should direct such pattern.

3.2 Materials and Methods

Study site

Serra Bonita mountain range (7.500 ha), is located at Camacan and Pau Brasil municipalities, in southern Bahia, Brazil. It covers one of the last forest patches in the region. Serra Bonita Private Reserve, the study site, at the middle part of this mountain complex, covers 2.000 ha of protected areas, between 300 and 1.080 m above sea level (Figure 3.1).
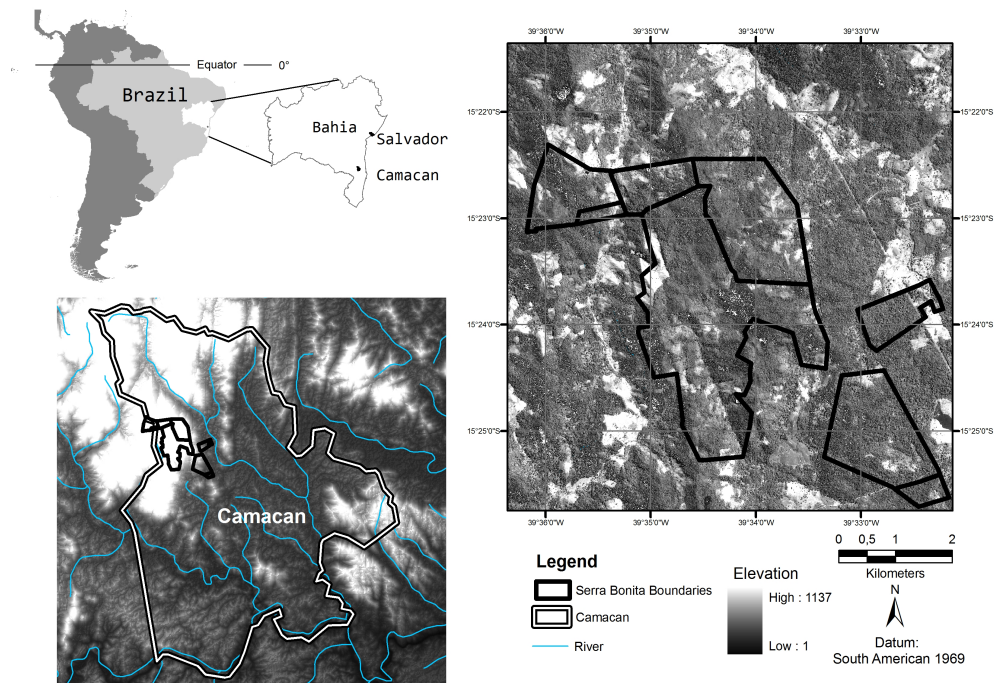
Figure 3.1: Serra Bonita Private Reserve location, indicating its boundaries and elevation, Camacan municipality, Bahia, Brazil.

The climate is warm and humid, with annual precipitation ranging from 1.500 to 1.800 mm, equally distributed along the year (Roeder, 1975). According to CEPEC data collected from 2000 to 2010, temperature on the study area varies from 20.1 °C to 28.8 °C, with 24.5 °C average and mean precipitation 100.5 per month. Total potential evapotranspiration ranges from 1.200 to 1.300 mm and the air relative humidity is around 80 percent. Serra Bonita Private Reserve forest cover ranges from dense sub-montane rain forest with elements of semideciduous forests to montane rain forest at the altitudinal gradient (Amorim et al., 2009).

The vegetation conservation status and physical structure vary greatly, from old-growth forests to different stages of regenerating forests over abandoned pasture, logging and agriculture areas (Amorim et al., 2009). Also, a road leading to a transmission tower on the Reserve's mountain top, resulted in the eradication of the original vegetation in that area (Amorim et al., 2009).

Even though the area still suffers from fragmentation effects, recent research has shown that these fragments shelter large number of rare and endemic species. Preliminary floristic studies have identified ca. 700 species of angiosperms (Amorim et al., 2009), 178 species of ferns and four lycophytes (Matos et al., 2010), with several new to science species, including a very notable bromeliad (Amorim and Leme, 2009) and three new fern species.

Community sampling

Survey plots were established following the procedure of Gentry (1982). Sample unit consists of ten 2 x 50 m plots aligned parallel to each other and separated by a distance of 20 m. Each sample unit covers a 1000 m^2 area. Three sample units were laid out on the Serra Bonita Private Reserve along an old-growth montane rain forest area, where there is feasible access by walking trails, distant 100 m from each other. Gentry's method was once developed for a rapid sample of arboreal species richness and density on a 0,1 ha area and since then it has been well disseminated, other taxa and multi-taxa studies inclusive (Magnusson et al., 2005).

All herbaceous ferns (i.e. terrestrial herbs, epiphyte herbs, hemiepiphyte herbs and rupestrial individuals) and tree ferns on soil and understory until 3 m high were quantified and identified. Epiphyte and hemiepiphyte ferns were sampled over four types of phorophytes: angiosperm trees, tree ferns, dead trunks I (i.e. dead trees fallen inside plots) and dead trunks II (i.e. dead trees still up). Voucher material was deposited in CEPEC herbarium and the species were classified in families according to Smith et al. (2006) classification system.

We collected soil and canopy variables for correlation with plant community structure data. For soil physical and chemical composition analysis we collected soil samples 0-20 cm and 20-40 cm deep from three sub-units of each transect. All soil samples from the same layer and sample unit were homogenized, totalizing six samples for the study

area. Soil samples were sent to CEPEC soil laboratory for physical (texture and conductivity) and chemical (pH, Ca, P, N e Mg) property analyses. Canopy openness was analyzed from digital images of forest canopy taken with a hemispherical lens attached to a digital camera and tripod and treated on the software Gap Light Analyzer (Frazer et al., 1999). Two photographs were shot on each plot of the sample units at 15 and 35 m, totalizing 60 photographs. We used total values per plot for correlation with community diversity calculated by Shannon and taxonomic distinctness.

Data analysis

In order to describe community structure we analyzed richness, diversity and taxonomy and phylogenetic indices. Statistical analyses were conducted on R software (R Core Development Team, 2009). We used vegan (Oksanen et al., 2010) and picante (Kembel et al., 2010) packages.

For Species Abundance Distribution (SAD) analysis we used functions from P. I. Prado (available at http://ecologia.ib.usp.br/let/doku.php?id=engl:tutorials:rcode). We tested SAD curve adjustment to broken stick, geometric series, Fisher's log-series and log-normal models based on maximum likelihood and Akaike Information Criterion (AIC).

We calculated phylogenetic measures by generating a phylogenetic tree from topological taxonomic information as in Kluge and Kessler (2010), instead of using adapted phylogenetic trees. For our proposal, our generated tree carried more information about species relatedness. From the communty sampled we analyzed taxonomic and phylogenetic diversity measures, and additive partitioning of diversity.

