PAULO HENRIQUE PEREIRA GUSMÃO

IDENTIDADE VS. CARACTERÍSTICAS DA PLANTA HOSPEDEIRA: O QUE IMPORTA MAIS PARA A DIVERSIDADE FUNCIONAL DE ARANHAS?

RECIFE-PE

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal Rural de Pernambuco – UFRPE, como requisito básico exigido para obtenção de grau de Mestre em Ecologia pelo referido programa.

Orientador:
Prof. Dr. Thiago Gonçalves Souza

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Dedico este trabalho aos meus quatro sobrinhos.

À sapequinha Giovanna: um dia ela disse que queria viajar "por aí" que nem o dindo dela: estude com amor e você vai muito além!

À estrelinha Felipe (*In Memoriam*): pequeno Felipe, presente de Deus, nos disse um "olá" e logo um "adeus". Te amo pra sempre!

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"*Não basta ensinar ao homem uma especialidade porque ele se tornará assim, uma máquina utilizável, mas não uma personalidade. É necessário que adquira um sentimento, um senso prático daquilo que vale a pena ser empreendido, daquilo que é belo, do que é moralmente correto. A não ser assim, ele se assemelhará, com seus conhecimentos profissionais, mais a um cão ensinado do que a uma criatura harmoniosamente desenvolvida.* "

(Albert Einstein).

RESUMO

Diversidade taxonômica é a variedade de espécies presentes em uma determinada comunidade, enquanto a diversidade funcional é a variedade de atributos que tem relação com o funcionamento dessa comunidade. Abordagens baseadas exclusivamente na identidade das espécies têm sido complementadas por estudos visando os atributos funcionais das espécies, já que a primeira possui certas limitações em estudos de comunidades. No presente estudo, testamos se a diversidade taxonômica e funcional de aranhas respondia mais significativamente a variação intraespecífica ou interespecífica de atributos de bromélias, sendo estas hospedeiras das espécies de aranhas estudadas. Lançamos mão de um método estatístico que quantifica a beta-diversidade de aranhas em resposta a variação intraespecífica e interespecífica de bromélias. Fizemos também uma decomposição dos atributos de bromélias na sua filogenia a fim de investigar se existia algum nó que contribuía desproporcionalmente para a diversidade de aranhas atual naquele local. Os dados deste estudo foram obtidos em uma área de Floresta Atlântica Neotropical localizada no estado do Espírito Santo, sudeste do Brasil. A diversidade funcional de aranhas foi obtida por meio de atributos relacionados ao uso do hábitat (atributos de resposta), enquanto os atributos das bromélias foram obtidos a partir da possibilidade de uso do hábitat pelas aranhas (atributos de efeito). Buscamos estudos filogenéticos recentes para decompor os atributos das bromélias na filogenia. Utilizamos a contribuição proporcional de variação intraespecífica e interespecífica dos atributos das bromélias como variáveis preditoras da diversidade de aranhas. Nossos resultados mostraram que a variação interespecífica de um dos atributos de bromélias afetou positivamente a diversidade beta de aranhas ($P < 0.05$), reafirmando a necessidade de se utilizar abordagens que extrapolem a identidade de espécies como medida única ou principal de diversidade.

Palavras-chave: História evolutiva. Interações não-tróficas. Filtro biótico. Artrópodes. Bromélias.

ABSTRACT

Taxonomic diversity is the variety of species present in a given community, while functional diversity is the variety of attributes that relates to the functioning of that community. Approaches based exclusively on species identity have been complemented by studies aiming at the functional attributes of the species, since the former has certain limitations in studies of Community Ecology. In the present study, we tested whether the taxonomic and functional diversity of spiders responded more significantly to intraspecific or interspecific variation of their host plants, bromeliads. We used a statistical method that quantified beta-diversity of spiders in response to intraspecific and interspecific variation of bromeliads. We also did a decomposition of the bromeliad attributes in the phylogeny in order to investigate if there was any node that contributed disproportionately to the current diversity of spiders. The data of this study were obtained in an area of Neotropical Atlantic Forest located in the state of Espírito Santo, southeastern Brazil. The functional diversity of spiders was obtained through traits related to habitat use (response traits), while the traits of bromeliads were obtained from the possibility of habitat use by spiders (effect traits). We searched recent phylogenetic studies to decompose bromeliad traits into their phylogeny. We used the proportional contribution of intraspecific and interspecific variation of bromeliad traits as predictors of spider diversity. Our results showed that the interspecific variation of one of the bromeliad traits positively affected spider beta diversity ($P < 0.05$), reinforcing the necessity to use approaches that extrapolate species identity as a single or main measure of diversity.

