UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Dissertação de Mestrado

Efeitos Funcionais e Filogenéticos nas Relações entre Forófitos e Epífitos Vasculares

Pedro Rates Vieira

Porto Alegre

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Pedro Rates Vieira

Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul (UFRGS), como um dos requisitos para obtenção do título de Mestre em Botânica.

Orientador: Prof. Dr. Jorge Luiz Waechter

Coorientador: Prof. Dr. Fernando Souza Rocha

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“É preciso variar, se não tivermos cuidado a vida
torna-se rapidamente previsível, monótona, uma seca”
José Saramago

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RESUMO

Dissertação de Mestrado

Programa de Pós-Graduação em Botânica

Universidade Federal do Rio Grande do Sul

Efeitos Funcionais e Filogenéticos nas Relações entre Forófitos e Epífitos Vasculares

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Orientador: Jorge Luiz Waechter

Os padrões de associação entre epífitos e forófitos não podem ser considerados espécie-específicos, mas as árvores que os epífitos colonizam também não são um conjunto aleatório das espécies forofíticas de um determinado local. Ao invés disso, parece haver uma preferência de certos epífitos por diferentes forófitos. No entanto, se conhece pouco sobre os fatores que determinam essa preferência. Nosso objetivo nesse trabalho é avaliar como os atributos funcionais e a filogenia dos epífitos vasculares influenciam na associação dos epífitos com os forófitos em uma Floresta Ombrófila Mista no sul do Brasil. Para isso nós (1) investigamos padrões de associação positiva e negativa entre grupos funcionais de epífitos e grupos de forófitos e como a diversidade e os atributos funcionais dos epífitos variavam em função do tamanho do forófito e (2) inferimos sobre a existência de sinal filogenético no uso de árvores hospedeiras pelos epífitos, procuramos por estrutura filogenética nas comunidades epifíticas e investigamos diferenças de composição filogenética de epífitos vasculares em diferentes clados de forófitos. Foram amostrados 70 forófitos compreendendo 15 espécies pertencentes a diversos clados e com arquiteturas e características variadas. A amostragem compreendeu 31 espécies epifíticas com os principais clados sendo Polypodiaceae, Bromeliaceae e Orchidaceae. A associação de grupos de epífitos vasculares com diferentes grupos de forófitos sugere que as características dos forófitos proporcionam ambientes contrastantes e que diferentes valores de atributos são necessários para colonizar esses ambientes. Mais especificamente espécies epifíticas com menor área específica foliar (SLA) parecem predominar em árvores maiores e maior SLA em árvores menores. Encontramos sinal filogenético na utilização dos forófitos, sugerindo que a conservação das interações com os forófitos deve ter sido importante ao longo da evolução dos epífitos. A tendência a agrupamento filogenético nas comunidades epifíticas sugere a influência de filtros ambientais representados pelas diferentes características dos forófitos estruturando as assembleias de epífitos. Clados mais basais de forófitos apresentaram composição filogenética distinta devido, sobretudo, a presença de diferentes clados de monilófitos epifíticos nessas árvores. Angiospermas epifíticas ocorreram principalmente em forófitos pertencente as eurosídeas. A preferência de epífitos por forófitos parece ser influenciada pelo surgimento de novidades morfológicas e ecofisiológicas em alguns clados, enquanto outros mantiveram o seu nicho ancestral. A composição florística das florestas quando da origem dos clados epifíticos também parece influenciar a associação entre epífitos e forófitos. Ao utilizar informações sobre os atributos e filogenia das espécies de epífitos vasculares nós podemos melhor compreender os mecanismos ecológicos e históricos que influenciam os padrões de associação entre epífitos e forófitos.

Palavras-chave: árvore hospedeira, associação de espécies, comunidades epifíticas, ecologia filogenética de comunidades, Estação Ecológica de Aracuri, estrutura filogenética, filtro filogenético de habitat, Floresta de Araucária, redes ecológicas, sinal filogenético, tipos funcionais,

ABSTRACT

Master's Thesis

Programa de Pós-Graduação em Botânica

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Functional and Phylogenetic Effects on the Relations between Phorophytes and Vascular Epiphytes

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Co-supervisor: Fernando Souza Rocha

Supervisor: Jorge Luiz Waechter

It has been shown that patterns of association between epiphytes and phorophytes can not be considered species-specific, although the trees that epiphytes colonize are not a random subset of phorophyte species in a particular location. Instead, there seems to be a preference of some epiphytes for different phorophytic species. However, little is known about the factors determining this choice. Our objective in this study is to assess how functional attributes and phylogeny of vascular epiphytes influence the association of epiphytes with the phorophytes in an Araucaria Forest in Southern Brazil. For that we (1) investigated the positive and negative association patterns between functional groups of epiphytes and groups of phorophytes and how functional diversity and functional traits of epiphytes varied with host tree size and (2) inferred about the existence of phylogenetic signal on the host trees use by epiphytes, looked for phylogenetic structure in the epiphytic communities and investigated differences in the phylogenetic composition of vascular epiphytes in different phorophyte clades. We used a sample of 70 phorophytes comprising 15 species and belonging to different clades and with different architectures and traits. The sample comprised 31 epiphytic species, the major clades being Polypodiaceae, Bromeliaceae and Orchidaceae. The combination of vascular epiphyte groups with different groups of phorophytes suggests that phorophyte traits provide contrasting environments and that different trait values are needed to colonize these environments. More specifically, epiphytic species with lower specific leaf area (SLA) seem to predominate on larger trees and with higher SLA values on smaller trees. We found phylogenetic signal on the host tree use, suggesting that conservatism of the interactions with phorophytes must have been important throughout the evolution of epiphytes. The tendency to phylogenetic clustering in the epiphytic communities suggests the influence of environmental filters represented by phorophyte traits structuring epiphyte assemblages. More basal clades of phorophytes showed different phylogenetic composition mainly due to the presence of different epiphytic monilophyte clades on these trees. Epiphytic angiosperms occurred mainly on those trees belonging to eurosids. The preference of epiphytes for phorophytes seems to be influenced by morphological and ecophysiological novelties in some lineages, while other clades kept their ancestral niche. The floristic composition of forests at the origins of epiphytic lineages also appears to influence the association between epiphytes and phorophytes. By using information about the traits and phylogeny of species of vascular epiphytes we can better understand the ecological and historical mechanisms that influence the patterns of association between epiphytes and phorophytes.

Keywords: Aracuri Ecological Station, Araucaria forests, ecological networks, epiphytic communities, functional types, host trees, phylogenetic community ecology, phylogenetic habitat filtering, phylogenetic signal, phylogenetic structure, species association.

INTRODUÇÃO GERAL

Duas disciplinas que têm tido sucesso nos últimos anos na tentativa de explicar os padrões atuais de riqueza, abundância e distribuição de espécies, bem como os processos ecológicos que geram esses padrões são a ecologia funcional e a ecologia filogenética de comunidades (Webb *et al* 2002; McGill *et al* 2006). Apesar das duas disciplinas terem fundações antigas dentro da ecologia, os avanços computacionais e metodológicos das últimas décadas têm impulsionado o aprimoramento teórico sobre a teoria de nicho nessas áreas, e um grande número de artigos vem sendo publicado a cada ano. A ecologia funcional integra como a forma e função das plantas se relacionam com gradientes ambientais e estuda as diferenças demográficas e funcionais das espécies interagentes e co-ocorrentes com com base nos seus atributos funcionais (Grime 2006; McGill *et al* 2006; Ackerly & Cornwell 2007). A ecologia filogenética de comunidades integra a biologia evolutiva com a ecologia de comunidades para compreender como fatores históricos interagem com processos ecológicos atuais, para melhor entender como as comunidades ecológicas estão organizadas (Webb *et al* 2002). Ambas as disciplinas têm bases históricas com a teoria de Darwin (1859) que afirma que todas as espécies tem uma origem em comum e que a luta pela sobrevivência deve ser mais forte em organismos relacionados e assim diferenças fenotípicas no modo como as espécies utilizam os recursos permitem sua coexistência. Assim, a ecologia funcional e a ecologia filogenética são inter-relacionáveis, uma vez que a expressão de atributos dos organismos é fruto de uma história evolutiva em comum, na qual a conservação do fenótipo e o surgimento de novidades evolutivas determinam os habitats que uma espécie está apta ou não a sobreviver (Donoghue 2008).

As assembléias de epífitos vasculares estão entre as mais ricas de formações florestais, sobretudo em florestas montanas neotropicais (Nieder *et al* 1999), e podem contribuir com mais de 50% do total local de espécies (Gentry & Dodson 1987). Já em uma escala global, os epífitos vasculares contribuem com cerca de 10% de todas as espécies de plantas vasculares, e estão concentradas nas florestas tropicais úmidas (Kress 1986). Apesar de constituírem um componente importante e rico de florestas úmidas, poucos estudos têm buscado compreender os mecanismos que mantém a diversidade e que permitem a coexistência das espécies de epífitos vasculares. Grande parte dos trabalhos publicados se restringe a estudos descritivos, sem uma análise quantitativa que permita fazer inferências acerca dos fatores que determinam a ocorrência de espécies epifíticas. A falta de estudos quantitativos deve-se em muito à dificuldade de acesso para se amostrar epífitos no dossel das florestas e à ausência de embasamento teórico que permita a formulação de hipóteses sobre os processos que geram a diversificação de epífitos vasculares nas copas das florestas (Burns & Zotz 2010).

Neste trabalho utilizamos as abordagens da ecologia funcional e filogenética de comunidades a fim de lançar luz sobre os processos determinantes para a coocorrência de epífitos vasculares, bem como essas comunidades estão estruturadas. Apesar de alguns estudos abordarem o modo como atributos estão associados com a sobrevivência de algumas espécies epifíticas, nenhum trabalho realizou essa abordagem em nível de comunidades com diversos clados de epífitos. Adicionalmente focamos em como as interações entre epífitos vasculares e árvores hospedeiras determinam as espécies que podem co-ocorrer sobre um mesmo forófito.

Relações entre epífitos vasculares e forófitos

Entender os fatores ecológicos e históricos determinantes no modo como os epífitos vasculares interagem e se associam com os forófitos (árvores hospedeiras) é de fundamental importância para compreender os padrões de distribuição e diversidade desta sinúsia. Classicamente, a noção de que a relação epífito-forófito é espécie específica foi utilizada como uma possível explicação para a alta diversidade de epífitos vasculares (Went 1940). Apesar de alguns poucos trabalhos suportarem a noção de que algumas espécies adotam uma especificidade, no sentido estrito, pelos seus forófitos (Ackerman *et al* 1989; Tremblay *et al* 1998; Moran & Russell 2004), as evidências para ampla ocorrência de espécie-especificidade em epífitos vasculares é muito escassa (Zimmerman & Olmstead 1992; Migenis & Ackerman 1993). Tampouco é possível falar em uma associação totalmente aleatória, na qual as árvores hospedeiras com as quais os epífitos interagem é uma representação aleatória do conjunto local de espécies forofíticas. Ao invés disso, diferentes espécies epifíticas parecem possuir uma preferência por determinados forófitos (Laube & Zotz 2006). Nesse sentido, um passo importante é compreender porque uma espécie epifítica está associada com uma espécie de forófito, enquanto é raramente encontrada em outra e quais fatores determinam as diferentes escolhas de epífitos vasculares com relação às árvores hospedeiras que eles colonizam. Por exemplo, porque pteridófitas epifíticas parecem estar mais associadas com pteridófitas arbóreas do que angiospermas arbóreas (Moran *et al* 2003) e porque algumas espécies de forófitos são largamente colonizadas por diversas espécies de epífitos enquanto outras parecem ser limitantes para quase todas as espécies (Vergara-Torres *et al* 2010)?

Para resolver essas questões ecólogos começaram a estudar como características dos forófitos poderiam influenciar na diversidade e na preferência dos epífitos por diferentes espécies. Kernan e Fowler (1995) sugeriram que diferentes características do substrato estruturam guildas de espécies epifíticas funcionalmente equivalentes. Estudos posteriores mostraram que características dos forófitos, como rugosidade e capacidade de retenção da água do ritidoma estão relacionadas com a preferência de epífitos vasculares por diferentes espécies forofíticas (Callaway *et al* 2002). Outros trabalhos têm demonstrado que características arquiteturais dos forófitos podem influenciar a diversidade e a preferência de epifitos vasculares (Hirata *et al* 2009; Aguirre *et al* 2010), embora nenhum deles considerem quais atributos dos epífitos estão associados a uma maior abundância destes em forófitos com características distintas. Apesar de alguns trabalhos relacionarem preferências de micro-habitats de epífitos ao longo de um mesmo forófito com seus atributos ecofisiológicos (Hietz & Briones 1998; Reyes-García *et al* 2008), não se sabe se os atributos funcionais de epífitos afetam a associação com diferentes tipos de forófitos. Como o fenótipo das espécies é que determina os habitats que elas estão aptas a ocupar e diferentes tipos estruturais de forófitos proporcionam ambientes distintos, espera-se que os atributos dos epífitos delimitem as árvores com as quais eles terão uma maior abundância e aqueles que eles não são capazes de colonizar.