We used taxonomic diversity (Δ) and distinctness indices (Δ^*) for evaluate taxonomic relatedness in relation to individual abundances. They are both phylogeny topological measurements. Taxonomy diversity index consists of mean pairwise taxonomic distance of random chosen individuals and incorporates species abundances and their taxonomic relationships. Taxonomic distinctness index consists of mean pairwise taxonomic distance of different species individuals (Clarke and Warwick, 1998; Warwick and Clarke, 1998). The notation Δ^+ is the presence/absence conversion of these indices and represents mean taxonomic distance between any given species (Clarke and Warwick, 1998).

We also evaluated phylogenetic influence on species richness by Phylogenetic Di-

versity (PD) and Evolutive History (EH). They are measures based on phylogenetic trees and do not include species abundance information. Phylogenetic diversity is a measure of the total branch length of the minimum spanning path (Faith, 1992). It corresponds to a measure dependent to species richness, which do not incorporate abundance information to diversity.

Evolutive history comprises the sum of branch lengths of a phylogenetic tree. As well as PD, EH is dependent to richness but can bottom up the uniqueness of a species and its contribution for the communtity evolution. When talking about conservation of ecological processes that generate the species and community biodiversity, both are useful measures to translate these issues.

For evaluate environmental effect on community we used correlation tests, such as Mantel test and Pearson's correlation analyses and regression analysis. We considered environmental effect of canopy openness and soil components.

Considering the two different spatial scales that emerge from the studied community, plots and transect, we adopted the additive partitioning of diversity so as to clarify the contribution of the beta diversity from epiphyte and non-epiphyte fern communities over the sample design. Additive partitioning of diversity considers the additive relation withing-community (α) diversity and among-community (β) diversity (i.e. gamma-diversity is partitioned into alpha and beta-diversities at multiple spatial and temporal scales) and its use to explain diversity distribution can assist the design of conservation strategies (Veech et al., 2002). We defined:

$$\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3$$

Where α_1 represents diversity within ferns on phorophytes and soil, β_1 represents diversity among ferns on phorophytes and soil, β_2 represents diversity among plots and β_3 represents diversity among sample units.

3.3 Results

Community description

We sampled 78 species belonging to 41 genus and 14 families, among 2433 individuals. The richest family was Polypodiaceae, harboring 20 species. Community species abundance distribution curve shows few abundant species and a considerable number of

rare species (Figure 3.2). The observed distribution fits Fisher's logarithmic series model (Fisher et al., 1943), according to maximum likelihood and AIC. We also represent SAD for angiosperm trees and tree fern community in Serra Bonita Private Reserve, that were sampled on other study on the same sample units (cite Diogo). Arboreal community also fits to Fisher's abundance distribution model.

Fern community presented *Asplenium auriculatum* Sw. (Aspleniaceae), an epiphyte herb, and *Lastreopsis amplissima* (C. Presl) Tindale (Dryopteridaceae), a terrestrial herb as the most abundant species. The most abundant species on the arboreal community were *Cyathea phalerata* Mart. (Cyatheaceae), a tree fern, *Eugenia schotiana* O. Berg (Myrtaceae), a canopy tree, *Guapira obtusata* (Jacq.) Little (Nyctaginaceae), an emergent tree, and *Bathysa mendocaei* K. Schum. (Rubiaceae), a shrub.
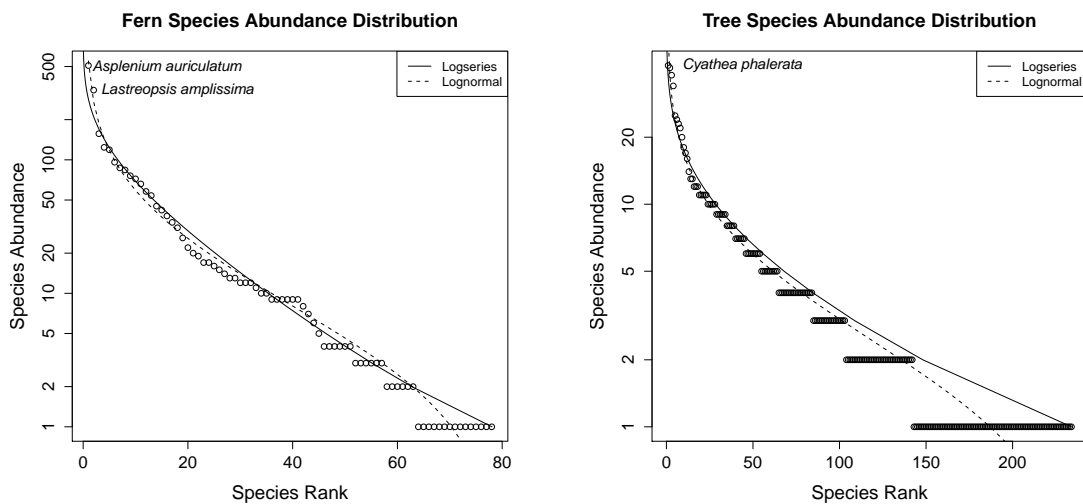
Figure 3.2: Species abundance distribution curve and its fitted model Fisher's logarithmic series, for the fern community studied and for angiosperm and tree fern community in Serra Bonita Private Reserve, Bahia, Brazil.

Environment and Community Diversity

Canopy openness (CO%) values were concentrated around four percent, the mean value, and did not vary greatly from it (Figure 3.3). CO% correlation with taxonomic distinctness and Shannon diversity were both significant, but presenting inverse relations (Figure 3.4).

Taxonomic distinctness presented positive correlation, while Shannon index presented negative correlation. In other way, plots with lower CO% values harbor lower
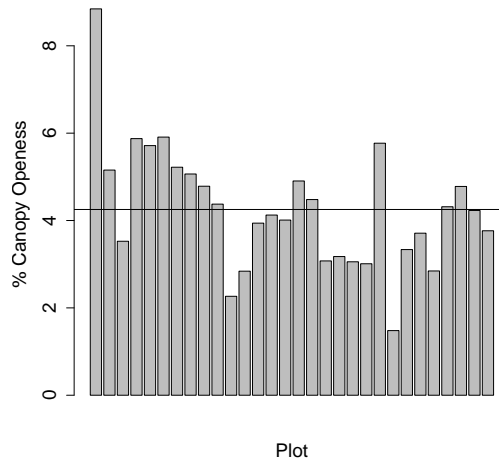
Figure 3.3: Canopy Openness percentage (CO%) for each plot on sample sites in Serra Bonita Private Reserve, Bahia, Brazil.