Keywords: Evolutionary history. Non-trophic interactions. Biotic filter. Arthropods. Bromeliads.

SUMÁRIO

1 INTRODUÇÃO

Comunidades ecológicas são assembleias de populações de espécies que co-ocorrem no espaço/tempo e interagem potencialmente entre si. A organização de tais comunidades resulta de processos bióticos como competição, predação e parasitismo (HUTCHINSON, 1959; LEIBOLD, 1989), abióticos como clima e solo (WEIHER & KEDDY 1995; CHASE 2003), que são continuamente moldados por processos evolutivos (TOFTS & SILVERTOWN, 2000; ACKERLY 2003). Como resultado, a estrutura (abundância, riqueza e composição) de comunidades muda constantemente por processos dinâmicos que são tipicamente variáveis no espaço e tempo. Por exemplo, Widenfalk et al. (2016) avaliaram a influência relativa de variáveis abióticas, bióticas e espaciais na diversidade de uma comunidade de colêmbolos, tendo como base a composição de espécies e seus atributos. Os autores demonstraram que espécies que co-ocorrem localmente são muito diferentes em vários atributos funcionais, mas além disso, o aumento da escala espacial, independente da variação abiótica, teve forte efeito sobre a composição de espécies e funcional.

Apesar disso, alguns aspectos permanecem não respondidos quando não compreendemos o papel evolutivo na variação funcional das comunidades (WEBB et al., 2002). Desse modo, o campo da ecofilogenética nos fornece percepções e avanços conceituais que nos ajudam a responder questões como o que causa a convergência (ou divergência) de atributos na comunidade (PROVETTE, 2013). De fato, a evolução pode determinar a força competitiva de linhagens que ocorrem no mesmo hábitat, uma vez que a semelhança (ou diferença) em seus atributos afetam (em termos de aptidão) a força da interação interespecífica e suas respostas a gradientes ambientais (HILLERISLAMBERS et al. 2012). Uma abordagem em que plantas podem ser consideradas um "habitat vivo" ainda não foi bem explorada, portanto requer estudos para entender os efeitos das interações interespecíficas na diversidade funcional e filogenética.

Tradicionalmente, descritores de riqueza de espécies e de diversidade taxonômica foram exaustivamente utilizados como principal dimensão da diversidade tanto na ecologia teórica quanto aplicada. Porém, a dificuldade em construir generalizações estimulou pesquisadores a explorar diferentes formas de diversidade (DÍAZ & CABIDO, 2001). O uso da riqueza de espécies como medida da diversidade foi amplamente aplicado ainda recentemente (MILDER et al., 2008; LARSEN & ORMEROD, 2010), apesar de haver algumas limitações como a de considerar que todas as espécies são equivalentes em sua resposta ou efeito no ambiente. Não obstante, a maioria dos estudos de comunidades de artrópodes são baseados em abordagens taxonômicas (incluindo composição e abundância de espécies; FOUNTAIN-JONES et al., 2015). Contudo, usar somente dados taxonômicos pode restringir o poder preditivo de estudos

de comunidades (MCGILL et al., 2006; MENEZES et al., 2010; BARTON et al., 2011), especialmente quando comparando áreas com diferentes *pools* de espécies (FOUNTAIN-JONES et al., 2015). Isto se confirma quando, de acordo com MCGILL et al. (2006), é verificável que diferentes áreas com comunidades funcionalmente semelhantes não necessariamente refletem uma comunidade taxonômica ou filogeneticamente semelhantes.