Uma vez que as características fenotípicas são conservadas ao longo da evolução das espécies devido à ancestralidade compartilhada, e se atributos conservados de epífitos estão relacionados à preferência por diferentes tipos de forófitos, espera-se que espécies mais relacionadas filogeneticamente habitem um conjunto semelhante de forófitos. Poucos esstudos têm utilizado essa abordagem para investigar as causas da preferência de epífitos por forófitos. Em um trabalho com orquidáceas epifíticas, Silva *et al* (2010) investigaram o quanto orquídeas filogeneticamente próximas colonizavam as mesmas espécies forofíticas, sem obter nenhum resultado significativo. No entanto, a família Orchidaceae representa apenas um clado no qual o hábito epifítico surgiu e uma abordagem que leve em consideração epifítos vasculares de uma maneira geral pode levar a resultados diferentes. Além disso, se tomarmos em consideração que as diferentes linhagens que compõe o epifitismo atual surgiram em diferentes tempos geológicos, faz sentido pensar que epífitos tenham adaptações que permitam colonizar forófitos que providenciem o ambiente mais semelhante com o existente no tempo de sua origem.

Considerando a ausência de informação sobre o papel dos atributos funcionais dos epífitos na associação com os forófitos em nível de comunidade e da influência de processos históricos nessas interações, o presente trabalho tem os seguintes objetivos: (1) analisar se as características do forófito permitem a colonização de epífitos devido à expressãode seus atributos funcionais; (2) avaliar se o uso de árvores hospedeiras é conservado ao longo da evolução dos epífitos vasculares; (3) inferir quais fatores históricos que são responsáveis pelos padrões atuais de associação entre epífitos e forófitos.

Sistema de vegetação e área de estudo

A vegetação do Planalto Sul-Brasileiro no Rio Grande do Sul é caracterizada por um mosaico de campos com florestas (Rambo 1956, Hueck 1972). A principal formação florestal neste sistema é a Floresta com Araucária ou Floresta Ombrófila Mista, que no contexto atual de um clima mais quente e úmido está se expandindo sobre a vegetação campestre (Behling *et al* 2004; Oliveira & Pillar 2004). As matas de araucária se configuram pelo planalto no fundo de vales, acompanhando os cursos da água em matas de galeria, em grandes extensões de mata e em capões de variados tamanhos (Rambo 1956).

Estruturalmente, *Araucaria angustifolia* (Bertol.) Kuntze é a espécie fisionomicamente dominante, sendo emergente em relação às outras árvores devido ao tronco comprido que pode elevar os ramos horizontais com as folhagens além do dossel. Outros componentes importantes da Floresta Ombrófila Mista são árvores das famílias Lauraceae (*Nectandra* spp., *Ocotea* spp.), Sapindaceae (*Cupania* spp., *Matayba* spp.), Aquifoliaceae (*Ilex* spp.), Winteraceae (*Drymis* spp.) e com destaque para diversas espécies de Myrtaceae (*Eugenia* spp.) (Rambo 1957; Pillar & Quadros 1997). Estas árvores bastante ramificadas formam o dossel abaixo das copas das araucárias. Outro elemento importante é o xaxim (*Dicksonia sellowiana* Hook.) uma samambaia arborescente que ocorre no sub-bosque e que tem uma preferência por ravinas úmidas (Mantovani 2004).

Levantamentos florísticos e fitossociológicos na Floresta Ombrófila Mista tem apontado que as principais famílias epifíticas nesta formação florestal são Orchidaceae, Bromeliaceae e Polypodiaceae (Borgo & Silva 2003; Buzatto *et al* 2008; Boelter *et al* 2011; Waechter 2009), um padrão que se repete para todas as formações florestais do sul do Brasil. A diversidade de epífitos nesse sistema parece estar relacionada principalmente com a heterogeneidade de substratos proporcionada pelas florestas nativas (Boelter *et al* 2011). Essa diversidade de substratos para epífitos emerge da ocorrência de diferentes forófitos como a araucária, o xaxim, mirtáceas e árvores com caule rugoso, que possuem composição taxonômica de epífitos muito distintas (Buzatto *et al* 2008; Waechter 2009).

Nosso estudo foi conduzido na Estação Ecológica de Aracuri, Rio Grande do Sul, Muitos Capões, Brasil (51º10'W; 28º13'S). A área é um fragmento de 272 ha de Floresta de Araucária localizada no Planalto Sul-Brasileiro a cerca de 900 m acima do nível do mar. No interior da mata a temperatura varia de uma média de 10ºC nos meses mais frios a 23ºC nos meses mais quentes (Cestaro 1989). O clima é subtropical úmido (Cfa) com a temperatura anual regional média de 14ºC e ocorrência de geada entre os meses de março e dezembro (Nimer 1990). Existem quatro tipos fisionômicos vegetais: banhado, campo, vassoural e mata com araucária, que comprende cerca de 25% da vegetação da Estação (Waechter *et al* 1984). A vegetação desta última fisiônomia é típica das demais florestas de araucária, dominada por *A. angustifolia*, *Sloanea monosperma*, e otras árvores das famílias Euphorbiaceae, Myrtaceae, Annonaceae e Sapindaceae (Jarenkow & Baptista 1987). Na área de estudo foi realizado um único trabalho com epífitos vasculares, da qual utilizamos a base de dados nos Capítulos 1 e 2 desta dissertação, que confirma a predominância das famílias Orchidaceae, Bromeliaceae e Polypodiaceae na Floresta de Araucária (Waechter 2009).

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Capítulo 1 - Phylogenetic Signal and Habitat Filtering in a Commensalistic Network of Vascular Epiphytes

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ABSTRACT

Phylogenetically related species share many traits what leads to ecological similarity between them. Interspecific interactions are an important part of the niche of a species, thus related taxa must interact with a similar set of species. Associations between vascular epiphytes and host trees are poorly understood and incorporting phylogenetic relatedness in studies of this type of interaction may highlight how comesalistic networks are assembled across evolutionary time. In this study we aimed to investigate if interactions are conserved through the phylogenies of the partners of a vascular epiphyte/host tree commensalistic network and if there is phylogenetic structure in communities of vascular epiphytes. We sampled vascular epiphytes on 70 host trees in a mixed-araucaria forest in southern Brazil. We evaluated phylogenetic signal on the network with the estimated generalized least-square (EGLS) procedure. Phylogenetic structure within vascular epiphyte communities was analysed by the net relatedness index (NRI) and phylogenetic structure across vascular epiphyte communities by an analysis of principal coordinates of phylogenetic structure (PCPS) extracted from a matrix of phylogeny-weighted species composition. EGLS procedure revealed a phylogenetic signal through epiphyte phylogeny but not through host tree phylogeny. We obtained eight significant NRI values, all of them in the direction of phylogenetic clustering. NRI mean values did not differ between host tree clades. PCPS analysis revealed that tree ferns and conifers host trees harbored a distinct epiphyte phylogenetic composition in relation to angiosperm trees. Phylogenetic signal found only through epiphyte phylogeny reveals an asymmetric importance of species interactions in commensalistic networks. Our results suggests that physiological and morphological novelties in some epiphytic clades, as well as niche conservatism in others were important in determining epiphyte-phorophyte associations and are a mechanism which generates phylogenetic habitat filtering.

Keywords: araucaria mixed-forest; Brazil; ecological interactions; host tree; principal coordinates of phylogenetic structure; phylogenetic community structure; phylogenetic habitat filtering.

INTRODUCTION

The advent of molecular phylogenies has stimulated new interest in how evolutionary history might affect patterns of community assembly (Webb 2000, Webb *et al*. 2002). The advances in the knowledge of the relatedness of species has allowed investigating the interplay between ecological and macro-evolutionary processes in shaping the structure of ecological communities (Cavender-Bares *et al* 2009). If we consider that related species have more phenotypic similarity just because they share more ancestry (Blomberg *et al* 2003) and that traits determine species ecological requirements (McGill *et al* 2006), we can expect that related species will have more ecological similarity (Burns & Strauss 2011), and that species should be phylogenetically filtered into communities, leading to phylogenetic clustering. Nonetheless, phylogenetic limiting similarity may exclude close relatives from communities, since very similar species are not able to persist in the presence of competition, generating phylogenetic overdispersion (MacArthur & Levins 1967, Violle *et al* 2011). Thus, by incorporating evolutionary history into ecological theory we can highlight the limitations of trying to explain ecological patterns purely by recent and current ecological factors. Accounting for phylogenetic relatedness will favor us to understand how species niche and interactions emerge (Wiens & Graham 2005, Ives & Godfray 2006).

Species-environment relationships are mediated by traits that may affect species growth and performance along environmental gradients, leading to demographic differences between contrasting habitat types (McGill *et al* 2006). As traits are phylogenetically conserved, keeping ancestral character state or changing in face of new environmental conditions may delimit ecological preferences of different lineages (Donoghue 2008). This can lead to ‘phylogenetic habitat filtering’ (Duarte 2011), where species are assembled into communities according to clade environmental requirements. So, phylogenetic habitat filtering may be an important factor delimiting species niche preferences.

The niche can be defined as a hypervolumetric space of environmental conditions and resources in which individuals of a given species are able to persist (Hutchinson 1957; Holt 2009).

Interspecific interactions constitute an important part of the niche of the majority of species (Chase & Leibold 2004). In general, the entangled bank of species interactions observed in nature can be interpreted as a web of interacting species linked together and generating ecological networks. Studying network structure and architecture and then accounting to how it may influence species extinction or persistence is fundamental to understand local community composition and has important implications to biodiversity conservation (Bascompte 2010). Recently, many studies have been carried out in order to understand how the structure of ecological networks is affected by assembly rules and how it responds to environmental change (Rezende *et al*. 2007; Valiente-Banuet & Verdú 2007; Verdú *et al.* 2010). One major goal in the study of ecological webs is to understand how the present pattern of entangled species interactions is affected by historical factors and how species coevolve when integrated in different types of complex webs (Jordano 2010).

A recent study has demonstrated that ecological interactions are conserved across the entire tree of life (Gómez *et al* 2010). The authors based their conclusions by checking that in seven different kingdoms close relatives of a same genus interact with a similar set of species. Although these results are consistent, the data set was comprised basically of mutualistic and antagonistic networks, and thus more information is necessary about commensalistic networks, in which one organism benefits while the other keeps neutral. One example is a facilitative network in which one neutral organism ameliorates environmental conditions to a beneficiary one (Callaway 2007). Nevertheless, facilitative interactions may become competitive as beneficiary plants shift to older ontogenetic stages (Miriti 2006; Verdú *et al* 2010). Epiphyte-tree associations can be considered as commensalistic interactions which not change its status along the ontogeny of both groups of organisms, since trees provide support for epiphytes and have neither cost nor advantage in this interaction (Piazzon *et al* 2011).

Although vascular epiphytes comprise more than 10% of all vascular plants (Benzing 1990), the lack of a theoretical framework to guide investigations has generated a gap in the understanding of vascular epiphyte communities (Burns & Zotz 2010). Network theory has elucidated some aspects of the assembly of vascular epiphytes communities, although only a few studies have been conducted properly with epiphyte networks (Burns 2007, Burns 2008, Burns & Zotz 2010, Silva *et al* 2010). One characteristic of epiphyte-phorophyte interactions is that they are generally not species-specific, in the sense that one epiphytic species colonizes only one species of phorophyte, but otherwise epiphytes on one host tree are not a random subset of the species pool. Rather, vascular epiphytes have some degree of preference for one or other phorophytic species (Laube & Zotz 2006), and host tree traits are shown to be an important factor for this preference (Callaway *et al* 2002). Regardless of the acceptance of this preference for a spectrum of phorophytes, we have very little information if it is conserved across the phylogeny of vascular epiphytes. Silva *et al* (2010) made the first attempt to investigate the existence of a phylogenetic signal on the host-use by epiphytic orchids, but could not find any evidence, maybe because they used mantel tests what may have inflated type-II error (Harmon & Glor 2010). If we consider vascular epiphytes as a whole we may find a different pattern, since epiphytism appeared many times in plant evolution and orchids represent only one clade with a distinct history where it has arisen (Benzing 1990). Once revealed if host-use is conserved through the phylogeny of vascular epiphytes, another interesting task is to check if different clades of phorophytes favor phylogenetic clustering or overdispersion of vascular epiphytes in response to limiting similarity or ecological filters. Further, distinct phorophyte clades may constitute different habitats for epiphyte growth and survival what can lead to phylogenetic habitat filtering of vascular.

In this study we aimed to investigate if interactions are conserved across the phylogenies of the partners of a vascular epiphyte-phorophyte commensalistic network and if there is phylogenetic structure and habitat filtering in the communities of vascular epiphytes. For this purpose we developed the following hypotheses: 1) host-use is conserved through the phylogeny of vascular epiphytes, but the set of epiphytes interacting with trees is not conserved through the phylogeny of phorophytes. This pattern emerges because the interaction is a commensalistic network in which epiphytes are beneficiated and phorophytes keep neutral; 2) phylogenetic habitat filtering structures the communities of vascular epiphytes since host tree traits comprise different habitats and are responsible for the preference of epiphytes for phorophytes.

METHODS

Study area - Mixed-araucaria forest is a subtropical humid ecosystem spread over the South Brazilian plateau, frequently forming mosaics with grasslands (*campos*) and marshes or peat-bogs (Hueck 1972). The most prominent species is the conifer *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae), which is potentially an emergent tree and dominates the forest physiognomy. Species of Myrtaceae, Lauraceae, Aquifoliaceae, Sapindaceae, Winteraceae, Podocarpaceae and Fabaceae dominate the intermediate and lower strata of the forest (Pillar & Quadros 1997). Another conspicuous species is *Dicksonia sellowiana* Hook. (Dicksoniaceae), a tree fern with aerial roots forming a thick root mantle over the caudex, providing a special environment for epiphyte establishment (Fraga *et al* 2008).