diversity, measured by taxonomic distinctness. Conversely, plots with lower CO% values harbors high diversity when measured by Shannon index.
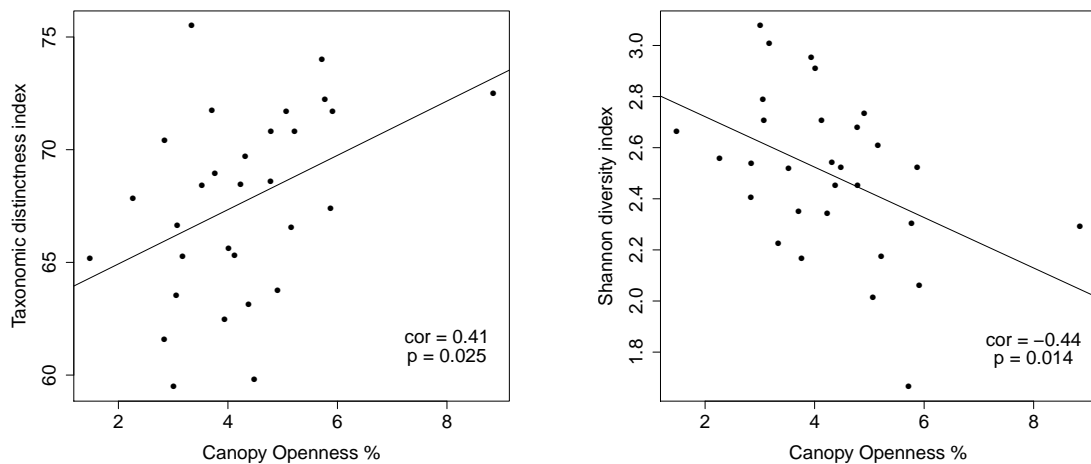
Figure 3.4: CO% correlation with Taxonomic Distinctness and Shannon Index for a fern community in Serra Bonita Private Reserve, Bahia, Brazil.

We also tested the relation between physical and chemical soil components and diversity measurements and found no significant results for correlation or multiple regression analyses, considering paired associations (Pearson's correlation) and multivariate analysis (Mantel test). Soil results show that our samples did not vary significantly on the study area, thus representing a homogeneous area concerning the edaphic characteristics.

Taxonomic and Phylogenetic Measures

In order to identify the taxonomic relationship among fern life forms we calculated different measures of species richness, abundance and relatedness. Our results (Table 3.1) clear out the behavior of different groups of ferns on the basis of different measures of diversity. First, the differences between abundance and richness are high among some groups, for example between epiphytes and hemiepiphytes. However, especially when considering the measures of phylogenetic diversity, it is noted that some groups with few species and individuals can be as diverse as the groups that stand out most in terms of Shannon index.

Table 3.1: Species Richness (S), Species Abundance (N), Shannon Index (H'), Phylogenetic Diversity (PD), Mean Pairwise Distance (MPD), Taxonomic Diversity (Δ) and Taxonomic Distinctness (Δ^*) for each life form for the fern community in Serra Bonita Private Reserve, Bahia, Brazil.

	S	N	H'	PD	MPD	Δ	Δ^*	$z(\Delta^+)$
Hemiepiphytic herb	4	369	1.63	365.8	46.3	43.70	56.23	-1.25
Epiphytic herb	53	1249	2.54	945.8	50.1	48.46	59.40	**-2.01**
Tree fern	5	143	1.16	94.9	13.5	15.21	24.63	**-4.64**
Terrestrial herb	35	624	2.02	767.6	49.0	48.92	68.65	-0.58
Rupestrial herb	5	48	1.30	315.4	47.9	31.73	60.26	-0.89
Total Community	2433	143	3.16	1352.2	62.0	65.40	71.10	
Total Community Expected				1352.0	62.2	67.52	59.48	

For example, it is worth noting the variation among hemiepiphyte measurements, which presented high values of mean pairwise distance (MPD = 50.1), taxonomic diversity ($\Delta = 48.46$) and distinctness ($\Delta^* = 58.40$) even with low values of richness (Table 3.1). Rupestrial and hemiepiphyte ferns, both groups with low values of abundance and richness, presented similar variation in index values.

As for groups with high values of abundance and richness, such as epiphytes and terrestrial herbs, we can observe a different response to the measures. In general, epiphytes presented higher diversity values, especially Shannon index (epiphyte $H' = 2.54$; terrestrial $H' = 2.02$). In terms of taxonomic distinctness, terrestrial herbs appear with the greatest diversity (terrestrial $\Delta^* = 68.65$; epiphyte $\Delta^* = 59.40$), instead.

Furthermore, with aggregation index $z(\Delta^+)$ we could point out life forms that correspond to groups of species that are more or less phylogeneticaly related. Epiphyte and tree ferns presented $z(\Delta^+) < -1.96$, which means phylogenetic aggregation pattern.

The other groups did not present patterns of aggregation or dispersal, and so did the total community.

Additive Partitioning of Diversity

Total community diversity was partitioned into four components: diversity within phorophytes (i.e. epiphyte and hemiepiphyte herbs) and soil (i.e. terrestrial herbs, rupestrial herbs and tree ferns) (α_1), diversity among phorophytes and soil, diversity among plots and diversity among transects (Figure 3.5). Alpha diversity was the principal component of diversity, but did not differ from null model distribution (i.e., p > 0.05 for t-test between α_{obs} and α_{mean}). Diversity among phorophytes and soil (β_1) was the major diversity gain observed (p < 0.01 for null model comparisons). In other words, β_1 contribution to total community diversity is determinant for community as a whole. Also, diversity among transect were significantly higher than null predictions (p < 0.01).
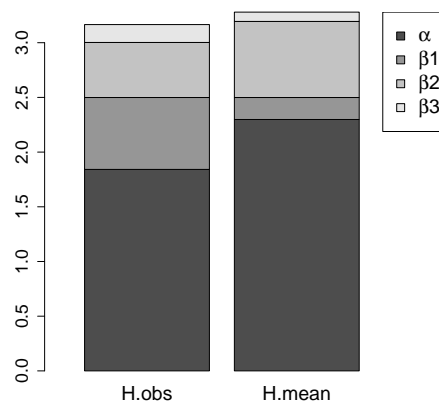
Figure 3.5: Additive partitioning of diversity based on Shannon Index (H'), for the fern community in Serra Bonita Private Reserve, Bahia, Brazil.

3.4 Discussion

Our research found 78 species in 0.3 ha of old-growth montane forest (850 m high), also, a floristic inventory on the area recorded 178 fern species (Matos et al. 2010), including reserve lower areas and human-disturbed sites. Excluding non-possible species from the species pool, we get 162 species from old-growth dense montane ombrophilous

forest areas of above 800 m. Our sample covered 53.5% of Evolutive History (EH) and 48% of species. Both studies highlighted the variety of the five life forms adding complexity to the community structure and composition.