De acordo com Tilman (1994), o espaço é um fator essencial que controla a estrutura de comunidades, em termos de diversidade funcional. Estudos de como essa substituição de espécies varia em resposta a processos em escala espacial e ambiental podem elucidar uma variedade de mecanismos que conduzem a distribuição e a diversidade de atributos funcionais (WIDENFALK et al., 2016). Por exemplo, Lapinski et al. (2015) estudaram a evolução de atributos funcionais de aranhas errantes e demonstraram que a morfologia das pernas continha elementos específicos associados a preferência de micro-habitat e habilidade de aderência, quando divididas em 3 sub-guildas. Entre esses elementos, destacava-se o padrão de escopulação das pernas, que eram surpreendentemente complexos e refletiam a preferência ecológica das aranhas. Corroborando com o exemplo anterior, Podgaiski et al. (2013) destacaram que abordagens baseadas em atributos funcionais possibilitam uma compreensão mecanicista da resposta das comunidades à variação ambiental, porém, ainda são raramente usadas para entender a ecologia de artrópodes terrestres. Além disso, nos deparamos com terminologias e metodologias inconsistentes (LAMBEETS et al., 2008; VANDEWALLE et al., 2010; BARRAGÁN et al., 2011; GERISCH et al., 2011; BIRKHOFER et al., 2015).

Há muito tempo os ecólogos têm estudado a influência da estrutura do habitat na montagem de comunidades biológicas (MACARTHUR, 1958; POUNDS, 1991; WILLIAMS et al., 2002). A heterogeneidade do habitat afeta entre outras coisas a composição e a diversidade de espécies (HUSTON, 1994; ROSENZWEIG, 1995; ELLINGSEN et al., 2002). Diversos estudos sugerem que existem relações intrínsecas entre as características estruturais do habitat e a morfofisiologia de animais e plantas (LAWTON, 1983; GONÇALVES-SOUZA et al., 2010). Mais recentemente, alguns trabalhos têm inclusive discutido que os estudos clássicos baseado em medidas taxonômicas podem ser ampliados e, de certa forma aprimorados, com a inclusão de previsões associadas com reflexos evolutivos nas comunidades. Porém, ainda não se sabe ao certo como e o quanto o hábitat vivo influencia e pode ser influenciado nessas relações. Podgaiski et al. (2013) demonstraram que aranhas ocorrendo em habitats mais diversos funcionalmente tiveram maior diversidade de atributos. O estudo clássico de Lawton (1983) demonstrou o papel das plantas no processo de montagem de comunidades e aumento da diversidade de artrópodes. O autor mostrou que diferentes atributos de plantas (nomeados por Lawton como "arquitetura"), como tamanho, forma de crescimento e variedade de

elementos aéreos influenciam positivamente a riqueza de insetos associados a elas (ver também SOUTHWOOD, 1978; MORAN, 1980). Além disso, alguns estudos demonstraram que plantas com arquitetura semelhante (e.g., tamanho, formato da folha) favorecem a ocorrência de comunidades animais compartimentalizadas (i.e., alta diversidade beta: GONÇALVES-SOUZA et al., 2015a; PRADO; LEWINSOHN, 2004). De fato, evidências apontam que a arquitetura do habitat pode afetar a morfologia corporal e a aquisição de recurso e, portanto, a história de vida de artrópodes predadores (PAKEMAN & STOCKAN, 2014; GONÇALVES-SOUZA et al., 2015b). Porém são necessários mais estudos para embasar melhor e dar força a essas evidências.