We conducted our study at Aracuri Ecological Station (272 ha), located in the municipality of Muitos Capões, Rio Grande do Sul, South Brazil (51º10'W; 28º13'S). The area is a mixed-araucaria forest fragment in the South Brazilian plateau, 900 m a.s.l. Climate is moist temperate (Nimer 1990). Regional mean annual temperature is *ca*. 14 ºC, with frost occurrence from March to December (Cestaro 1989), but evidently concentrated during the winter months (Nimer 1990), from June to August. Mean annual rainfall is around 1700 mm, generally well distributed throughout the year (Waechter *et al* 1984). Forest vegetation in the Station is is mostly a disturbed mixed-araucaria forest, dominated by *A. angustifolia* and *Sloanea monosperma* Vell. and several species of trees in the Euphorbiaceae, Myrtaceae, Annonaceae and Sapindaceae (Jarenkow & Baptista 1987).

Sampling procedures – For this study we used a data set from Waechter (2009). In the data set phorophytes were sampled along three transects with five sampling points each. At each point, the nearest host-tree (d.b.h $\geq$ 30 cm) was sampled in each of four quadrants (point-centered quarter method). In addition to 60 phorophytes sampled according to this method, Waechter (2009) also sampled 10 adult individuals of the arborescent monilophyte *D. sellowiana*, since it represents a distinct linage with unique traits allowing the colonization of a very distinct group of epiphytes (Waechter 2009). Abundance of vascular epiphyte species was noted for all host trees, with ranks from 0 to 5 according to their prevalence along the phorophyte. Sampling was carried out mostly by climbing the trees, which allowed the detection of small-sized species (e.g. *Capanemia micromera*). Whenever it was possible or necessary, complementary observations were made with the aid of binoculars and the survey of fallen branches at the basis of tall individuals of araucaria.

Data analysis – We used binary matrices of species interactions to analyze the epiphyte-phorophyte network, wherein epiphyte species are rows and phorophyte species are columns. Whenever an epiphytic species interacted with a phorophytic species a value of 1 was assigned and 0 otherwise. From this matrix we calculated network nestedness and connectance. We used NODF (nestedness based on overlap and decreasing fills) metric to calculate nestedness (Almeida-Neto *et al* 2008). Connectance was calculated as the realized number of pairs of interactions between species in relation to all possible pairs of interactions. Nestedness significance was calculated after running 1000 randomizations of the CE null model as implemented in ANINHADO software (Guimarães & Guimarães 2006). We accounted for the species degree as the number of species each species interacted with.

We used the phylogenetic tree R20100701 (available at <http://svn.phylodiversity.net/tot/megatrees>), with family relationships based on APG III (APG 2009) to construct the phylogenetic trees for phorophytes and vascular epiphytes of our sampling by the software Phylocom 4.1 (Webb *et al* 2008). We calibrated our megatree with age estimates from Wilkström *et al* (2001) and undated nodes were evenly distributed between dated nodes.

We calculated the strength of association between epiphytes and phorophytes as the rate of use of host species *k* by epiphyte species *i* (A_{ik}), accordingly to equation 4 in Ives and Godfray

(2006):

$$A_{ik} = -\log\left(1 - \frac{F_{ik}}{H_i}\right)$$

where H_i is the total abundance of epiphyte species *i* and F_{ik} is the abundance of epiphyte species *i* on host tree species *k*. Note the typo in the original article, indicating H_i/F_{ik} instead of F_{ik}/H_i (see Verdú *et al* 2010 for a personal communication with A.G. Ives).

In hand of phylogenies for phorophytes and vascular epiphytes present in our sampling and the measure of strength of association (A_{ik}), we calculated the phylogenetic signal on the interaction following the estimated generalized least-squares procedure (EGLS; Ives & Godfray 2006). It is similar to the generalized least-squares (GLS) procedure of Blomberg *et al* (2003), which estimates phylogenetic signal for traits with continuous values. In our case, the target trait was the matrix of strength of associations between vascular epiphytes and phorophytes. This method calculates the phylogenetic signal for the phylogenies of vascular epiphytes and phorophytes, independently, at the same time. The method is based on the Ornstein-Uhlenbeck model of evolution, accounting for stabilizing selection, and calculates a parameter *d*. When this parameter is $d = 0$ it indicates absence of phylogenetic signal and when $d = 1$ it indicates a phylogenetic signal under the assumption of a Brownian motion. Goodness of fit of the different models was calculated by comparing the mean squared error (MSE) under the full model (MSEd), under a star phylogeny (MSEs) and under a Brownian evolution model (MSEb). The lower is the MSE the best is the model fit (Ives and Godfray 2006). The significance of the parameter *d* was accessed by calculating 95% bootstrap confidence intervals (hereafter, 95% CI) as in Appendix S1 in Ives and Godfray (2006). We measured phylogenetic signal also with presence and absence data. In this case H_i was the total frequency of epiphyte species *i* and F_{ik} the frequency of species *i* on host tree species *k*. We performed these analyses including and excluding *D. sellowiana*. All analyses were run on R 2.14.1 (R Development Core Team 2011) with the auxiliary of 'pblm' function of the package 'picante' (Kembel *et al* 2010).

To test for phylogenetic structure of vascular epiphyte communities we used two approaches. The first, the Net Relatedness Index (NRI; Webb *et al* 2002) is a measure of phylogenetic structure within communities. High values of NRI indicate phylogenetic clustering, while low NRI values reveal phylogenetic evenness (Webb *et al* 2002). NRI significance for each community was tested by comparing the observed values against the 1000 NRI values generated by a null model which randomly reshuffled the epiphytic species on the tips of the phylogenetic tree. We excluded from this analysis seven phorophytes which harbored only one species of vascular epiphyte. We used 'picante' for this analysis (Kembel *et al* 2010).

As a phylogenetic filter could be acting in a metacommunity scale, and thus generating distinct phylogenetic composition in different host tree clades, we applied the 'phylogenetic fuzzy-weighting' method as our second approach (Pillar & Duarte 2010). This procedure generates a **P** matrix where local communities or phorophytes are defined by phylogeny-weighted species composition. For this, a matrix **W** is necessary, which describes each community by its floristic composition, and a phylogenetic distance matrix **D** with the species contained in matrix **W**, obtained from our vascular epiphyte phylogenetic tree. Our **D** matrix was then transformed into a matrix of phylogenetic similarities **S**. With a fuzzy algorithm, phylogenetic similarities of matrix **S** were used to weight species composition in matrix **W**, and generating a matrix **Q**. Matrix **Q** is a species vs. species matrix where the cells indicate the degree of phylogenetic belonging of epiphyte species *j* in relation to epiphyte species *i*. Multiplying matrix **Q** by matrix **W**, gives us matrix **P**, with the phylogenetic representation of each epiphytic species on each host tree (see Pillar & Duarte 2010 for detailed method description). We extracted a principal coordinate analysis from matrix **P**, utilizing the square root of Bray-Curtis distance to obtain principal coordinates of phylogenetic structure (PCPS), which indicate orthogonal phylogenetic gradients on the metacommunity (Duarte 2011). We produced the matrix **P** in R 2.14.1 (R Development Core Team 2011) with the package 'SYNCSA' (Debastiani 2011). PCPS were generated with the software PCO (by M.J. Anderson, avaiable at <http://www.stat.auckland.ac.nz/~mja/Programs.htm>).

In order to analyze whether phorophyte evolution structures community phylogenetic composition of vascular epiphytes, we grouped the sampled phorophytes into six major clades: tree ferns, conifers, magnoliids, fabids, Sapindales and Myrtales. We then compared NRI and PCPS values between groups of sample units through analysis of variance (ANOVA) with permutation tests (Pillar & Orlóci 1996). Euclidean distances between sample units were used as measures of dissimilarity and test criterion was the sum of squared-distances between groups of sampling units (Qb statistics; Pillar & Orlóci 1996). We used 100 000 permutations in each ANOVA. Whenever statistical analyses were significant we compared groups of sampling units (host tree major clades) by phylogenetic independent contrasts (*e.g.* tree ferns against seed plants, conifers against angiosperms, magnoliids against rosids and so on). We used Bonferroni tests to correct for multiple comparisons with PCPS axes.

RESULTS

We sampled 31 species of vascular epiphytes, 16 being monilophytes and 15 angiosperms. Monilophytes were concentrated in the family Polypodiaceae (9 species), being followed by Hymenopyllaceae (3) and Aspleniaceae (2). Blechnaceae and Pteridaceae were representated by only one species. Angiosperm families were more equally represented by number of species, with Bromeliaceae (5 species), Orchidaceae (4), and Cactaceae and Piperaceae (3); (Figure S1; Table S1). Phorophytes belonged to 15 species, with an unequal number of species across the five major clades. Malvids predominated (6 species), followed by magnoliids (4) and fabids (3). Conifers and tree ferns were represented by one species each. Although some clades were constituted by very few species, comparisons between clades were allowed because these species were represented by a relatively large number of individuals, like the conifer *Araucaria angustifolia* with 13 individuals, and the tree fern *Dicksonia sellowiana* with 10 individuals (Figure S2; Table S2).

The network structure was highly nested (NODF = 43.63; $P \leq 0.001$). Connectance had an intermediate value of 0.34. Phorophyte species degree was positively correlated with phorophyte abundance ($\rho = 0.55$; $t_{13} = 2.35$; $P = 0.035$) as well as epiphyte species degree was positively correlated with epiphyte abundance ($\rho = 0.92$; $t_{29} = 12.98$; $P \leq 0.001$). The bulk of interactions was represented only by a few generalist phorophytic and epiphytic species and specialists tended to interact with generalist species (Figure 1).

Phylogenetic signal on the network was detected through the phylogeny of vascular epiphytes but not through the phylogeny of phorophytes (Table 1). Mean squared error estimations were lower under the full model (MSEd) than under the assumptions of a star phylogeny (MSEs) or a Brownian motion evolution (MSEb). Parameter *d* was 0 through phorophyte phylogeny, suggesting no signal, and less than 1 through the phylogeny of vascular epiphytes, indicating lower values than expected under the Brownian motion evolution model (Table 1). Very close values of MSEd and MSEs indicate a very weak phylogenetic signal.

Phylogenetic community structure was random in most epiphyte communities. However, we observed a tendency of communities being phylogenetically clustered instead of overdispersed (Figure 2). We obtained eight significant and five marginally significant NRI values, all of them in the direction of phylogenetic clustering. Furthermore, by examining carefully all NRI values, we could observe a general trend of probabilities of NRI being nearer of phylogenetic clustering than overdispersion. Five out of the eigth NRI values were found in malvid host trees, two in fabids and only one in conifers. Nevertheless, host tree clades did not differ with respect to mean NRI values ($P = 0.77$; Figure S3).

Principal coordinate analysis applied to matrix **P** generated 65 PCPS. We restricted subsequent analysis of variance to the first 6 PCPS, since they accounted for more than three quarters of matrix **P** variation. All remaining PCPS accounted individually for less than 3% of the total variation. After Bonferroni corrections ($P = 0.05/6 = 0.0083$) only the first three PCPS differed between host tree major clades (Figure 3). Differences in phylogenetic composition found in PCPS1 and PCPS3 can be explained by the fact that tree ferns harbored only monilophytes, while other tree clades were additionally colonized by angiosperm epiphytes. Some of these monilophytes were found exclusively on tree ferns, reinforcing the differences. PCPS2 was characterized by phylogenetic differences between rosids and non-angiosperm host trees because a marked presence of monilophytes and *Tillandsia* spp. on *A. angustifolia* in the former and a more heterogeneous phylogenetic composition on the latter.

DISCUSSION

Our findings largely corroborate our initial hypotheses on the existence of phylogenetic signal in a commensalistic network and about the phylogenetic structure of vascular epiphyte communities. We found that species interactions are conserved through the phylogeny of vascular epiphytes but not through the phylogeny of phorophytes. Furthermore, we got evidence for some degree of phylogenetic structure within vascular epiphyte communities, although every major clade of host tree had the same level of phylogenetic community structure. The conserved character of host use associated with the clustered pattern found in some communities agree with the prediction of an environmental filter acting on vascular epiphyte communities (Webb *et al* 2002; Kraft *et al* 2007) . Because host tree clades evolved generating traits which may affect epiphyte performance and survival, different epiphyte clades are able to colonize host trees with traits that provide contrasting habitats. Indeed, when we accounted for variation in phylogenetic composition in a metacommunity scale we observed that communities belonging to different host tree clade are phylogenetic distinct.

Overall epiphyte commensalistic network structure was similar to plant-animal networks (Jordano *et al* 2003). The network was highly nested, but many of the potential interactions could not be observed. The entangled bank of interactions are maintained by a very few abundant generalist species which interact between them and forming a well-connected network core. Furthermore, many specialist species have very few links, preferentially with generalist ones. Although the overall epiphyte network properties was very similar to other plant-animal network (Jordano *et al* 2003), the same did not happened with the phylogenetic structure.

The phylogenetic signal found in the epiphyte-phorophyte network occurs through the phylogeny of epiphytes but not through the phylogeny of phorophytes. This result means that closely related epiphytes tend to establish with the same set of host trees, but closely related phorophytes do not harbor the same set of epiphytes. Because trees provide support and substrate for epiphytic growth and survival and are not affected by them, it is expected that they do not conserve interactions with epiphytes during the course of evolution. On the other hand, vascular epiphytes take evident benefit from this interaction, so conserving the set of trees with they interact must had been historically favored. It makes sense if we consider that environments constituted by host trees are very distinct and that epiphytes perform differently between habitats. In fact, it has been demonstrated that host traits affect epiphyte growth, a mechanism which generates epiphyte preference (Callaway *et al* 2002). Phylogenetic signal was very weak, since MSEd and MSEs values were almost the same. It suggests an effect of strong stabilizing selection and that a phylogenetic host association was defined early on epiphyte phylogeny and stabilized subsequently.