Other fern community studies on tropical high diversity areas reported fewer species on larger sample areas, such as 50 species in 1 ha of Bolivian Amazonia (Poulsen and Nielsen, 1995); 140 species in 50 ha of Central Amazonia, Brazil (Tuomisto et al., 2002); 40 species in 4 ha of Equatorian and Peruan Amazonia (Tuomisto and Poulsen, 2000); 36 species in 4.4 ha of Central Amazonia, Brazil (Zuquim et al., 2009); in Southern Bahia, Brazil a study on lowland areas reported 60 species in 4.5 ha (Paciencia and Prado, 2005); in south Brazilian montane forests 81 species were reported in a 1 ha plot (Dittrich et al., 2005). Our sampling was therefore appropriate to assess the diversity of the area. On the other hand, we could not find support on literature for sample suficience for fern communities and our findings are based on simple comparisons with previous studies.

Fern and arboreal communities on the same sample units adjusted to Fisher's logarithmic series model for SAD (Figure 3.2), which means that we found a biological model that explains fern species abundance distribution in the area. Based on it, we can infer that these communities result from regular time intervals of species arriving at unsaturated habitats (May, 1975; Magurran, 2004). Additionally, this distribution implies that the community did not present one or few environmental or biological factors determining it, but there are several factors generating the pattern observed (Magurran, 2004). Different processes can generate the same SAD, in the case of log-series distribution, it can be caused by neutral or maximum entropy processes, but, we cannot infer about which processes generate the pattern observed, just analyzing the pattern alone (Stevens, 2009). As fern and arboreal communities fitted this model, we are bound to consider that on our study area plant communities respond similarly to factors regulating and generating them.

Correlation between canopy openness percentage (CO%) and different diversity measures clarified the processes that are responsible for community colonization. We found that lower canopy openness values reflect on high diversity communities considering species number, but on low diversity when talking about generic and family level diversity. It is important to consider that CO% did not present a large range of variation, but its increase or decrease from mean values had clearly influenced diversity. As light gaps

appear in the community, different fern species arise (different taxa). In contrast, over more complex and low light environments we found higher values of species diversity, but more related taxa, which implies on lower taxonomic distinctness values. This is a simple empirical perception from field studies that derives from our analysis. A study from Brazilian Central Amazonia found an increase of fern diversity as light gaps became smaller and also with small canopy openness variation (Zuquim et al., 2009). For the studied fern community it seems that canopy openness may act as environmental filter.

Additionally, on our SAD curve, we emphasize the species with more individuals on the sample, being one an epiphytic (*Asplenium auriculatum*) and the other a terrestrial herb (*Lastreopsis amplissima*). The fact that most abundant species belong to different life forms indicates that dominant species do not compete for habitat. Similar results occurred on angiosperm and tree ferns SAD curve, where most abundant species have different life forms, being a tree fern, a canopy tree, an emergent tree and a shrub (D. Rocha, *pers.com.*). Not only did fern and arboreal communities present the same model adjustment, but they also presented similar patterns of dominance within life forms. This seems to indicate that different taxa present similar mediate coexistence processes.

One important issue in community ecology is to understand how processes related to community evolution shape species relations on a local scale. In order to understand this issue, we asked what the relationship between life form and community evolution is. For a fern community, life forms directly related with phylogenetic traits are epiphytic herb and tree fern. Others, such as rupestrial and terrestrial herbs, evolved separately and several times along the group history (Schuettpelz and Pryer, 2009). For instance, as we found phylogenetic aggregation within epiphyte and tree fern life forms, we clearly see how fern species present different strategies for life form coexistence on a local scale. When considering the whole community, we found more taxonomic distinctness than expected from a random community. This may occur as the proper result from the distinctness among some life forms and within others. Aggregation inside some groups did not shape an aggregated pattern for the entire community. Conversely, random structure from other groups defined the general pattern.

In our work, only epiphyte and tree ferns presented phylogenetic aggregation, and correlated with canopy openness. According to Webb et al. (2002), a clustered community may be structured by habitat filtering, as a consequence of a phenotipic attraction.

Based on this assumption, we may infer that less opened canopies represent environmental filtering driving to lower taxa diversity communities but with higher species diversity. Considering the whole community we found a random phylogenetic structure, similar to results from fern community studies in Costa Rica (Kluge and Kessler, 2010).

Epiphytic ferns present considerable species and generic diversity (Schuettpelz and Pryer, 2009) and are often emphasized on community structure studies (Watkins Jr et al., 2006). If we are referring to species diversity, it is a significant group, but, when looking at taxonomic or phylogenetic measures, we clearly see that terrestrial herbs are as diverse as them. As epiphytic ferns are, in part, directly related to phylogeny, they are represented by fewer families and orders than herbaceous ones, which is re-enforced on phylogenetic measures. These diversity measure variations must be considered when using community ecology studies as basis for conservation issues.

For instance, in terms of Evolutive History (EH), our sampled community represents an amount of 2704, i.e. the sum of leaves in the community phylogeny, which is based on the number of species and its evolutive age. Among all taxa surveyed, if we decide to direct our conservation effort to the most diverse and exclusive epiphytic family, the Polypodiaceae and its 20 species, we will have only 25% of community EH. On the other hand, if we attempt select 20 species at random (near 25% of species richness) we will have 46% of community EH. This is a warning to our biased look to species conservation when we should care for evolutive processes conservation, as suggested by the work that proposed this measure (Nee and May, 1997), and the trends in phylogenetic community structure (Webb, 2000; Webb et al., 2002).

Furthermore, the assumptions that come from the diversity measures described above converge to diversity additive partitioning results. When analyzing diversity gain on the β_1 level (within ferns over soil and phorophytes), there is a significant gain compared to a null model. Also, it is important to mention that on additive partitioning analysis, as plot scale is influenced by dependency of the sample unit (plots represent sub-units of the transect and not independent units), diversity among transect presented higher value than expected, probably because it represents a more complex sample unit (i.e. composed by the sub-units). On this scale and for sample aspects it is an expected result.

These results suggest that differences within ferns on these two types of habitats are an important component of total community diversity and when deciding how to

manage conservation areas we must look at terrestrial herbs vs. epiphyte herbs both as priority groups. Therefore, when directing conservation strategies to maintain a local fern community and the evolutive processes that generate it, we must consider the complex structure of forms and strict site occupied (i.e. phorophyte, soil, rock) and the different fern species sensibility to light disturbances.

Ferns are a plant group that is usually neglected from inventories and rapid research directed to select conservation areas. Our study brings up the potential for the group to be used as model taxa for conservation strategies, as it is easier to be dealt with on the field and harbors less species than angiosperm trees to be treated on laboratory, which represents more efficiency on conducting the work. These issues also emerged from previous works of evaluating edge effects (Paciencia and Prado, 2005) and landscape fragmentation (Faria et al., 2007; Pardini et al., 2009) on southern Bahia, Brazil.