Relações mutualísticas entre animais e plantas são comuns na natureza, porém as forças que regem essas interações são mediadas por diversos fatores. Bronstein (1994) afirmou que existe uma magnitude dos benefícios para ambas as partes, e isso resulta em um *continuum*, o que dificulta a categorização e até mesmo a evolução de certas relações mutualísticas. Por exemplo, a quantidade e a qualidade da proteção que formigas oferecem é variável, a depender do tamanho da agregação da planta hospedeira mutualista (fornecedora de exsudatos, abrigo, etc) e da abundância local de predadores (BRONSTEIN, 1994). Ao contrário de interações amplamente estudadas como polinizador-planta, dispersor-planta e formigas-plantas mirmecófitas, as relações entre predadores (como aranhas) e plantas são relativamente desconhecidas. Relações estreitas entre aranhas (sejam elas bromelícolas ou bromelígenas) e bromélias são relatadas na literatura em alguns estudos (e.g., DIAS & BRESCOVIT, 2004; ROMERO & VASCONCELLOS-NETO, 2005; DE OMENA et al., 2017;), e até mesmo benefícios para ambas as partes são relatados (revisão em ROMERO 2005), porém carecem de mais evidências na literatura.

Em um cenário onde aranhas e bromélias coexistem e parecem responder mutuamente a seus atributos funcionais, estudamos os efeitos dessa relação na morfologia de ambos os grupos, utilizando uma abordagem filogenética e funcional para responder perguntas que envolvem questões ecológicas e evolutivas. Em especial, esperamos que a relação estreita entre aranhas e plantas pode ser compreendida a partir de correspondências morfologia-morfologia entre os organismos em interação. Por exemplo, a variação espacial da composição (e morfologia) de espécies de bromélias gera resposta similar (em termos de composição taxonômica e funcional) de aranhas? Esta variação é independente da identidade das espécies de bromélias? Entre outras palavras, será que aranhas são mais afetadas por atributos de bromélias do que por relações espécie-específicas, como vemos comumente em sistemas mutualistas?

2 OBJETIVOS

2.1 GERAL

- Investigar as relações ecológicas e evolutivas entre bromélias e aranhas, utilizando uma abordagem filogenética e funcional.

2.2 ESPECÍFICOS

- Quantificar a resposta da diversidade funcional de aranhas à variação na diversidade funcional de bromélias, considerando-se variações intraespecíficas e interespecíficas desses grupos;
- Identificar os atributos funcionais de bromélias que contribuem mais significativamente para o aumento da diversidade de aranhas;
- Buscar evidências na filogenia de bromélias que apontem inovações funcionais em determinados grupos que contribuam mais fortemente para o aumento da diversidade de aranhas;
- Qualificar o tipo de relação que ocorre entre bromélias e aranhas (sem distinção, se bromelícolas ou bromelígenas).

3 **ARTIGO**

REVISTA ALVO: ECOLOGICAL ENTOMOLOGY – QUALIS A2

Interspecific plant functional variation prevails over intraspecific in driving spider beta-diversity

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Running title: Plant traits affect spider beta-diversity

Abstract

1. Non-trophic interactions between plant and animals can affect community structure and species traits composition. However, most studies investigated mutualistic interactions and currently it is unclear how intra and interspecific morphological trait changes in plant species affect non-trophic interactions at metacommunity scale. Also, whether plant evolutionary history determine taxonomic and functional diversity of plant-living predators is an open question.

2. To address these gaps, we used a published dataset with spiders living exclusively over bromeliads to investigate if: (i) host plant intra and interspecific morphological trait variability affect taxonomic and functional diversity of spiders, and (ii) bromeliad trait evolution determines present-day patterns of spider trait diversity.

3. We measured spider and bromeliad traits and used a new statistical framework to quantify spider beta-diversity response to intra and interspecific trait variation of bromeliads. In addition, we decomposed bromeliad traits across its phylogenetic tree to verify if current bromeliads morphological trait variability is a result of ancestral or recent diversification.

4. Whereas leaf length variation between bromeliad species exerts a positive effect on spider functional beta diversity, intraspecific variation did not affect it. Interestingly, the most ancestral split between two subfamilies explained most of bromeliad species variability, which suggest that spider functional diversity represent an outcome of bromeliad evolutionary history.

5. Overall, our results imply that the evolution of organisms that do not feed directly on plants tissues is also driven by host plant evolutionary history which, in turn, indicates that non-trophic interactions can be evolutionarily stabilized.