Studies on the phylogenetic structure of phylogenetic networks have shown that mutualistic and antagonistic interactions are generally evolutionary conserved through the phylogenies of both interactors (Ives & Godfray 2006; Rezende *et al* 2007; Rezende *et al* 2009; Gómez *et al* 2010). Considering that in these types of interactions both partners are positively or negatively affected, we would expect this pattern of phylogenetic signature to happen. The contrasting pattern found in our commensalistic network suggests that distinct network types are differently structured in the phylogenetic sense. Accordingly, Verdú *et al* (2010) found that interactions in a commensalistic facilitation network were conserved through the phylogenies of facilitated plants, but not through the phylogenies of nurse plants. When the interactions had an ontogenetic shift becoming a competitive network, phylogenetic signal was encountered through phylogenies of both partners. This elucidates the importance of distinguishing and studying commensalistic networks, as their structure differs from other networks. In fact, a study on epiphyte-phorophte networks revealed that they are more nested than mutualistic and antagonistic networks, contrasting from what was previously expected (Piazzon *et al* 2011).

We found some communities of vascular epiphytes that were significantly clustered, and some that were only marginally significant. Even though these constituted a minority of all communities, we observed that most communities had NRI values much nearer from the phylogenetic clustering threshold, instead of phylogenetic overdispersion, revealing a trend in direction of phylogenetic attraction (Figure 2). A problem associated with analyses proposing to investigate phylogenetic attraction and overdispersion concomitantly (*e.g.* Webb *et al* 2002; Helmus *et al* 2007a) is that factors with opposed effects may be acting in the communities, obscuring each other's effect (Helmus *et al* 2007b; Pausas & Verdú 2010). Phylogenetic clustering suggests an increased influence of environmental filtering in relation to biotic interactions among vascular epiphytes. It is argued that competitive interaction plays a less important role in the assembly of vascular epiphyte communities because a great proportion of the trunks of phorophytes is uncovered by living plants, attenuating the effects for resource competition (Zotz & Vollrath 2003). So, epiphyte growth and survival on phorophytes seems to be ultimately an effect of environmental filters, such as the traits of phorophytes (Kernan & Fowler 1995; Callaway *et al* 2002), water stress (Laube & Zotz 2003; Werner & Gradstein 2008) and disturbance (Hietz 1997; Köster *et al* 2009). It is interesting to think that biotic interactions between epiphytes and phorophytes generate phylogenetic clustering, instead of phylogenetic overdispersion. Nevertheless, patterns of negative co-occurrence of vascular epiphytes found by Burns and Zotz (2010) may be explained by competition. Thus, some degree of competition might be mitigating the effects of environmental filters in the phylogenetic structure of vascular epiphyte communities.

Comparing results of NRI and PCPS values between major clades of host trees leaves us with contrasting conclusions. This happens because NRI is a within-community metric of phylogenetic structure, while PCPS measures phylogenetic structure across communities (Duarte 2011). In PCPS analysis, the first principal coordinate capture phylogenetic variation on matrix **P** related to the most basal nodes of the vascular epiphyte phylogeny. Each subsequent PCPS captures each time more variation respective to recent nodes on the phylogeny, explaining why the differences in vascular epiphyte phylogenetic composition between host tree major clades in the first PCPSs are relative to deep nodes in the phylogeny, while subsequent principal coordinates captured differences in a finer phylogenetic scale (Duarte *et al* 2012).

The main differences captured by PCPS analysis are between ancestral and derived host tree clades. PCPSs 1, 2 and 3 captured variation of non-angiosperm phorophytes in relation to eurosids, while magnoliids differ from other clades in PCPS4. Tree ferns constitute a very distinct group of phorophytes because the aerial root mantle covering the trunks provides a much higher water content and water retention favoring the survival of hygrophylous species (Mehltreter *et al* 2005). Indeed, some studies have shown that these phorophytes have a very distinct epiphyte composition with high predominance of ferns (Moran *et al* 2003; Mehltreter 2005; Schneider & Schmitt 2011). The only conifer tree in the study area was *A. angustifolia*, a heliophylous species which drives forest succession in the South Brazilian plateau (Duarte & Dillenburg 2000; Duarte *et al* 2006). Adult trees are characterized by very tall vertical trunks which eventually raise the horizontal branches and leaves beyond all other trees, characterizing a sunny canopy. Vascular epiphytes colonizing araucaria trees are mainly ferns, *Tillandsia* spp. and some orchids (Boelter *et al* 2011). The predominance of monilophytes on two so contrasting habitats as those provided by *A. Angustifolia* and *D. sellowiana* seems to be intriguing. However, a more careful examination reveals that fern trees are characterized by Hymenophyllaceae, *Blechnum* and *Vittaria*, while araucaria trees harbor mainly Polypodiaceae, a derived clade within monilophytes. Even though fern epiphytism has arisen several times as a phenomenon from the beginning of the Cenozoic (Schuettpelz & Pryer 2009), different monilophyte clades seem to have different adaptations to epiphytism. Indeed, physiological and morphological traits of epiphytic ferns have shown to correlate with their ecological distribution (Hietz & Briones 1998). While the species of Hymenophyllaceae desiccate completely within hours in moderately dry air, Polypodiaceae have coriaceous leaves, more or less succulent rhizomes and high cell wall elasticity (Hietz & Briones

1998). So, evolutionary novelties may have favored the Polypodiaceae to expand their niches to host trees with more xeric conditions, like conifers and angiosperms, becoming one of the more widespread epiphytic families around the world (see Benzing 1990). On the other side, niche conservatism may have restricted other epiphytic species of monilophytes to the lower forest strata and to the most water-retaining phorophytes.

Angiosperm epiphytes showed an overall pattern in being more diverse angiosperm host trees. Vascular epiphytes are known to have their diversity peak in the wettest rain forests (Gentry & Dodson 1987). Angiosperm epiphytic clades in our study radiated and started to diversify after the appearance of angiosperm-dominated modern rain forests (Burnham & Johnson 2004; Smith *et al* 2008; Gustafsson *et al* 2010; Calvente *et al* 2011; Givnish *et al* 2011). Association with angiosperm trees, at least in part, must be due to the high predominance of this group of plants during the multiple origins of angiosperm epiphytism. Adaptations to more widespread host tree traits, like bark chemicals and microorganisms, must had been advantageous in relation to adaptations to less common non-angiosperm tree traits. Additionally, angiosperm morphological and physiological traits leaded to environmental transformations, such as a wetter climate, triggering epiphytism in angiosperm-dominated rain forests (Boyce *et al* 2009). In contrast, *Tillandsia* spp. were more associated to the conifer *A. angustifolia*. Extreme xerophytism is a widespread characteristic within the genus *Tillandsia*, manifested by several traits enabling many species to cope with very dry conditions (*e.g.* leaf succulence, absorptive trichomes, crassulacean acid metabolism; Crayn *et al* 2004; Quezada & Gianoli 2011). Specialization to the driest canopy conditions might have prevented many atmospheric *Tillandsia* species to compete with other vascular epiphytes.

Many studies have attempted to investigate which factors are responsible for associations between epiphytes and phorophytes (Kernan & Fowler 1995; Callaway *et al* 2002; Moran *et al* 2003; Flores-Palacios & García-Franco 2006; Laube & Zotz 2006). Although these studies brought important insights about the mechanisms that generate host preferences, they rely only on ultimate ecological factors. Since plant species share a long ancestry, we incorporated phylogenetic relationships to understand how evolution may affect epiphyte-phorophyte associations. We found that physiological and morphological novelties, niche conservatism and environmental transformations can explain phylogenetic associations of epiphytes with different major clades of host trees. So, epiphyte environmental preferences are determined by trait stasis in some clades and trait adaptations in others, limiting the phorophytes that might be occupied, which leads to phylogenetic habitat filtering (Donoghue 2008; Duarte 2011). Future works in community ecology of epiphytes must to consider phylogenetic affinities between species and the evolutionary past, in order to better understand epiphyte correlations with different environment dimensions.

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Table 1. Phylogenetic signal in epiphyte-phorophyte association for epiphyte abundance and presence data in which d_{epiphyte} and $d_{\mathrm{phorophyte}}$ measure the signal strength through the epiphyte and phorophyte phylogenies, respectively. Bootstrap 95% confidence intervals are given inside the parentheses.

Data	d_{epiphyte}	$d_{\mathrm{phorophyte}}$	MSEd	MSEs	MSEb
Abundace	0.045 (0.005, 0.131)	0 (0, 0.003)	0.0342	0.0355	0.1182
Presence	0.047 (0.007, 0.137)	0.004 (0, 0.065)	0.0334	0.0348	0.1193

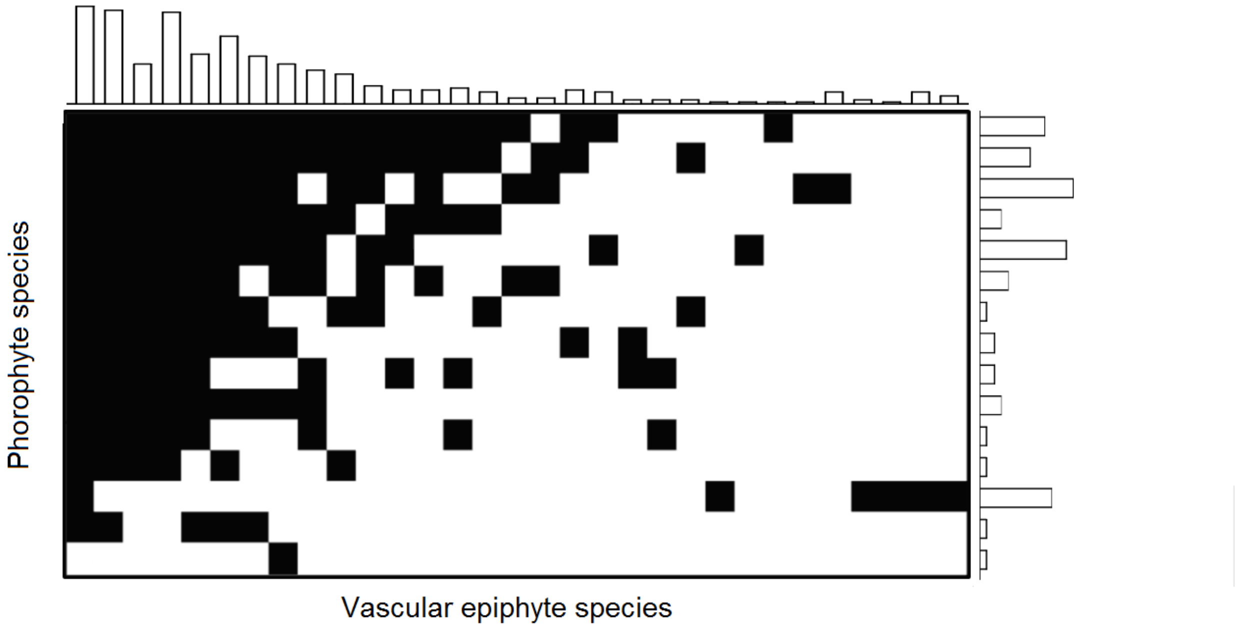

Figure 1. Maximally packed interaction matrix between vascular epiphyte species (columns) and phorophyte species (rows). Black squares represent interaction between pairs of species. Vertical bars denote relative abundances of vascular epiphyte species and horizontal bars denote relative abundances of phorophyte species. The matrix is ordered according to the number of links of vascular epiphyte and phorophyte species links.