In addition, the group presented the same Species Abundance Distribution (SAD) model that arboreal community diversity, which gives more basis for generate information on plant community studies. One decisive issue in terms of conservation cost-effectiveness is the capability of a determined taxa to respond to structural variation on the ecosystem coupled with low field and laboratory costs (Gardner et al., 2008). In this case, we suggest that ferns meet those needs. Also, we recommend the use of ferns as model taxa in this kind of research, due to their capability to translate empirical and theoretical backgrounds into simple and elegant measures of diversity.

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4   CAPÍTULO 2

Epiphyte ferns conservation: metacommunity and phorophyte analyses based on ecological networks in a Tropical Montane Forest, Brazil[1]

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ABSTRACT

We analyzed an epiphyte fern community in two aspects: species co-occurence and epiphyte-host interactions in order to test which interaction is the most funtamental to define the epiphyte metacommunity structure. We found high levels of robustness in epiphyte-epiphyte interactions, which presented six compartments. We also found high specialization level for epiphyte-host interaction. As epiphyte host interactions are specialized, epiphyte fern conservation must occur in the shadow of arboreal community conservation. Aditionally, epiphyte-epiphyte robustness and compartmentalization evidenced a balance of facilitation and competition, where facilitation processes may be stronger on generating metacommunity structure. Another important issue of our study is the contribution of dead trees for mantaining epiphyte richness.

Keywords: robustness; specialization; co-occurence; ecological interactions.

4.1   Introduction

Epiphyte and its host plants, i.e. phorophytes, are interacting entities. These interactions can be considered comensalistic, but some times with benefits for some or both parts (Benzing, 1990). Epiphytes can be favored by host substrate and epiphytes can contribute for the microclimate and herbivory control (Benzing, 1990). Even though there are some works describing epiphyte and host interactions (Benzing, 1990), the ecological network approach became more widespread with recent research involving epiphyte-phorophyte interactions (Burns, 2007; Silva et al., 2010; Burns and Zotz, 2010).

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[1]In preparátion to Biotropica Journal

Ecological networks, or complex networks, deals with ecological interactions considering species as nodes and their connections as interactions. They provide a more accurate representation of interactions among species and clears out their interdependence aspects (Bascompte 2009). They were once applied in community ecology to describe food web relations, and, later, to host-parasitoid interactions and mutualistic webs, such as plant-pollinator and plant-frugivore (Jordano et al., 2002; Ings et al., 2009). While mutualistic networks represent interactions that benefit both partners, food web and host-parasitoid interactions are considered antagonistic (Ings et al., 2009).

Plant-plant interactions received more attention with Burns (2007) and became more widely spread in the context of ecological networks with epiphyte-phorophyte (Burns, 2007; Blick and Burns, 2009; Silva et al., 2010), liana-phorophyte (Blick and Burns, 2009; Sfair et al., 2010) and mistletoes-phorophyte works (Blick and Burns, 2009).

For epiphyte-phorophyte interactions, metacommunity concept is also adopted (Burns and Zotz, 2010). In a fine-scale, epiphyte communities on phorophytes are connected by dispersal and this approach may help to identify co-occurrence patterns (Burns and Zotz, 2010).

Network structure analysis allows the identification of nested and compartmentalized patterns in community interactions. It can be measured by nestedness and compartment. Nestedness is measured from many metrics, but the most commonly used is NODF, nestedness metric based on overlap and decreasing fill (Almeida-Neto et al., 2008; Ulrich et al., 2009). Compartment comprises sub-groups of interactions and is mostly measured by modularity (Olesen et al., 2007; Fortuna et al., 2010). Additionally, using networks as a conceptual framework for community interactions we can forecast consequences of community disturbances when one or a group of species are lost (Bascompte, 2009).

We used ecological network approach to test ecological interactions between epiphyte ferns and its host trees, also, epiphyte vs. epiphyte networks. Epiphyte ferns represent one-third of all fern species, with families such as Aspleniaceae, Hymenophyllaceae e Polypodiaceae harboring 59 to 93 percent of epiphyte species (Dubuisson et al., 2009). One hypothesis for its considerable diversity is based on a recent diversification of ferns as consequence of the rise of angiosperms in the Cretaceous period, where epiphytes had a successful establishment, within this character evolving separately on different groups (Schneider et al., 2004; Schuettpelz and Pryer, 2009). Furthermore, ferns seemed

to present patterns of epiphyte-host interactions, exhibiting preference for tree ferns as hosts, due to favorable subtracts for spore establishment and attachment rather than angiosperms trunks (Moran et al., 2003).

In this study we analyzed epiphyte-host preferences from a fern epiphyte community, in terms of network structure and specialization patterns. Also, we analyzed species co-occurrence patterns and metacommunity process as well.

4.2   Materials and Methods

Study site

Serra Bonita mountain range (7.500 ha), is located at Camacan and Pau Brasil municipalities, in southern Bahia, Brazil. It covers one of the last forest patches in the region. Serra Bonita Private Reserve, the study site, at the middle part of this mountain complex, covers 2.000 ha of protected areas, between 300 and 1.080 m above sea level.

The weather is warm and humid, with annual precipitation ranging from 1.500 to 1.800 mm, equally distributed along the year (Roeder, 1975). According to CEPEC data collected from 2000 to 2010, temperature on the study area varies from 20.1 °C to 28.8 °C, with 24.5 °C average and mean precipitation 100.5 per month. Total potential evapotranspiration ranges from 1.200 to 1.300 mm and the air relative humidity can reach 80 percent. Serra Bonita Private Reserve forest cover ranges from dense sub-montane ombrophilous forest with elements of semidecidual forests to dense montane ombrophilous forest at the altitudinal gradient (Amorim et al., 2009).

The vegetation conservation status and physical structure vary greatly, from old-growth forests to different stages of regenerating forests over abandoned pasture, logging and agriculture areas (Amorim et al., 2009). Also, a road leading to a transmission tower on the Reserve's mountain top, resulted in the eradication of the original vegetation in that area (Amorim et al., 2009).

Even though the area still suffers from fragmentation effects, recent research has shown that these fragments shelter large number of rare and endemic species. Preliminary floristic studies have identified ca. 700 species of angiosperms (Amorim et al., 2009), 178 species of ferns and four lycophytes (Matos et al., 2010), with several new to science species, including a very notable bromeliad (Amorim and Leme, 2009) and three new fern

species.

Sampling and analysis

We quantified the occurrence of epiphyte fern species on ferns and angiosperms in a Montane forest, Bahia, Brazil on three 0.1 ha transects following Martini et al. (2007) adaptation of Gentry's method (Gentry, 1982).