Keywords: evolutionary history, non-trophic interactions, biotic filter, arthropods, bromeliads

Introduction

Ecological and evolutionary processes can drive species distribution as well as their functional traits through space and time, dictating community assembly process. For a given site, there is a non-random selection of functional traits from the regional pool (Siefert, 2012). These functional traits express the history and evolutionary processes responsible for species ecological roles, affecting their persistence and coexistence in ecological communities (McGill et al., 2006; Violle et al., 2007). For example, plant height determines plant competitive dominance and tolerance to resource fluctuation. Thus, by affecting the ability of plants to establish, grow and reproduce, this trait can determine species coexistence and community assembly (McGill et al., 2006). However, there is little information about how changes in different types of plant traits may affect coexistence of non-plant species. In addition, the relevance of plants evolutionary changes in shaping morphological traits of plant-living predators remains unclear.

In general, animals are labile organisms which allow them to move from or adapt to new environmental conditions (DeWitt et al., 1998). In an adaptive way, selective pressures imposed by the environment would be expressed as physiological, behavioral or morphological modifications through successive generations (McGill et al., 2006). Because of that, the physical environment might influence patterns of community structure as much as species intra and inter-specific interactions. When animals are used to forage and breed in a

"biotic environment" (e.g. plants), both organisms are susceptible to each other selection pressure, which could result in distinct evolutionary pathways compared with classic trait-environment association. For example, plants with open flowers (rather than those with narrow and tubular structures) allow the pollination by large body size and short mouthparts visitors (Garibaldi et al., 2015). Therefore, spatial variation on plant species (and their traits) might affect specific traits of coexisting species. Accordingly, ancient changes in plant morphology and present-day ecological processes may interactively determine the trait diversity of species that live on plants. This can be stronger in plant families with distinct morphological structures or architectures, such as domatium-bearing plants (Chomicki & Renner, 2015) and the Bromeliaceae family. Some plants such as bromeliads are widely known by their water accumulation in a central tank which creates an important ecosystem for invertebrates, bacteria, zooplancton, etc. (Srivastava et al., 2004, Romero & Vasconcellos-Neto, 2005). Those organisms provide nutrients for plants, becoming crucial for their survivorship (Romero et al., 2006). Conversely, bromeliads might protect spiders against disturbance regimes such as fire (de Omena et al., 2018). Therefore, this intrinsic association between bromeliads and organisms might be a good model to detect legacy effects of ancient changes in present-day communities upon bromeliads.

In the Neotropics, associations between spiders and bromeliads could be very common (Romero, 2006) which opens a fruitful and wide field to investigate how associations throughout evolutionary time are molting spiders' bodies, like flattening their dorso-ventral shape and increasing (or decreasing) their body size (Gonçalves-Souza et al., 2014). For example, recent studies have shown that spiders occurring in plants with similar traits could share similar body sizes because plant morphology has favored the selection of specific morphological types (Podgaiski et al., 2013; Gonçalves-Souza et al., 2014). In addition, bromeliad leaves arrangement could favor species able to forage in tight space, such as spiders with compressed bodies. Therefore, bromeliads represent a very distinctive architecture compared to the surrounding vegetation, which can favor specialization (de Omena & Romero, 2010). They even might be very distinctive among other bromeliads, which highlights a strong interspecific variation. Furthermore, spiders can respond to bromeliad morphological variation because of the dependence of plant characteristics for web attachment, conduction of vibratory signals and foraging, as suggested in other spider-plant systems (Riechert & Gillespie, 1986; Uetz, 1991).

The association between spiders and bromeliads comprises a good system to understand effects of habitat heterogeneity (measured as morphological variation within and between plant species) on beta diversity components, because they live in an intimate

relationship (de Omena & Romero, 2008; 2010). However, even though spiders are not restricted to this type of habitat, previous studies have already shown that spiders diversity tend to respond positively to habitat heterogeneity (Podgaisky et al., 2013). Conversely, bromeliads can also be positively affected (e.g., increasing in size) by spiders, because they control herbivore pressure and may increase nutrient provisioning (Romero et al., 2006; Gonçalves et al., 2011). But the way spiders respond to those plants modifications and how evolutionary changes in plant and spider morphologies are affecting each other is still unclear and may highlight the processes that lead them to the current association.