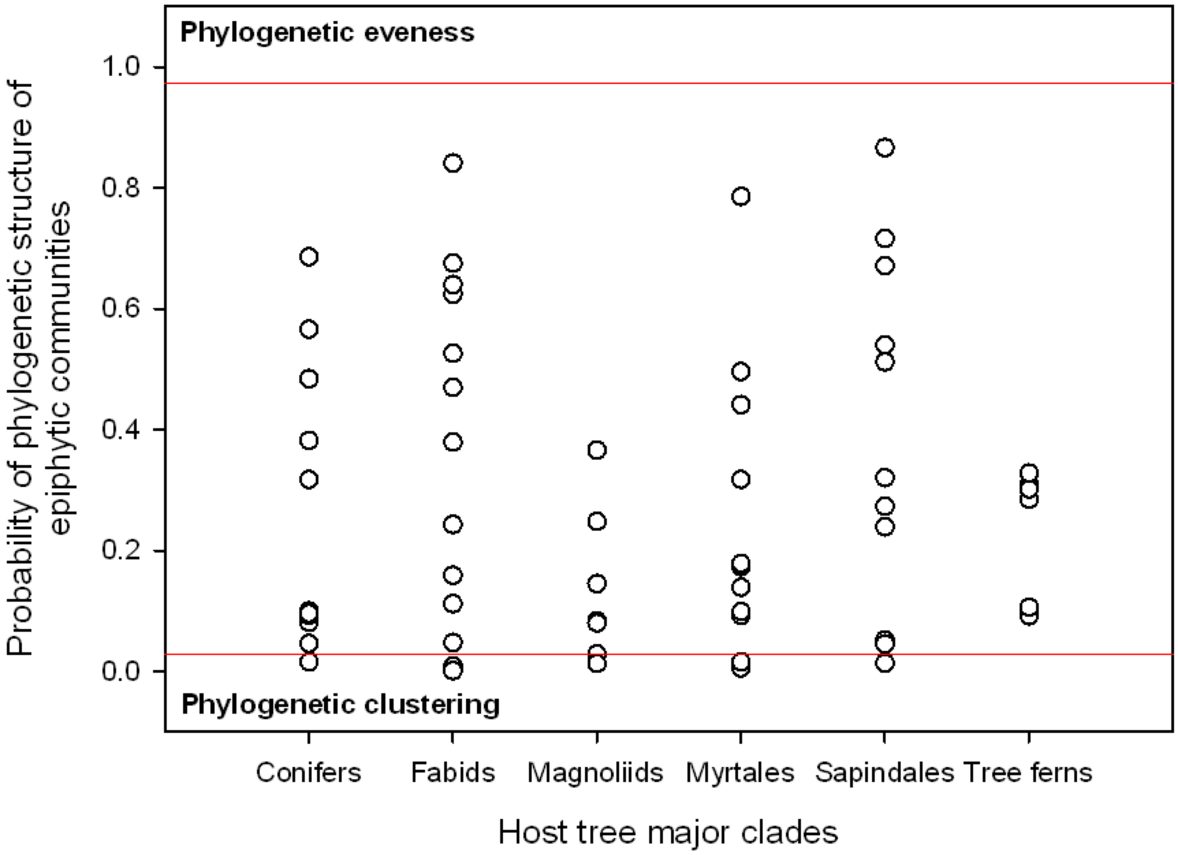

Figure 2. Probability of phylogenetic structure in communities of vascular epiphytes, represented by major clades of host trees. Values of net relatedness index with a probability rank ≤ 0.025 indicate phylogenetic clustering and ≥ 0.975 indicate phylogenetic eveness.

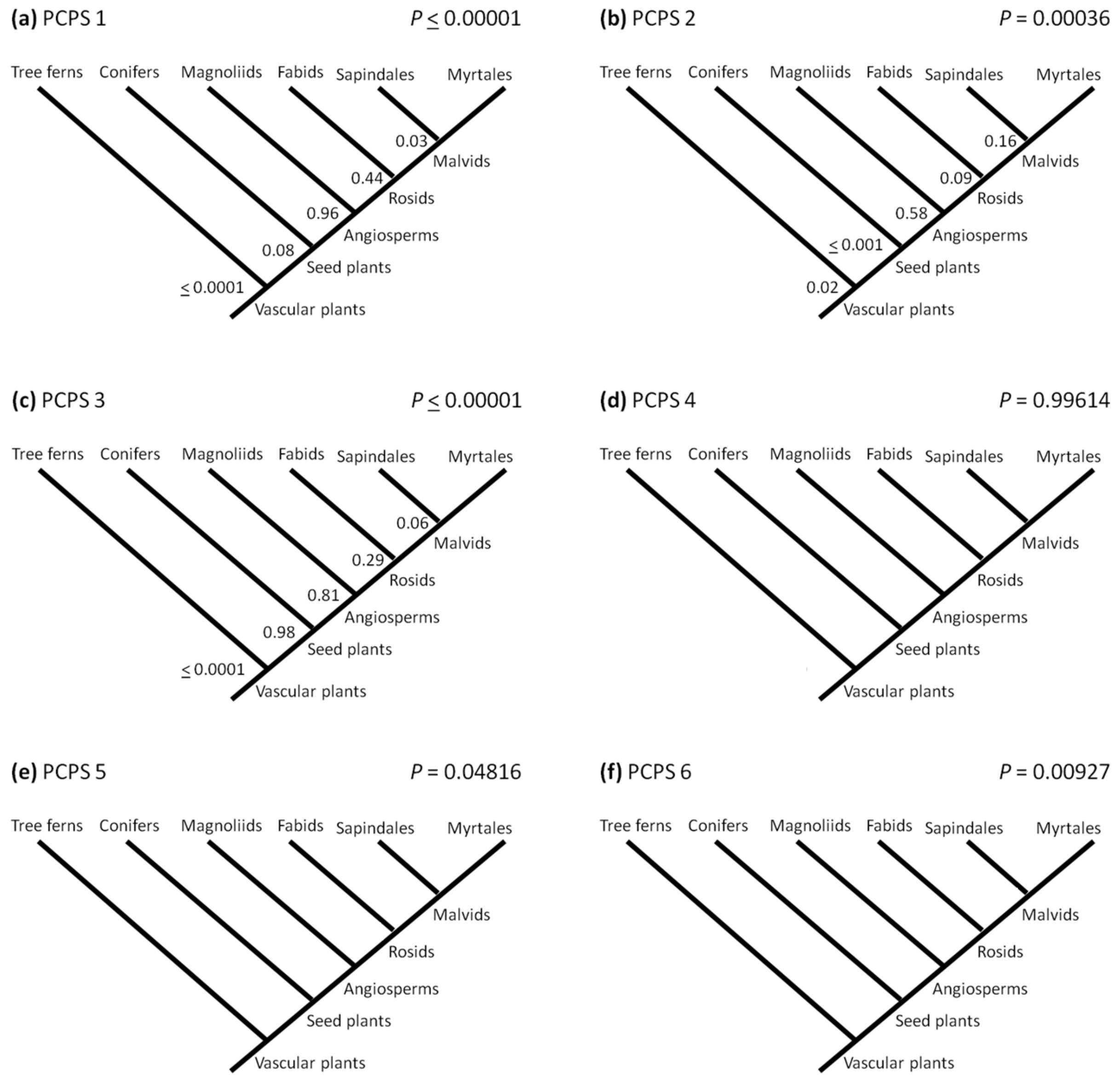

Figure 3. Analysis of variance with permutation for the first six (a to f) principal coordinates of phylogenetic structure (PCPS) of vascular epiphyte communities on different host tree major clades. After correcting alpha-value with Bonferroni method (α = [0.05/6] = 0.0083), variation between host tree major clades was significtive for (a), (b) and (c). Whenever *P*-values were significant, contrasts were evaluated for all the nodes of the phylogenetic tree of the host tree major clades. *P*-values of the contrasts are given next to the node evaluated.

Table S1. Taxonomic hierarchy of vascular epiphytic species in Aracuri Ecological Station, Muitos Capões, Rio Grande do Sul, Brazil.

Major clade	**Order**	**Family**	**Species**
Monilophyte	Hymenophyllales	Hymenophyllaceae	*Trichomanes anadromum* Rosenst.
Monilophyte	Hymenophyllales	Hymenophyllaceae	*Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson
Monilophyte	Hymenophyllales	Hymenophyllaceae	*Didymoglossum hymenoides* (Hedw.) Desv.
Monilophyte	Polypodiales	Pteridaceae	*Vittaria lineata* (L.) J. Smith
Monilophyte	Polypodiales	Blechnaceae	*Blechnum binervatum* (Poir.) C.V. Morton
Monilophyte	Polypodiales	Aspleniaceae	*Asplenium gastonis* Fee
Monilophyte	Polypodiales	Aspleniaceae	*Asplenium raddianum* Gaudich.
Monilophyte	Polypodiales	Polypodiaceae	*Campyloneurum nitidum* C. Presl
Monilophyte	Polypodiales	Polypodiaceae	*Campyloneurum austrobrasilianum* (Alston) de la Sota
Monilophyte	Polypodiales	Polypodiaceae	*Pleopeltis hirsutissima* (Raddi) de la Sota
Monilophyte	Polypodiales	Polypodiaceae	*Pleopeltis macrocarpa* (Willd.) Kaulf.
Monilophyte	Polypodiales	Polypodiaceae	*Pleopeltis pleopeltifolia* (Raddi) Alston
Monilophyte	Polypodiales	Polypodiaceae	*Pleopeltis squalida* (Vell.) de la Sota
Monilophyte	Polypodiales	Polypodiaceae	*Pecluma sicca* (Lindm.) M.G. Price
Monilophyte	Polypodiales	Polypodiaceae	*Pecluma singeri* (de la Sota) Price
Monilophyte	Polypodiales	Polypodiaceae	*Microgramma squamulosa* (Kaulf.) de la Sota
Magnoliid	Piperales	Piperaceae	*Peperomia catharinae* Miq.
Magnoliid	Piperales	Piperaceae	*Peperomia tetraphylla* (G. Forst.) Hook & Arn.
Magnoliid	Piperales	Piperaceae	*Peperomia trineura* Miq.
Monocot	Poales	Bromeliaceae	*Aechmea recurvata* (Klotzsch) L.B. Sm.
Monocot	Poales	Bromeliaceae	*Tillandsia aeranthos* (Loisel) L.B. Sm.
Monocot	Poales	Bromeliaceae	*Tillandsia recurvata* (L.) L.
Monocot	Poales	Bromeliaceae	*Tillandsia stricta* Sol.
Monocot	Poales	Bromeliaceae	*Tillandsia usneoides* (L.) L.
Monocot	Asparagales	Orchidaceae	*Acianthera dutrae* Pabst
Monocot	Asparagales	Orchidaceae	*Bulbophyllum regnellii* Rchb. f.
Monocot	Asparagales	Orchidaceae	*Capanemia micromera* Barb. Rodr.
Monocot	Asparagales	Orchidaceae	*Gomesa bifolia* (Sims) M.W. Chase & N.H. Williams
Caryophyllales	Caryophyllales	Cactaceae	*Rhipsalis floccosa* Salm-Dyck ex Pfeiff.
Caryophyllales	Caryophyllales	Cactaceae	*Lepismium houlletianum* (Lem.)Barthlott
Caryophyllales	Caryophyllales	Cactaceae	*Lepismium lumbricoides* (Lem.) Barthlott

Table S2. Taxonomic hierarchy of host trees in Aracuri Ecological Station, Muitos Capões, Rio Grande do Sul, Brazil, and their abundances as phorophytes in a vascular epiphyte survey.

Major clade	**Order**	**Family**	**Species**	**N**
Monilophyte	Cyatheales	Dicksoniaceae	*Dicksonia sellowiana* Hook.	10
Gymnosperm	Coniferales	Araucariaceae	*Araucaria agustifolia* (Bertol.) Kuntze	13
Magnoliid	Canellales	Canellaceae	*Cinamodendron dinisii* Schwanke	4
Magnoliid	Laurales	Lauraceae	*Ocotea pulchella* (Nees) Mez	1
Magnoliid	Laurales	Lauraceae	*Nectandra lanceolata* Nees	1
Magnoliid	Laurales	Lauraceae	*Nectandra megapotamica* (Spreng.) Mez	2
Fabid	Rosales	Rosaceae	*Prunus myrtifolia* (L.) Urb.	1
Fabid	Ericales	Elaeocarpaceae	*Sloanea monosperma* Vell.	3
Fabid	Oxalidales	Euphorbiaceae	*Sebastiania commersoniana* (Bill.) L.B. Sm. & Downs	9
Malvid	Myrtales	Myrtaceae	*Eugenia pyriformis* Cambess.	3
Malvid	Myrtales	Myrtaceae	*Campomanesia xanthocarpa* O. Berg	12
Malvid	Sapindales	Rutaceae	*Zanthoxylum rhoifolium* Lam.	1
Malvid	Sapindales	Sapindaceae	*Matayba elaegnoides* Radlk.	2
Malvid	Sapindales	Sapindaceae	*Cupania vernalis* Cambess.	7
Malvid	Sapindales	Sapindaceae	*Allophylus edulis* (A.St.-Hl. e*t al*) Radlk.	1

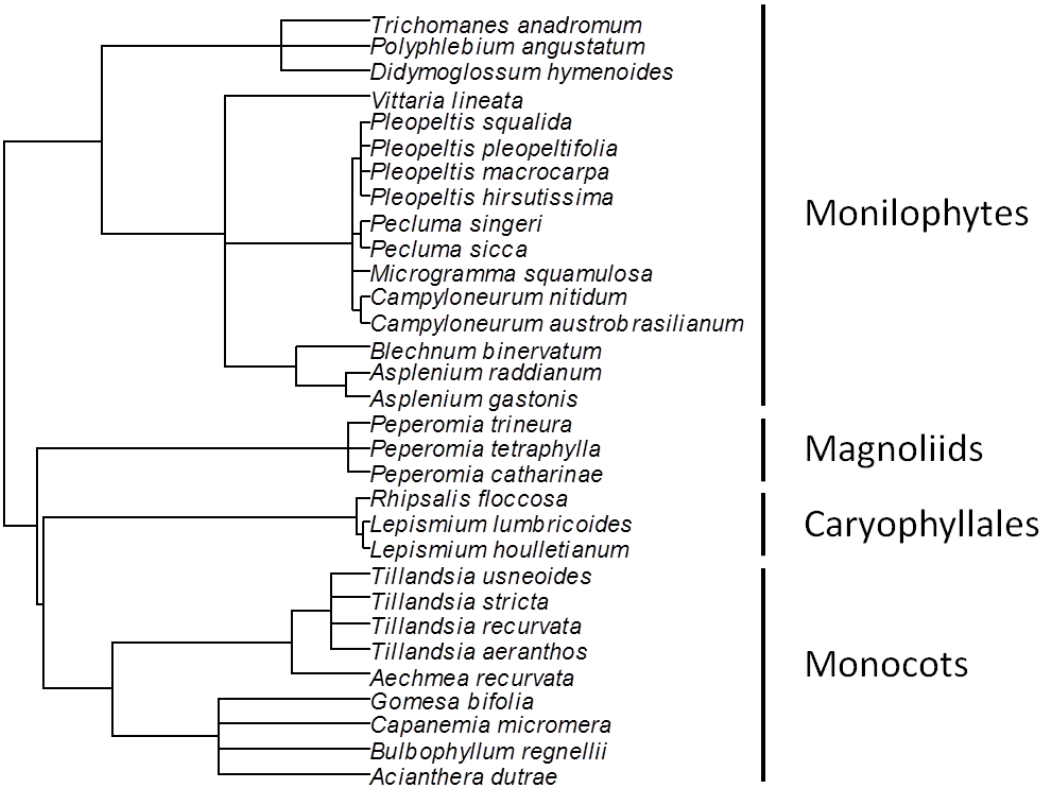

Figure S1. Phylogenetic tree for the species of vascular epiphyte occurring on different clades of phorophytes. Undated nodes are evenly distributed between dated nodes (Wilkström *et al* 2001).