Each transect consists of ten 2 x 50 m plots aligned parallel separated by a 20 m distance. We sampled all epiphyte ferns until 3 m high on tree ferns, arboreal angiosperm and dead trees phorophytes inside the samples. The host trees and tree ferns were also collected and identified. Voucher materials from each epiphytes and its host species were deposited in CEPEC Herbarium.

We classified phorophyte in four types: angiosperm trees, tree ferns, dead trees I (i.e. dead trees fallen inside plots) and dead trees II (i.e. dead trees still up), which were considered on general epiphyte community analysis. We constructed two matrix interactions: epiphyte-epiphyte and epiphyte-phorophyte in order to identify their structure and in which way they reflect metacommunity processes.

We calculated nestedness from NODF, which consists on overlap and decreasing fill resulted from the interaction matrix (Almeida-Neto et al., 2008). We also analyzed number of compartments in the networks based on correspondence analysis (Lewinsohn et al., 2006) and subgroups of interactions was by modularity (M). This metric considers a network as a graph (i.e. networks between two disjoint sets of vertices) and its subgroups as subgraphs and calculates how modular the graph division is (Newman and Girvan, 2004; Fortuna et al., 2010).

At last, we tested specialization level for epiphyte and phorophyte interactions using Blüthgen et al. (2006) index which describes selectiveness of a bipartite network. For extinction simulations we based our calculations on robustness of the system to species loss (Memmott et al., 2004; Burgos et al., 2007).

We also analyzed epiphyte preferences for hosts in terms of circumference at breast hight (CBH) by correlation analysis and height, considering 0-1, 1-2 and 2-3 m, by Jaccard similarity analysis.

Data analyses were conducted on R software (R Core Development Team, 2009), packages bipartite (Dormann et al., 2008, 2009) and igraph (Csardi and Nepusz, 2006).

We used Aninhado Software (Guimarães Jr and Guimarães, 2006) for NODF and null models analyses.

4.3 Results

Ecological Networks

We found 51 epiphyte species on 545 phorophytes, belonging to 146 species in our 0.3 ha sample area. Each analyzed network performed in a particular way in terms of interactions and nestedness (Figure 4.1).

(a)   (b)
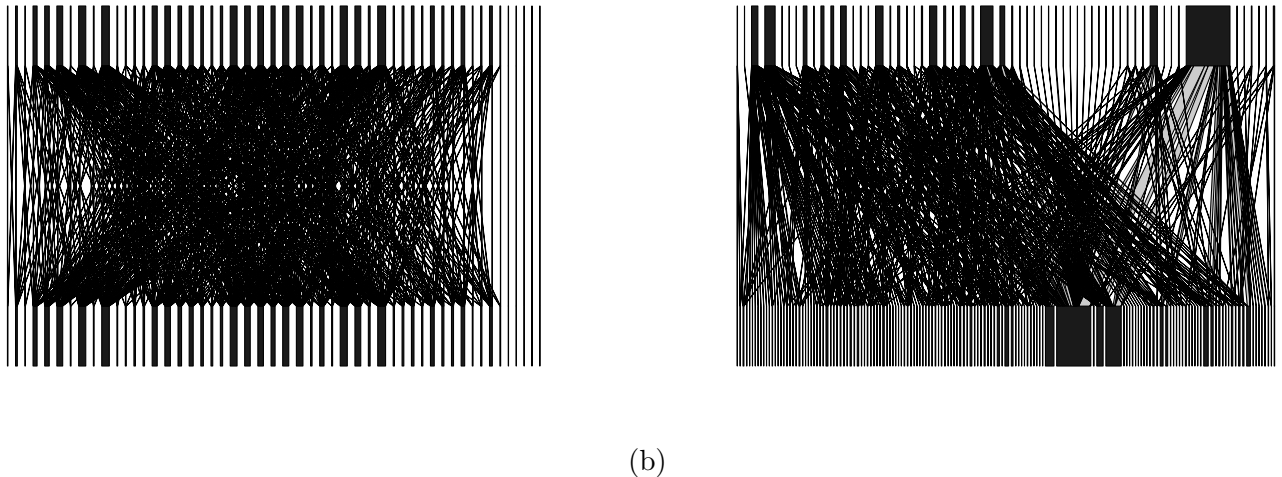
Figure 4.1: (a) Epiphyte-epiphyte and (b) epiphyte-phorophyte network structure of a fern community in Serra Bonita Private Reserve, Bahia, Brazil.

Both studied network did not presented nested structure (Table 4.1). Epiphyte-epiphyte networks presented significant values for robustness. On the other hand, epiphyte-phorophyte networks with and without dead trees were significantly specialized.

Table 4.1: Matrix Metrics for studied networks of a fern community in Serra Bonita Private Reserve, Bahia, Brazil.

Network Metric	Epiphyte-epiphyte	Epiphyte-phorophyte	Epiphyte-phorophyte (excluding dead trees).
NODF	0.43	0.07	0.07
Matrix fill	0.23	0.06	0.06
Specialization	0	0.22*	0.30*
Robustness	0.81*	0.50	0.55

$*p < 0.05$ when compared with null model

Epiphyte-epiphyte network presented a high robustness value, which can be represented by low slope extinction curves (Figure 4.2). For epiphyte-phorophyte networks primary extinctions occured on phorophyte level. Epiphyte-phorophyte network were more sensitive to species loss. The x-axis of the graphic features the proportion of exterminated participants, while the y-axis depicts the proportion of secondary extinctions.
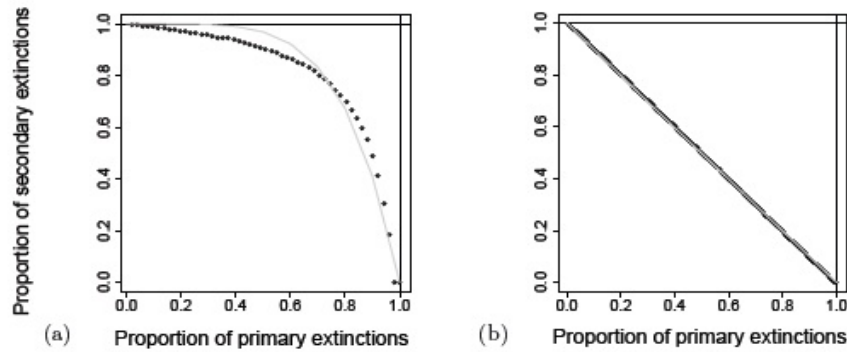

Figure 4.2: Proportion of extinctions based on proportion of primary extinction *vs.* proportion of secondary extinction for the fern community in Serra Bonita Private Reserve, Bahia, Brazil. (a) Epiphyte-epiphyte extinctions. (b) Epiphyte-phorophyte extinctions based on loss of phorophyte species

Considering the subgroups of interactions, epiphyte-epiphyte networks presented six compartments and a significant modularity value. Epiphyte-phorophyte networks did not exhibit patterns of subgroups interactions, i.e. presented only one compartment and did not presented significant modularity values.