In this way, understanding how bromeliad-spider relationships are structured through spatial and temporal scales can be addressed using a phylogenetic and functional beta diversity approach. Therefore, by using such approaches we could highlight the roles of bromeliad lineages to spider species and traits turnover (phylogenetic framework) (Leprieur et al., 2012); also, the turnover of bromeliad functional traits might affect spider communities (Villéger et al., 2013). For instance, natural or disturbance-induced changes in plant morphology could affect spiders' traits diversity (e.g. Podgaiski et al., 2013). Furthermore, how changings in plants might cascade down to spiders' morphological traits may also affect phylogenetic structure is an unanswered question.

In the present study, we aim to demonstrate how intra and interspecific variation in bromeliad morphological traits affect functional traits of bromeliads-dwelling spiders, and whether there is a pattern on bromeliad traits distribution over their phylogeny, explaining spiders' functional diversity. We tested the following hypothesis: (1) non-trophic relationships between spiders and host plants molt spiders' traits through evolutionary processes. We predicted that spiders' traits will respond positively to bromeliads trait variation, presenting greater functional beta diversity in areas where bromeliad traits exhibit greater interspecific variation. This prediction indicates species specific responses revealing deepest evolutionary relationship between spiders and their plant hosts. As a result, bromeliad traits affect spider functional diversity but not taxonomic diversity. Conversely, the alternative hypothesis is that (2) any morphological variation of plants will affect spider morphology. Thus, we expect that bromeliad species identity is unimportant to spiders, because intraspecific variation generates short term changes in spider performance and, consequently, it affects taxonomic and functional diversity of spider. To successfully compare whether intra or interspecific trait differences of bromeliad species affect the associated spider predators, we performed auxiliary analyses to untangle how evolutionary changes in bromeliad morphology could determine present-day patterns of spider diversity. By doing so, we can provide a deeper

investigation of historical and contemporary processes driving trait-to-trait responses in non-trophic interactions.

Material and Methods

Study area

We used the data collected by Gonçalves-Souza *et al.* (2011) in Estação Biológica Santa Lúcia (EBSL), a Neotropical rainforest area located in the municipality of Santa Teresa, Espírito Santo, Brazil (19º57'S, 40º31'W). The EBSL comprises an area of 440 ha with elevations ranging from 600 to 900 m in a highly undulated topography with abundant rocky outcrops. The average annual rainfall is 1,868 mm, with the highest precipitation events in November and the lowest ones in June (Mendes & Padovan, 2000). As described by Gonçalves-Souza *et al.* (2011), bromeliads dominate the understory of this area and generally grow in multispecies clusters, being found between the forest and rocky outcrops in structurally poor ground environments with patch size varying from 0.005 to 0.93 ha (see also Wendt et al. 2008). The rainforest bromeliads species richness is one of the highest in the Neotropics (n = 75 species; Wendt et al., 2008). In some areas, a single patch can present several bromeliad genera, each one presenting natural morphological traits variation (such as plant shape, number of leaves, leaf width and leaf length). The genera that present the greatest species richness on the Family Bromeliaceae are Vriesea (n = 12 species), Aechmea (n = 11) and Nidularium (n = 4), and the most common species are Nidularium procerum, Aechmea lamarchei and Neoregelia macrosepala (Wendt et al. 2008). The genus Vriesea belongs to the subfamily Tillandsioideae, whereas Aechmea, Neoregelia and Nidularium belong to the subfamily Bromelioideae. These distinctions will be important for further analysis.