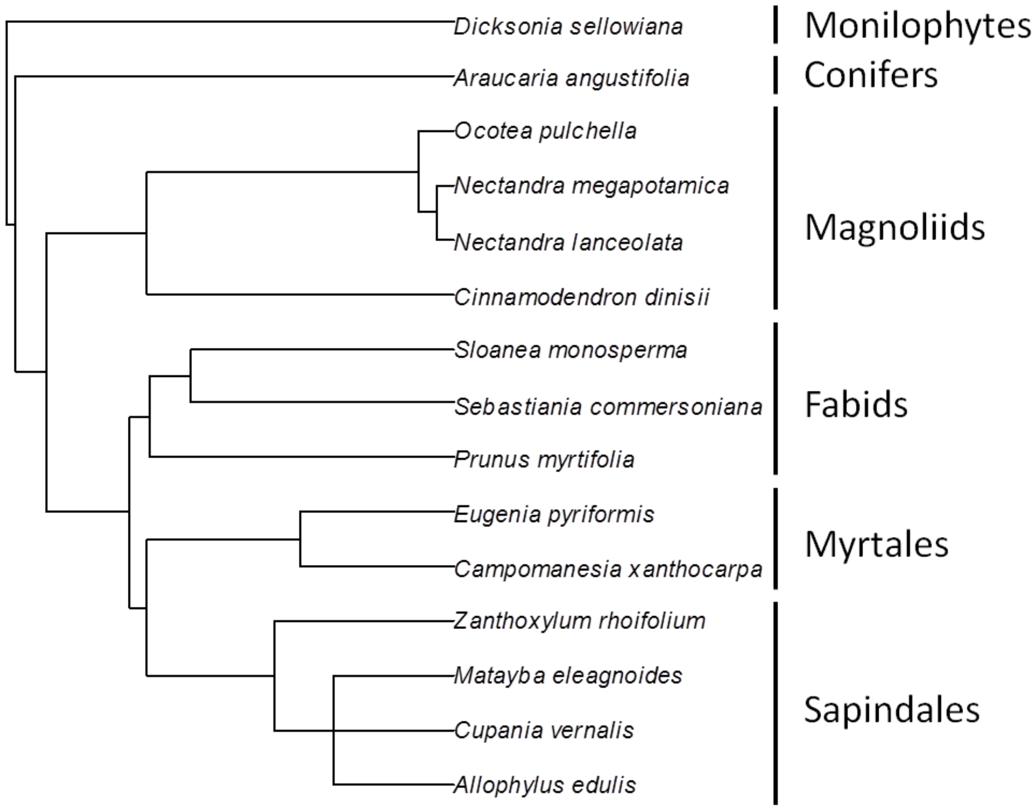

Figure S2. Phylogenetic tree of the species of phorophytes species sampled in a survey of vascular epiphytes in Aracuri Ecological Station, South Brazil. Undated nodes are evenly distributed between dated nodes (Wilkström *et al* 2001).

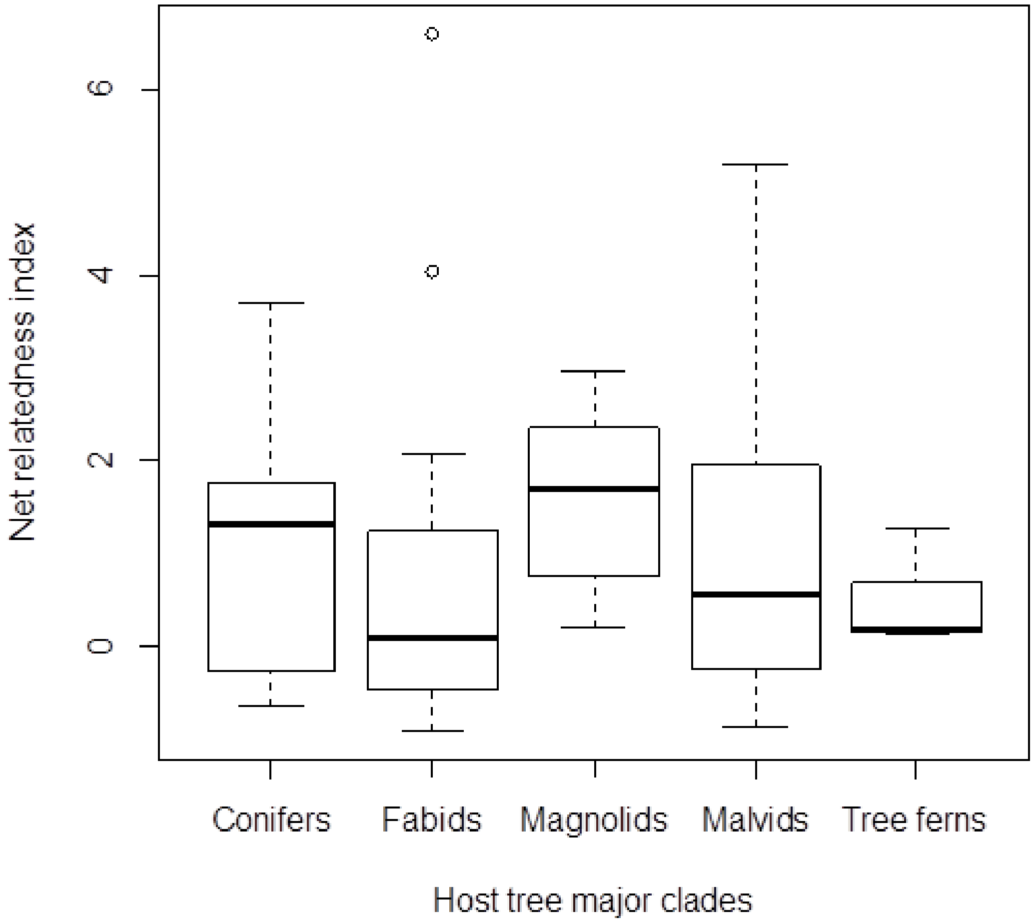

Figure S3. Analysis of variance with permutation for the net relatedness index in communities of vascular epiphytes on different major clades of host trees (*P* = 0.77). Box plots encompass 25th and 75th percentiles, with a line at the median; error bars define 10th and 90th percentiles; open circles represent outliers.

Capítulo 2 – Functional Traits Explain Host Preference by Vascular Epiphytes

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ABSTRACT

In this paper we evaluate positive and negative associations of vascular epiphyte functional groups with phorophyte groups and the influence of phorophyte size on epiphyte functional diversity, specific leaf area (SLA) and succulence. We conducted our study in a mixed-araucaria forest in the highlands of Southern Brazil by sampling vascular epiphyte composition on 70 phorophytes. We used epiphyte SLA, succulence, and poikilohydry presence and phorophyte diameter at breast height, height, bark type, crown shape, branching pattern and forest stratum of grown individuals to generate epiphyte and phorophyte groups, respectively. We measured negative and positive associations between epiphyte and phorophyte groups with Indicator Value index (IndVal). We used Rao Quadratic Entropy to estimate epiphyte functional diversity. We then related host size with epiphyte functional diversity, mean SLA and mean succulence. Different epiphyte functional groups were positively associated with distinct phorophyte groups, but only the tree fern *Dicksonia sellowiana* was negatively associated with epiphyte groups. Host tree size only correlated with mean SLA of vascular epiphytes. Epiphyte-host association seems to be mediated by trait complementarity between groups of species. The main traits involved in this interaction seem to be phorophyte size and vascular epiphyte SLA. As host trees grow up and their crowns get into the forest canopy seems to be a change in the strategy of the epiphytes which colonize it. Incorporating functional traits in the research agenda of vascular epiphyte communities may be a great help to understand the processes which structure these assemblages.

Keywords: araucaria mixed-forest; epiphytic communities; phorophytes; specific leaf area; trait complementarity

INTRODUCTION

Understanding the way species interact with each other is an important task in community ecology. For a long time ecologists used to see species interactions as highly species-specific, where one species interacts with one or very few other organisms (Ehrlich & Raven 1964; Bronstein 1988; Nilsson 1988). However, more recently some studies have shown that most systems present an entangled interaction pattern, in which partners usually interact with one or a few (*i.e.* specialists) to a high number of species (*i.e.* generalists) (Bascompte *et al* 2003; Bascompte & Jordano 2007; Thébault & Fontaine 2010). While interactions with anatomical association (*e.g.* endosymbionts) are characterized by modularity and specialist species, the same is not true for non-symbiotic interactions, where networks are highly nested and species are more generalists (Guimarães *et al* 2007, Gómez *et al* 2010). Many factors may influence the pattern of species interactions, like species abundance (Vázquez *et al* 2007), interaction type (Guimarães *et al* 2007) and phenotypic complementarity (Rezende *et al* 2007), where traits of one interaction partner match traits of the other (*e.g.* tolerance to secondary metabolites, fruit size in relation to animal size).

Vascular epiphyte communities often provide a species-rich system to test for the effects of trait complementarity on species associations. Epiphytes encompasses more than 10% of the vascular plants (Benzing 1990), being very rich in the humid tropics and subtropics, and forming highly diverse assemblies in wet forests (Nieder *et al* 1999). Even though, there are a few examples of extreme host-specificity among vascular epiphytes (*e.g.* Ackerman *et al* 1989; Tremblay *et al* 1998; Moran & Russell 2004), there is little evidence for a strict species-specific association in this life-form (Zimmerman & Olmstead 1992). Nevertheless, this kind of interaction is not characterized by randomness, since some epiphytes show pronounced preference for different species of phorophytes (Laube & Zotz 2006). Some studies have shown that tree traits are very important in determining epiphyte host preference (Kernan & Fowler 1995; Callaway *et al* 2002; Hirata *et al* 2009; Aguirre *et al* 2010). However, there is no information associating epiphyte traits to host preference, with only a few studies that investigate correlations between host tree zones in a same phorophyte and epiphyte functional traits (Hietz & Briones 1998; Reyes-García *et al* 2008).

By considering how functional traits vary in function of environmental gradients we can move from questions as which species occur in a given environment to which kind of species occur in a given environment (McGill 2006). Evaluating trait patterns in coocurring species has provided important insights about the processes structuring plant communities (*e.g*. Kraft *et al* 2008; Carlucci *et al* 2012). Using information about vascular epiphyte traits and how they are affected by environmental conditions may help to better understand the factors structuring these communities and fill the gap of knowledge about epiphytic assemblages (Burns & Zotz 2010).

A host trait that affects epiphytic communities and has been constantly investigated is phorophyte size. The diversity of vascular epiphytes is known to be influenced by host diameter at breast height (d.b.h; Zotz & Vollrath 2003; Flores-Palacios & García-Franco 2006; Aguirre *et al* 2010; Köster *et al* 2011). In general, epiphyte richness increases with phorophyte size and age (Zotz & Vollrath 2003). There is a certain discussion about how this trend is a question of more time available for epiphyte colonization, and how much it is a question of new niches that appear as a phorophyte grows up (Flores-Palacios & García-Franco 2006). If new niches are available, we would expect an increase in epiphyte functional diversity, since the habitats that a particular species can occupy are determined by functional traits (McGill *et al* 2006). So, the higher the number of habitats to be occupied on a tree the higher the number of functional alternatives to colonize a phorophyte. Furthermore, species with different functional trait values may be able to colonize trees of different sizes.

In this paper we studied the influence of functional traits on host preference by vascular epiphytes in a mixed-araucaria forest in southern Brazil. For this purpose we (1) measured positive and negative associations between groups of phorophytes with host trait similarities and functional groups of vascular epiphytes, and (2) correlated epiphyte functional diversity with host tree size, epiphyte mean specific leaf area and epiphyte mean succulence index. We aimed to ask whether phenotypic complementarity mediates associations between epiphytes and their hosts and whether phorophyte growth enhances epiphytic functional diversity by creating open niches.

METHODS

Study area - We performed this study in Aracuri Ecological Station (AES), Rio Grande do Sul, Brazil (51º10'W; 28º13'S). AES is a 272-ha fragment of mixed-araucaria forest located on the South Brazilian highlands plateau, 900 m a.s.l. Climate is humid subtropical (Cfa) , and regional annual mean temperature is *ca*. 14 ºC, with frost occurrence concentrated in June-August (winter), but also occasionally occurring from March to December (Nimer 1990). Mean annual rainfall is about 1700 mm, fairly well distributed throughout the year (Cestaro 1989).