Epiphyte ferns preferences

Epiphyte richness ranged from 1 to 7 species on each phorophyte, with mean value around 1.8 species. We compared epiphyte richness on different types of phorophytes by rarefaction curves (Figure 4.3). We found more species on dead trees still up (dead trees I) than in angiosperm or tree ferns. Considering the same phorophyte number (N = 75) we had 38 fern species on dead trees I and 38 species on angiosperm trees.

We also found positive correlation ($p < 0.01$) for both epiphyte richness and abundance with phorophyte Circumference at Breast Height (CBH). This means that larger phorophytes present higher epiphyte diversity. We did not identify differences in epiphyte diversity in a vertical variation from 0 to 3 m. We found a value of 0.9 for Jaccard
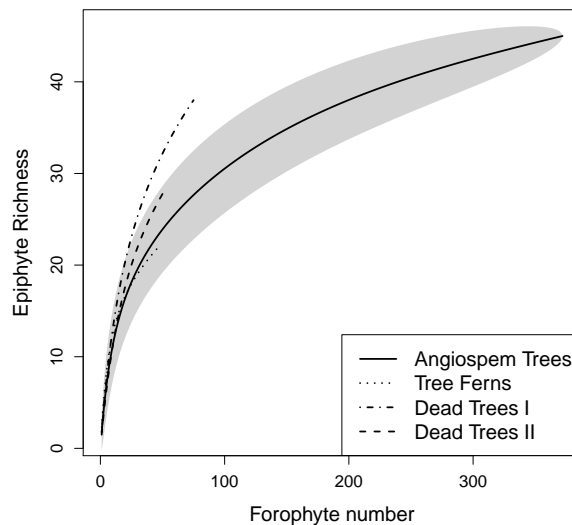
Figure 4.3: Richness comparison of epiphyte ferns on different kind of phorophytes by rarefaction curves in Serra Bonita Private Reserve, Bahia, Brazil. Dead trees I = dead trees fallen inside plots; Dead trees II = dead trees still up.

similarity for all comparisons among 0-1 m, 1-2 m and 1-3m.

4.4   Discussion

As we found random network structure for both epiphyte-epiphyte and epiphyte-phorophyte networks, this may suggest that nested structure did not emerge from comensal interactions, such as epiphyte-phorophyte. In contrast, nestedness is commonly reported for mutualistic networks (Ulrich et al., 2009). Epiphyte-phorophyte network random structure was also reported for orchids on Brazilian gallery forests (Silva et al., 2010), although epiphyte-epiphyte network in New Zealand forests presented a nested structure (Burns, 2007).

Distinctions from these epiphyte-phorophyte networks may occur due to differences on structural complexity between Brazilian Tropical and New Zealand Temperate forests (Sfair et al., 2010). Network structure may vary from higher diverse systems to simpler ones even when dealing with the same kind of interaction (Sfair et al., 2010). Our work confirms these issues.

The fact that our epiphyte-phorophyte network is not nested is supported by the specialization values found. Specialization implies that species with few network links

interact with species with few interactions also. Alternatively, nestedness is a result of species with few links interacting with generalist species. Specialization and nestedness concepts explain our findings. Furthermore, orchid-host networks study on tropical Brazilian forests also presented specialized interactions and discussed an opposite relation to nested structure (Silva et al., 2010).

Epiphyte-epiphyte network was compartmentalized, but we could not identify if compartments were related to host preferences. This occurred because it wasn't possible identify compartments or significant modules on epiphyte-phorophyte networks.

In our epiphyte-epiphyte network, compartments may emerge from a balance between facilitation and competition forces from epiphyte co-occurrence. As epiphyte-epiphyte is a robust network we inferred that these interactions may be structured from facilitation processes. In this case, when one one species arises it facilitates the establishment of another. Yet, facilitation processes occur on the epiphyte subgroups found.

For conservation purposes robustness is an important characteristic of epiphyte-epiphyte network, indicating that metacommunity interactions on host trees prevent species loss (Burns and Zotz, 2010). On the other hand, as we found high specialization levels for epiphyte-phorophyte interactions, we assumed that conservation of arboreal structure and diversity is crucial for fern epiphyte community maintenance.

Another relevant characteristic for epiphyte community establishment is phorophyte circumference. More structured arboreal communities, which present bigger trees in terms of CBH, favored fern abundance and richness. Epiphyte richness ranged from 1 to 7 species per phorophyte and larger phorophytes favored more individuals and different species colonization.

In addition, we did not found higher richness and abundance on fern trees, as suggested on previous literature (Moran et al., 2003). In contrast, we highlighted the dead trees contribution to epiphyte metacommunity diversity, as it presented higher species richness values than the others (Figure 4.3). For conservation purposes this is an important issue, because management practices for increasing diversity would not care for dead trees removal. In this case, we indicate not removing this kind of phorophytes.

In our study of epiphyte fern community, we emphasized forest structure and complexity as maintainers of fern diversity and processes modeling interactions between them and among epiphytes and its hosts.

What comes from our work is that specialization in epiphyte-phorophyte network is crucial for its maintenance. Also, as the interactions between epiphytes presented high robustness, they are as important in structuring the metacommunity as the epiphyte-host interactions. Thus, we identify a balance between the specificity of epiphytes with its hosts and the epiphyte facilitation relations in determinating community structure. This leads us to think about the epiphyte ferns conservation in a broad sense, including conservation of interactions in two levels: among metacommunities and between metacommunities and its hosts.

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5   CONSIDERAÇÕES FINAIS

Os aspectos da estrutura filogenética e das interações na comunidade de samambaias estudada traduziram de maneira mais clara relações de co-ocorrência entre e as formas de vida e, no caso das epífitas, as relações inter e intra-metacomunidades. Ficou claro que as métricas adotadas permitem captar informações acerca dos processos subjacentes à estrutura e funcionamento da comunidade.

Dessa maneira, esperamos que os resultados sirvam para direcionar os esforços de conservação das samambaias em processos e interações, ao invés de seguir abordagens tradicionais de conservação de espécies.

O trabalho foi concluído com menor esforço de coleta e reduzido tempo de laboratório para identificação das espécies do que trabalhos com o mesmo delineamento amostral envolvendo comunidades arbóreas. Isso mostra o potencial do grupo para uso em estudos de comunidades de plantas, com um baixo custo e alta capacidade de responder questões ecológicas e de conservação.