Database

The database used in this study comes from Gonçalves-Souza et al. (2011). In that study, the authors sampled spiders in nine bromeliad patches spaced from 125 to 1,031 m apart from each other, in 24 permanent plots within the patches. The samplings were performed seven times monthly or bimonthly between February 2006 and July 2007. Because patches vary greatly in size, they adjusted plot size and used six 7 x 3 m plots for small patches (varying from 0.005 to 0.14 ha) and eighteen 20 x 3 m plots for large patches (varying from 0.43 to 0.93 ha). In summary, they surveyed spiders in nine bromeliad patches varying

from one to six plots per patch. The first step was to identify all bromeliads. In each plot spiders were manually collected from all foliage surfaces (live and dead leaves), rosette interiors and leaf axils in up to 10 bromeliads individuals (maximum height at vegetation 1.5 m), totalizing 1,110 bromeliads belonging to 39 species. They performed bromeliads sampling using non-destructive methods. In each plot where bromeliads exceeded 10 individuals, we sampled the ten ones, which were more widespread in that plot. This spatial division of hyperabundant species was done to circumvent the problem of sampling ramets. Then, because of the high abundances of some species (e.g. Nidularium procerum and Aechmea lamarchei) and increasing probability of sampling ramets, a maximum of 10 individual bromeliads per species per plot were considered. However, we removed bromeliad species with less than five individuals to calculate intra vs. interspecific variability (see analysis below). Spiders were fixed in 75% alcohol, and voucher species were deposited at the Instituto Butantan (IBSP; curator: A.D. Brescovit).

Morphological traits

We chose bromeliad effect traits (sensu Violle et al., 2007) that affect spider response traits (Gonçalves-Souza et al., 2014). In this way, we attempted to choose some spider traits that could reflect their association with bromeliad traits, as predicted by theory (see above). For example, Gonçalves-Souza et al. (2014) have shown that bromeliad with greater leaf length increase spiders' body compression. Also, the number of leaves might be one of the most distinguishable trait, since spiders like Salticidae can select its host plant by visual cues (de Omena & Romero, 2010; de Omena et al., 2017). Moreover, other studies have found that these plant traits adequately predict the spatial distribution of spiders on bromeliads (e.g. Romero & Vasconcellos Neto, 2005; de Omena & Romero, 2008). Thus, we measured three bromeliad effect traits (leaf length, leaf width and number of leaves) and four spider morphological traits (prosoma height, prosoma length, prosoma width and opisthosoma length) to test our predictions concerning plant-spider trait matching. All collected spiders were photographed and measured (mm) in a stereoscopic microscope (Leica MZ 16). Bromeliads, in turn, were measured with a tapeline (cm) during the field work did by Gonçalves-Souza et al. (2011).

Decomposition of bromeliad trait diversity on bromeliad phylogeny

We manually produced a consensus tree topology with the software Mesquite (Maddison & Maddison, 2017), describing phylogenetic relationships among 39 bromeliad species based on the phylogenetic hypothesis proposed by Givnish et al. (2011). We then decomposed the pattern of bromeliad trait diversity across the phylogeny nodes using the methodology proposed by Pavoine et al. (2010), where each node has a trait value attributed as a function of trait diversity among clades descending from it. By decomposing trait across nodes, the sum of all internal nodes values will represent the total trait diversity of the clade. This approach allowed us to find whether some bromeliad nodes contribute disproportionately to their morphological variability (Pavoine et al., 2010). Basically, if there is a random variation of trait diversity across, for example, 11 nodes of a 12-species phylogeny, the average node contribution should be close to 9%. Consequently, this method tests whether one or few nodes explain more variability than expected by chance. Specifically, it uses 999 permutations to evaluate if trait diversity is concentrated (i) in phylogeny root (Ro test: root/tips skewness), (ii) in a single node (SN test: single-node skewness test), (iii) or in few-nodes (FN test: few-nodes skewness test) (more details in Pavoine et al., 2010). This is an auxiliary analysis to improve our comprehension of possible evolutionary processes increasing plant functional diversity (i.e., morphological variation between species) which, in turn, may cascade down to spider taxonomic and trait diversity.

Data analysis

Species from communities under different environmental conditions suffer changes in trait averages that can be caused either by intraspecific trait variability (ITV) or a change in species composition (turnover) or, most frequently, a combination of ITV and turnover. Likewise, effects of bromeliad traits on spider diversity may be affected by individual and species level bromeliad morphological variation. Therefore, to find out whether bromeliad traits influenced spider trait distribution we decomposed both bromeliad and spider intraspecific and interspecific variability to be able to answer which mechanism (species turnover or intraspecific bromeliad variation) was responsible for spider trait variation on the community (see Leps et al., 2011).