Vegetation is typical of mixed-araucaria forest, dominated by *Araucaria angustifolia* (Bertol.) Kuntze, *Sloanea monosperma* Vell. and other tree-species belonging to the Euphorbiaceae, Myrtaceae, Annonaceae and Sapindaceae families (Jarenkow and Baptista 1987). These trees constitute hosts with very distinct traits which may affect epiphyte colonization (Waechter 2009). For example, *A. angustifolia* is potentially an emergent tree with a very high trunk which eventually raises its branches and leaves beyond the forest canopy. Trees of Myrtaceae often have a peeling bark (Sobral 2003). The tree fern *Dicksonia sellowiana* Hook. has aerial roots forming a mantle over the caudex, which may favor epiphyte establishment (Fraga *et al* 2008).

Sampling procedures – We used the survey of vascular epiphytes on 70 phorophytes of Waechter (2009). In that study 60 phorophytes were sampled along three transects, each one with five sampling points. At each point thye adopted the point-centered quarter method to sample the four nearest trees with a d.b.h. $\geq$ 30 cm. Additionally, 10 individuals of *Dicksonia sellowiana* were sampled separately, as this species occurs more or less restricted along riverines and represents a very distinct phorophyte with unique traits. Abundance of vascular epiphyte species was noted on all host trees, with ranks from 0 to 5 according to their prevalence along the phorophyte.

Phorophyte traits – Original data by Waechter (not published) contain tree height (m) and dbh (cm) measured in the field at the time of sampling. For other traits we reviewed information in the literature. We used the following four categorical traits (with categories in the parentheses): forest stratum of grown individuals (canopy, subcanopy and understory); crown shape (globular, umbella-like and flattened); branching pattern (upward, horizontally divergent, absent); kind of bark (peeling, rough, aerial root mantle).

Epiphyte traits – We got vascular epiphyte traits from field collections and literature information. We used the following traits for each species: specific leaf area (SLA, according to Cornelissen *et al* 2002); succulence index (fresh weight/dry weight ratio) of the ramet; presence of poikilohydry. We used traits related to water stress tolerance since this feature has been shown as a major factor limiting epiphytic growth (Laube & Zotz 2003). Due to the diversity of epiphyte forms we had to adapt SLA measures. Cactaceae are leafless and we measured SLA for the photosynthetic cylindrical stems. For ferns, we measured SLA for the entire fronds.

Data analysis – In order to obtain groups of phorophytes we performed a cluster analysis with the UPGMA linkage method. We used a bootstrap procedure with 10,000 iterations to check the sharpness of groups (Pillar 1999). For this analysis each individual phorophyte was considered as a sampling unit, and host traits were considered as variables. Because we had distinct types of variables (*e.g.* continuous, categorical) we used Gower index as a resemblance measure between sampling units. Simulations have shown that this method has a reduced type-II error with $\alpha = 0.1$, which was adopted as a significance level (Pillar 1999). We used the same procedure to generate functional groups of vascular epiphytes. In this case, the species of vascular epiphytes were considered as sampling units and their traits as variables. For both cluster analyses we used the software MULTIV v.2.63b (Pillar; avaiable at <http://ecoqua.ecologia.ufrgs.br/ecoqua/MULTIV.html>).

We tested whether functional groups of epiphytes were associated with phorophyte groups with an indicator species index (IndVal; Dufrêne & Legendre 1997). This index was originally developed to determine indicator species for conservation purposes for its properties of combining specificity and fidelity of an object by a site in a same measure. In our case, the former was represented by a group of vascular epiphytes and the latter by a group of phorophytes. This index has the advantage that the association between an object and a site is entirely independent from other objects. Finally, the index can also measure negative association between objects and sites by a modification of the original IndVal metric (Dufrêne & Legendre 1997). By utilizing appropriate null models, it is possible to detect if the observed values of IndVal differ significantly from the expected ones (De Cáceres & Legendre 2009).

For computing IndVal_{ij} of epiphytic functional group i in phorophyte group j we accounted for two parameters: (i) $A_{ij}=\text{Nindividuals}_{ij}/\text{Nindividuals}_{i}$, where the numerator is the mean number of epiphyte group individuals of species i on phorophyte group j, and the denominator is the mean number of individuals of the epiphte group i in all phorophyte groups; (ii) $B_{ij}=\text{Nsites}_{ij}/\text{Nsites}_{j}$, which is the relative frequency of occurrence of epiphyte group i on phorophyte group j. A_{ij} is a measure of specificity, while B_{ij} is a measure of fidelity. By multiplying these two parameters we obtained IndVal_{ij}. The indicator value for dissociations is given by replacing A_{ij} by the relative mean of nonrealized abundance of epiphte group i on phorophyte group j and B_{ij} by the relative frequency of absences (see details in Dufrêne & Legendre 1997). We tested IndVal_{ij} significance with permutation tests by reallocating trees among phorophyte groups. We run 9 999 permutations and ranked observed IndVal_{ij} against expected ones. We adopted $\alpha = 0.05$ for one-tailed tests (as we were testing whether IndVal was higher than expected) and adopted Bonferroni corrections to adjust P-values for multiple-tests within epiphyte functional groups. IndVal analyses were run on R 2.14.1 (R Development Core Team 2011) with the package 'indicspecies' (De Cáceres & Legendre 2009).

We measured epiphyte functional diversity with Rao Quadratic Entropy (Rao 1982). This diversity measure can, optionally, take into account differences between species, in our case, functional differences. We used the Gower index to measure functional distances between species. We evaluated if functional diversity, the mean SLA and mean succulence index of epiphytic individuals inhabiting a phorophyte were affected by host tree size with linear regressions. Mean SLA values were log-transformed. These analyses were performed on R 2.14.1 (R Development Core Team 2011).

RESULTS

We sampled 31 species of vascular epiphytes distributed on 15 phorophyte species. Polypodiaceae was the main family with nine species, followed by Bromeliaceae (5), Orchidaceae (4), Piperaceae, Cactaceae and Hymenophyllaceae (each with three species). Other families summed a total of four species. Cluster analysis revealed a total of five sharp epiphytic functional groups (Figure 1a). Epiphyte Group 1 (EG1) was characterized by non-poikilohydric species with low to intermediate SLA. Group 2 (EG2) was defined by the orchid *Capanemia micromera* Barb. Rodr. which had a very high SLA and Group 3 (EG3) was defined by *Peperomia catharinae* Miq. with a high succulence. Epiphyte Group (EG4) comprised poikilohydric ferns with high SLA and intermediate succulence index, the filmy ferns, while Group 5 (EG5) comprised poikilohydric ferns with low to intermediate SLA and low to intermediate succulence (Table 1).

Phorophytes showed very distinct traits and architecture. Cluster analysis also indicated six sharp groups of phorophytes (Figure 1b). Phorophyte Group 1 (PG1) comprised the majority of species, characterized by usual canopy trees, with rough bark and dichotomous ramification. Group 2 (PG2) was formed by trees with a peeling bark, as occurring in several species of Myrtaceae. *Araucaria angustifolia*, which comprised Phorophyte Group 3 (PG3), is potentially a very tall conifer with an apical crown achieving the forest canopy, and eventually above this layer as an emergent tree. In adult trees the trunk is usually not ramified until 20m-high. One big *A. angustifolia* and one big *Sloanea monosperma* formed two independent clusters which we tied together in Group 4 (PG4) due to their size. *Dicksonia sellowiana*, which defined Phorophyte

Group 5 (PG5) is an understorey tree fern with indeterminate non-ramified trunks covered by a thick root mantle (Table 2).

Indicator value analysis showed that most functional groups of epiphytes are associated with one phorophyte group (Table 3). Indicator values ranged from 0.00 to 0.86 (Table S1). The epiphytic group which was composed by *P. catharinae* was the only one which was not associated with any phorophyte group. On the other hand, PG1 was associated with *C. micromera* and EG5, while tall-sized host trees were associated with EG1 and *D. sellowiana* was associated with EG4 (Table 3). Negative associations were found between *D.sellowian* and EG1 and EG5 (Table 4).

Rao functional diversity showed considerable variation between sample units (0.04±0.025; mean±standard deviation). Nevertheless, phorophyte size had no influence over functional diversity ($F_{1,61}$ = 0.27; P = 0.61; Figure 2a). On the other hand, mean SLA was shown to decrease with increasing phorophyte size ($F_{1,68}$ = 20.42; R^2 = 0.23; $P \leq 0.0001$; Figure 2b). This pattern was kept even when excluding small *D. sellowiana* tree ferns from the analysis ($F_{1,58}$ = 4.91; R^2 = 0.08; P = 0.03). Succulence index did not change with phorophyte size ($F_{1,68}$ = 0.19; P = 0.67; Figure 2c).

DISCUSSION

Our results partially corroborated our initial hypotheses concerning the correlation between phorophytes and epiphytic traits. We expected these associations should be driven by trait matching of the interaction partners. Significant positive and negative associations of epiphytic functional groups with phorophyte groups defined by tree traits suggests that trait complementarity is an important mechanism for host preference and host limitation (Callaway *et al* 2002; Laube & Zotz 2006; Vergara-Torres *et al* 2010). On the other hand, phorophyte size did not correlate with epiphyte functional diversity, as well as epiphyte succulence, though epiphyte mean SLA showed to decrease with tree size. These results indicate a change in the functional pattern of species which colonize trees of different size, despite the abscence of change in functional diversity. So, how do these distinct responses of functional ecology of vascular epiphytes arise?

Functional diversity is expected to be high when species in a community are functionally complementar, meaning that the range of trait values or states is higher in functional diverse communities (Díaz & Cabido 2001). While the range of trait values did not vary in all spectra of tree size, mean epiphyte SLA had a rapid decrease on bigger trees. So, vascular epiphyte species with low SLA values were replaced by high-SLA species, while functional diversity was kept constant. SLA is a good proxy for stress tolerance, with tolerant species having low SLA (Poorter & de Jong 1999; Cornelissen *et al* 2003). The main limiting factor epiphytes have to cope is water avaiability (Laube & Zotz 2003). In the forest understorey and on small hosts epiphytes are less susceptible to water stress, since lower temperatures and sun irradiance reduce evapotranspiration. Furthermore, low nutrient supply on small twigs due to low debris accumulation may also be a factor of stress for high-canopy dwelling epiphytes. SLA seems to be an important trait defining niche partitioning of epiphytes along forest layers in vascular epiphytes. On the other hand, epiphyte succulence was not influenced by phorophyte size and its importance seems to be related to other niche dimensions.

Association of EG1 with PG4 is consistent with higher SLA mean values on higher trees. EG1 is composed by non-poikylohdric species, mainly with low SLA, while PG4 is characterized by large trees. Phorophyte Group 1 was positively associated with EG2 and EG5. EG2 was composed only by *C. micromera*, and it is hard to distinguish whether this preference is related to the traits which define the functional group (high SLA in *C. micromera*) or to specific traits of the species itself. Indeed, EG2 was functionally distinct from EG5, which was characterized by poikylohidry, low succulence and low to intermediate SLA. Phorophyte group 1 is the most widespread type of host trees in the study area, since most of the sampled species constitute this group. These trees reach the forest canopy, have a rough bark and have much ramified crowns. Additionally, this type of phorophyte provides a set of habitat conditions along the tree, often represented as phorophyte zones (Johansson 1974; Zotz 2007). The considerable variation in SLA and succulence of EG5 may favor the occupancy of most of these zones. EG3 was not associated with any phorophyte group because it was represented by only one species with very low frequency (it occurred only on three phorophytes). EG4, constituted by filmy ferns, was highly associated with PG3, composed by the tree fern *D. sellowiana*. Tree ferns, and especially in the genus *Dicksonia*, are characterized by a root mantle around the trunks providing a unique substrate that retains humidity (Mehltreter *et al* 2005). Furthermore, *D. sellowiana* is an understorey tree that occurs in very wet microhabitats (Mantovani 2004). These characteristics provide a highly favourable habitat for filmy ferns, which have to inhabit humid environments, since they usually lack cuticule, differentiated epidermis and stomata (Andrade & Nobel 1997; Parra *et al* 2009). When we considered the negative associations, *D. sellowiana* was the only phorophyte dissociated from some epiphytic functional groups. These functional groups, EG1 and EG5, were the most widespread and abundant epiphyte groups, characterized by lower SLA values. Furthermore, many of these species have a thick cuticule, which might not allow growing in understorey conditions.

Trait complementarity is one of the mechanisms proposed to explain linkage patterns in ecological networks (Santamaría & Rodríguez-Gironés 2007). In this work, the most important traits responsible for epiphyte-phorophyte associations were host tree size and epiphyte SLA. Even when we considered significant associations between groups it seems to represent a gradient of associations of small trees with high-SLA epiphytes to large trees with low-SLA epiphytes. Negative associations of low-SLA species with small *D. sellowiana* trees act as 'forbidden links' (Jordano *et al* 2003) due to trait mismatch. Strategies adopted by canopy dwelling epiphytes probably do not allow them to prevail in the same way in the humid understorey. Ecophysiological novelties have allowed angiosperm clades to cope with drier environments (Boyce *et al* 2009; Brodribb *et al* 2009). Analyzing the composition of epiphyte functional groups we observe that those groups associated with larger trees are mainly composed by angiosperm epiphytes, while other groups associated with lower trees are mainly composed by ferns. In the light of this observation, future research should account for the influence of evolutionary history in the association between vascular epiphytes and phorophytes.