Ainda, tanto para as medidas de diversidade filogenética, como para as redes de interação, a partir dos resultados gerais não foi possível encontrar diferenças significativas em relação a modelos nulos.

Diante disso, a pergunta que permanece é se a aleatoriedade da comunidade seria um efeito de amostragem em uma pequena escala, i.e, um único sítio de floresta montana no sul da Bahia, ou se seria esse o padrão resultante dos efeitos de heterogeneidade ambiental e deriva ecológica para uma comunidade de samambaias.

APÊNDICE

Lista de espécies de samambaias amostradas em 0.3 ha de floresta ombrófila densa montana, RPPN Serra Bonita, Bahia, Brasil.

Família	Espécie	Abundância	Forma de vida
Aspleniaceae	*Asplenium angustum*	26	erva epífita
Aspleniaceae	*Asplenium auriculatum*	509	erva epífita
Aspleniaceae	*Asplenium feei*	54	erva epífita
Aspleniaceae	*Asplenium pteropus*	10	erva epífita
Aspleniaceae	*Asplenium scandicinum*	66	erva epífita
Aspleniaceae	*Asplenium* sp.	1	erva epífita
Aspleniaceae	*Asplenium triquetrum*	17	erva rupícola
Aspleniaceae	*Asplenium truncorum*	7	erva epífita
Blechnaceae	*Blechnum acutum*	84	erva hemiepífita
Cyatheaceae	*Alsophila setosa*	11	arborescente
Cyatheaceae	*Cyathea delgadii*	34	arborescente
Cyatheaceae	*Cyathea glaziovii*	20	arborescente
Cyatheaceae	*Cyathea phalerata*	96	arborescente
Cyatheaceae	*Cyathea rufa*	1	arborescente
Cyatheaceae	*Cyathea* sp.	1	arborescente
Dennstaedtiaceae	*Dennstaedtia cornuta*	9	erva terrestre
Dennstaedtiaceae	*Dennstaedtia dissecta*	14	erva terrestre
Dennstaedtiaceae	*Dennstaedtia globulifera*	1	erva terrestre
Dennstaedtiaceae	*Dennstaedtia obtusifolia*	1	erva terrestre
Dryopteridaceae	*Ctenitis distans*	1	erva terrestre
Dryopteridaceae	*Ctenitis submarginalis*	4	erva terrestre
Dryopteridaceae	*Cyclodium meniscioides*	45	erva terrestre
Dryopteridaceae	*Elaphoglossum insigne*	119	erva epífita
Dryopteridaceae	*Elaphoglossum lingua*	15	erva epífita
Dryopteridaceae	*Elaphoglossum peltatum*	2	erva epífita
Dryopteridaceae	*Elaphoglossum rigidum*	38	erva epífita
Dryopteridaceae	*Elaphoglossum* sp.	58	erva epífita
Dryopteridaceae	*Elaphoglossum vagans*	2	erva epífita
Dryopteridaceae	*Lastreopsis amplissima*	333	erva terrestre
Dryopteridaceae	*Lomagramma guianensis*	2	erva hemiepífita
Dryopteridaceae	*Megalastrum canescens*	9	erva terrestre
Dryopteridaceae	*Megalastrum connexum*	4	erva terrestre
Dryopteridaceae	*Megalastrum eugenii*	2	erva terrestre
Dryopteridaceae	*Olfersia cervina*	5	erva terrestre
Dryopteridaceae	*Polybotrya speciosa*	124	erva hemiepífita
Hymenophyllaceae	*Abrodyctium rigidum*	12	erva terrestre
Hymenophyllaceae	*Didymoglossum reptans*	22	erva epífita
Hymenophyllaceae	*Hymenophyllum caudiculatum*	72	erva epífita
Hymenophyllaceae	*Hymenophyllum hirsutum*	4	erva epífita
Hymenophyllaceae	*Hymenophyllum polyanthos*	8	erva epífita
Hymenophyllaceae	*Polyphlebium angustatum*	9	erva epífita
Hymenophyllaceae	*Polyphlebium diaphanum*	31	erva epífita
Hymenophyllaceae	*Polyphlebium hymenophylloides*	42	erva epífita
Hymenophyllaceae	*Trichomanes polypodioides*	12	erva epífita
Hymenophyllaceae	*Vandenboschia collariata*	1	erva epífita
Lindsaeaceae	*Lindsaea lancea*	13	erva terrestre

Lomariopsidaceae	*Lomariopsis marginata*	9	erva hemiepífita
Lomariopsidaceae	*Nephrolepis rivularis*	1	erva epífita
Marattiaceae	*Danaea geniculata*	76	erva terrestre
Oleandraceae	*Oleandra articulata*	3	erva epífita
Polypodiaceae	*Campyloneuron acrocarpon*	157	erva epífita
Polypodiaceae	*Campyloneuron angustifolium*	3	erva epífita
Polypodiaceae	*Cochlidium serrulatum*	1	erva epífita
Polypodiaceae	*Lellingeria suspensa*	3	erva epífita
Polypodiaceae	*Melpomene melanosticta*	1	erva epífita
Polypodiaceae	*Microgramma acatallela*	19	erva epífita
Polypodiaceae	*Microgramma lycopodioides*	9	erva epífita
Polypodiaceae	*Microgramma tecta*	9	erva epífita
Polypodiaceae	*Micropolypodium achilleifolium*	1	erva epífita
Polypodiaceae	*Pecluma pilosa*	13	erva epífita
Polypodiaceae	*Pecluma plumula*	3	erva epífita
Polypodiaceae	*Pecluma* sp. 1	1	erva epífita
Polypodiaceae	*Pecluma* sp. 2	1	erva epífita
Polypodiaceae	*Phlebodium aureolatum*	2	erva epífita
Polypodiaceae	*Pleopeltis pleopeltidis*	6	erva epífita
Polypodiaceae	*Pleopeltis pleopeltifolia*	4	erva epífita
Polypodiaceae	*Polypodium monoides*	3	erva epífita
Polypodiaceae	*Serpocaulon catharinae*	10	erva epífita
Polypodiaceae	*Serpocaulon fraxinifolium*	87	erva epífita
Polypodiaceae	*Terpsichore taxifolia*	1	erva epífita
Pteridaceae	*Polytaenium lineatum*	4	erva epífita
Pteridaceae	*Pteris angustata*	1	erva terrestre
Pteridaceae	*Vittaria scabrida*	4	erva epífita
Saccolomataceae	*Saccoloma inaequale*	3	erva terrestre
Woodsiaceae	*Diplazium ambiguum*	16	erva terrestre
Woodsiaceae	*Diplazium lechleri*	12	erva terrestre
Woodsiaceae	*Diplazium leptocarpon*	17	erva terrestre
Woodsiaceae	*Diplazium mutilum*	2	erva terrestre