Despite the many studies which investigated factors underlying epiphyte host tree associations, these usually relate species to habitat preference without considering epiphyte traits (Migenis & Ackerman 1993; Callaway *et al* 2002; Laube & Zotz 2006; Zotz & Schultz 2008). Some studies taking functional traits into consideration do not provide a direct link between traits and environment (Hietz & Briones 1998; Reyes-García *et al* 2008; Parra *et al* 2009). In this study we found direct associations between functional traits of epiphytes and environment, represented by host tree traits, in a community context. Moving towards a functional-based approach allows us to understand what traits perform better in contrasting environments and further determine species occurrence and abundance (McGill *et al* 2006). We expect that by associating functional traits with epiphyte environmental preferences we will improve our capacity to understand the processes behind the structure of epiphytic communities, and will help us to fill the gap of knowledge concerning these assemblages.

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Table 1. Functional groups of vascular epiphytes with main characteristics and representative taxa.

Epiphyte group (PG)	Main characteristics	Representative taxa
EG 1	Non-poikilohydrous species with low to intermediate specific leaf area (SLA)	Angiosperm epiphytes, *Asplenium* spp., *Campyloneurum* spp.
EG 2*	Non-poikilohydrous species with high SLA	*Capanemia micromera*
EG 3*	Non-poikilohydrous species with high succulence and SLA	*Peperomia catharinae*
EG 4	Poikilohydrous species with high SLA and low to intermediate succulence	Filmy ferns (Hymenophyllaceae)
EG 5	Poikilohydrous species with low to intermediate SLA and low succulence	*Pleopeltis* spp., *Pecluma* spp.

* A single species group

Table 2. Groups of Phorophytes with main characteristics and representative taxa.

Phorophyte group (PG)	Main characteristics	Representative taxa
PG 1	Canopy trees with dichotomous ramification and rough bark	Sapindaceae spp., Lauraceae spp., *Sebastiania commersoniana*
PG 2	Canopy trees with dichotomous ramification and peeling bark	Mytaceae spp., *Allophylus edulis*
PG 3*	Trees with a very high trunk and emergent crowns	*Araucaria angustifolia*
PG 4**	Very high trees (d.b.h $\geq$ 100 cm)	*Araucaria angustifolia*, *Sloanea monosperma*
PG 5*	Non-ramified, understorey trees with trunk involved by a root mantle	*Dicksonia sellowiana*

* Single species groups

** Only one individual of the species mentioned. This group, actually, is represented by two independent groups of one individual of *A. angustifolia* and one individual of *S. monosperma*, but we tied it together due to the great high of these individuals.

Table 3. Probabilities of strength of IndVal of epiphyte functional groups in each phorophyte group being random for **positive** associations. Significant values are in bold. Alpha-value was corrected with Bonferroni method (α = [0.05/5] = 0.01).

	Phorophyte group 1	Phorophyte group 2	Phorophyte group 3	Phorophyte group 4	Phorophyte group 5
Epiphyte group 1	0.4440	0.9993	0.9957	**0.0001**	1.0000
Epiphyte group 2	**0.0009**	0.0908	1.0000	1.0000	1.0000
Epiphyte group 3	0.2959	1.0000	0.1660	1.0000	1.0000
Epiphyte group 4	0.9821	1.0000	1.0000	1.0000	**0.0001**
Epiphyte group 5	**0.0073**	0.6199	0.7876	0.1213	1.0000

Table 4. Probabilities of strength of IndVal of epiphyte functional groups in each phorophyte group being random for **negative** associations. Significant values are in bold. Alpha-value was corrected with Bonferroni method (α = [0.05/5] = 0.01).

	Phorophyte group 1	Phorophyte group 2	Phorophyte group 3	Phorophyte group 4	Phorophyte group 5
Epiphyte group 1	0.9996	**0.0058**	0.0446	1.0000	**0.0002**
Epiphyte group 2	0.9981	0.6365	0.0250	0.5708	0.0515
Epiphyte group 3	0.9263	0.4466	0.9279	0.9160	0.6195
Epiphyte group 4	0.0221	0.0616	0.1294	0.7409	1.0000
Epiphyte group 5	0.9999	0.2532	0.1464	0.8205	**0.0001**

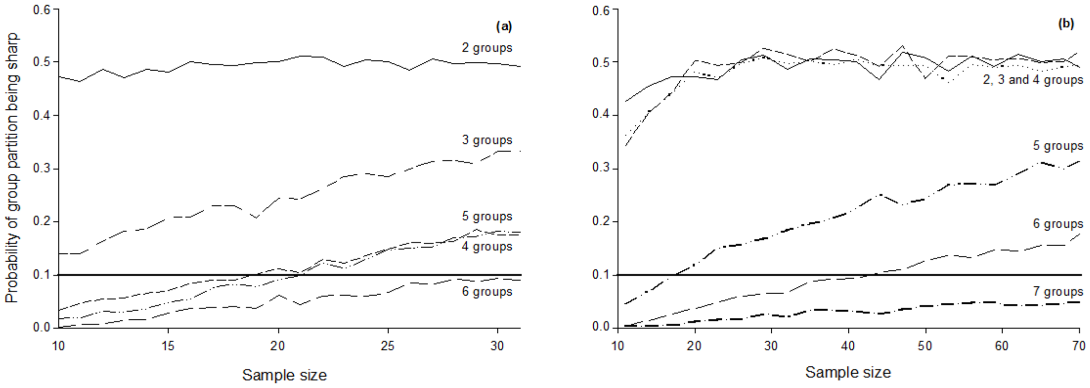

Figure 1. Probabilities of forming sharp groups in UPGMA cluster analyses for different partition levels with increasing sample sizes. Groups are fuzzy when $P \leq 0.1$ and sharp otherwise. Groups are defined by vascular epiphyte traits (a) and phorophyte traits (b).

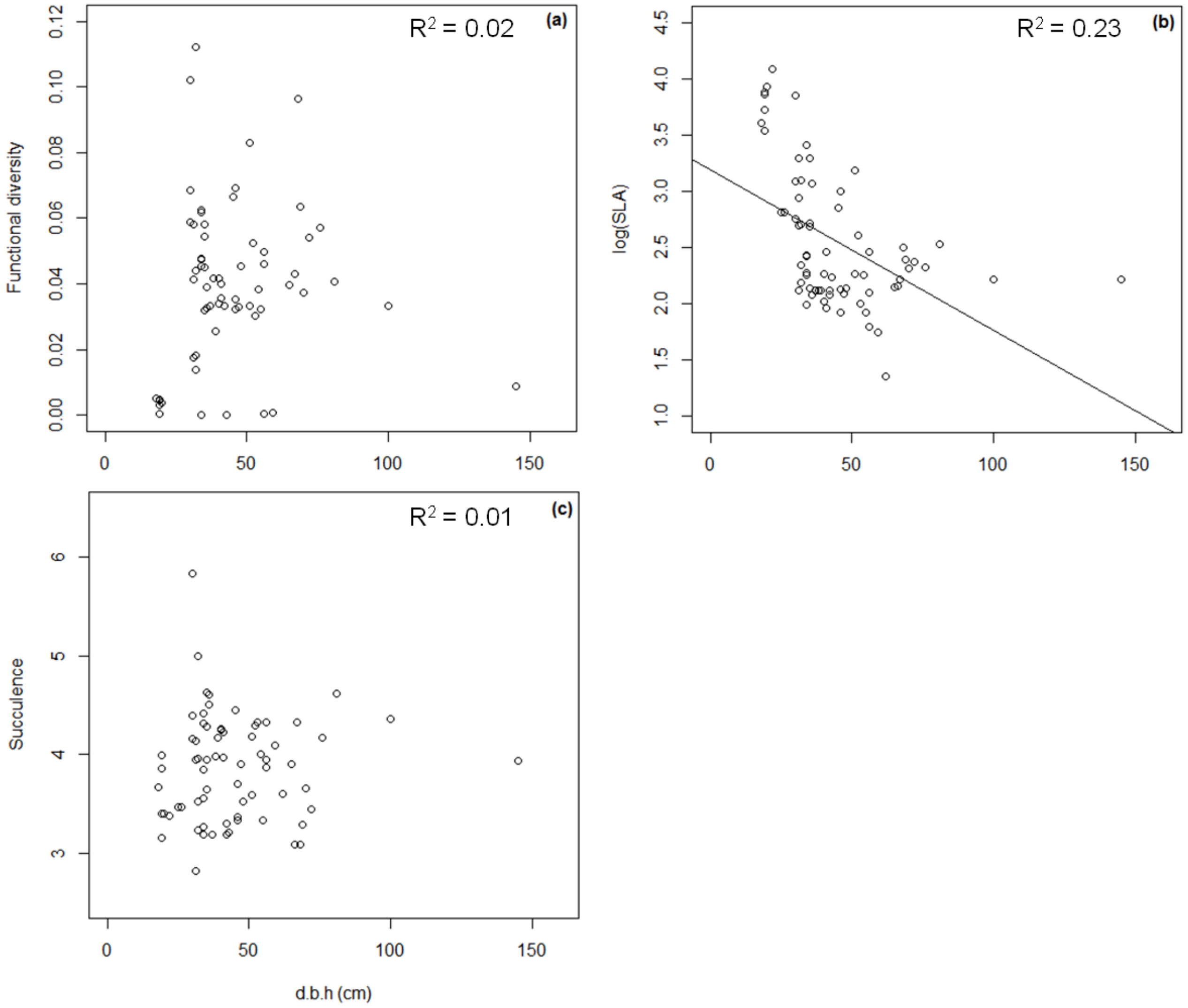

Figure 2. Relationships between phorophyte diameter at breast height (d.b.h) and vascular epiphyte functional diversity (a), mean specific leaf area of epiphyte individuals inhabiting a host tree (b) and mean succulence of epiphyte individuals inhabiting a host tree (c).

Table S1. Strength of IndVal of epiphyte functional groups in each phorophyte group.

	Phorophyte group 1	Phorophyte group 2	Phorophyte group 3	Phorophyte group 4	Phorophyte group 5
Epiphyte group 1	0.79	0.34	0.31	0.34	0.19
Epiphyte group 2	0.57	0.25	0.00	0.00	0.00
Epiphyte group 3	0.21	0.00	0.17	0.00	0.00
Epiphyte group 4	0.07	0.00	0.00	0.00	0.86
Epiphyte group 5	0.73	0.42	0.28	0.21	0.00

CONSIDERAÇÕES FINAIS

Uma das principais questões dos ecólogos que estudam as comunidades de epífitos vasculares é compreender o padrão complexo e emaranhado de interações entre espécies epifíticas e árvores hospedeiras. Neste trabalho utilizamos a filogenia e os atributos funcionais das espécies para determinar quais os principais fatores na preferência de epífitos por forófitos. Assim, ao integrar informações sobre as relações evolutivas dos organismos e suas características fenotípicas, conseguimos identificar processos históricos e respostas adaptativas a variações ambientais proporcionadas pelas árvores hospedeiras, que ajudam a entender o padrão atual de associação entre epífitos e forófitos.

No Capítulo 1 identificamos que grupos funcionais de epífitos vasculares estão associados de maneira positiva e/ou negativa a diferentes grupos de forófitos. Essa ligação se dá pela complementaridade de atributos entre os interagentes dessa associação. Para que um epífito possa colonizar e sobreviver sobre um forófito é necessário que ele tenha os atributos fenotípicos que o habilitem a lidar com as condições ambientais geradas pelas características da árvore portadora. Este aspecto fica mais bem evidenciado pela relação de decréscimo na área específica foliar (SLA) média dos epífitos com o aumento do tamanho do forófito. Enquanto em árvores pequenas apenas indivíduos com um alto valor de SLA estão presentes, em árvores maiores existe uma preponderância de indivíduos com baixo valor de SLA e espécies com alto valor de SLA são encontradas em baixa abundância na base dos troncos.

No Capítulo 2 encontramos evidência de que o conjunto de forófitos colonizados é conservado ao longo da evolução dos epífitos vasculares. Ao utilizar métricas distintas pudemos inferir sobre diferentes aspectos de fatores históricos estruturando as comunidades epifíticas. Por exemplo, a ação de filtros ambientais parece ter sido mais importante do que as interações bióticas na organização dessas comunidades, mas a intensidade dos filtros não parece diferir entre os clados de forófitos. Contudo, as diferentes linhagens de forófitos diferem na composição de clados epifíticos que aportam. A manutenção do nicho original em algumas linhagens epifíticas, bem como o surgimento de novidades fisiológicas e morfológicas, que permitiram a alguns clados colonizarem novos habitats parece ser responsável por esse padrão. Esses efeitos filogenéticos na associação entre forófitos e epífitos fazem sentido se considerarmos que essa interação tem uma longa história evolutiva. As preferências dos epífitos por forófitos se devem, em grande parte, pelo tipo de ambiente e pela fisionomia florestal preponderante na época de origem e radiação dos diferentes clados epifíticos.

Mesmo se restringindo a uma escala local, este trabalho é inovador ao relacionar diretamente atributos funcionais de epífitos vasculares com variações nos diferentes forófitos em uma escala de comunidades, assim como é o primeiro a utilizar relações filogenéticas entre diversos clados de epífitos para inferir sobre a estruturação dessas comunidades e processos históricos influenciando as associações com os forófitos. Essas abordagens nos permitiram concluir sobre fatores determinantes nessa associação, o que não seria possível levando em consideração apenas a identidade taxonômica das espécies. Esperamos que este estudo incentive novos autores a utilizarem essas abordagens em diferentes contextos e escalas, para lançar luz acerca dos processos agentes na estruturação das comunidades de epífitos vasculares, um grupo altamente diverso e ainda relativamente pouco estudado.