To test whether trait variation between bromeliad species increases spider functional beta diversity we combined two different approaches. The first one is a premise test and the second one compares relationships between bromeliads and spiders. First, it is necessary to evaluate the variation of spider traits within and between species and plots. Thus, we decomposed the variance of spider traits across different organizational levels: (i) population

($T_{IP/IC}$: trait variance of individuals within the same species relative to the variance of the community within plot), (ii) community ($T_{IC/IR}$: trait values of all individuals but ignoring species identity; this metric compares all individuals within a plot with individuals from all plots), and (iii) regional ($T_{PC/PR}$: community-wide variance using population-level means compared with all plots). This metric was called T-statistics by Violle et al. (2012), which is used to calculates ratios of variances (intra and interspecific) through different scales. $T_{IP/IC}$ is a measure of niche packing and represents overlap of intraspecific variation in spider morphology. Accordingly, it quantifies how individuals within the same species differ from other co-occurring species in a plot. In doing so, $T_{IP/IC}$ allows the comparison of internal filters (density dependent processes) affecting individual differences and species coexistence. $T_{IC/IR}$, in turn, quantifies whether external filtering (for example, abiotic differences between plots) increases population variance (independent of species identity). Last, $T_{PC/PR}$ compares species averages to all traits in the region and thus can be used to test how external filtering affects differences between species (details in Violle et al., 2012). Specifically, we used the T-statistics to decompose spider trait variance as a premise testing and, consequently, we expect that internal filters (density-dependent processes mediated by habitat structure, i.e., host plant morphology) should be more important than external filters. This premise means that spider population co-occurring in host plants within the same bromeliad patch are morphologically packed compared with spiders from the whole region. This test is essential because those predictions concerning responses of spiders to bromeliad traits are more realistic (in terms of its evolutionary prevalence) when there are density-dependent processes affecting fitness and competitive differences.

The second approach was organized in four steps. First, we quantified the amount of bromeliad trait variance explained by intraspecific variability (W), the variability due to species turnover (interspecific) (B) and their covariance (Leps et al., 2011) and use the proportional contribution of each part (W and B) as predictor variables of spider functional and taxonomic diversity. This method uses total sum of squares in a series of general linear models to decompose the variance explained by individual terms (i.e., within fixed averages, intraspecific trait variability and specific averages) using plot as a sampling unit. As a result, by summing each term we obtain the total variance (100%), and individual term contribution (i.e., percentage explained by intra (W) vs. interspecific variation (B) within each plot). This calculation was repeated for each bromeliad trait. Second, the percentage explained by each term [between species variance (B) and within species variance (W)] of the three bromeliad traits was used as predictor variable of spider (functional and taxonomic) beta diversity. To visualize how the relative importance of between- and within-species bromeliad variability to

spider beta diversity, we created a statistical test referred to as BW-statistics, which diminishes the between-species (B) variability minus within-species variance (W). BW varies from -1 (when total variance is explained solely by within-species variance) to +1 (variance totally explained by between-species variance). Third, we used spider beta diversity (taxonomic or functional) as dependent variable (y axis) and BW as the independent variable (x axis). We predict that increasing BW ($\rightarrow$ +1) will increase spider functional beta-diversity. Fourth, we calculated spider functional and taxonomic beta diversities within each plot using the methodology proposed by de Bello et al. (2011). It quantifies these values using the Rao quadratic entropy index (Rao, 1982). This method uses functional (Euclidean index) and taxonomic (Simpson index) distances within and between plots to decompose γ-diversity into α and β components. We used Jost's correction to control for differences in α diversity between plots. It produces a distance matrix with average functional (or taxonomic) beta diversity between plots. We then implemented a Permutational Multivariate Analysis of Variance (PERMANOVA) to test whether differences between bromeliad intra (W) and interspecific (B) variability (the BW-statistics) affect spider functional (or taxonomic) beta-diversity. Previous studies have advocated that PERMANOVA has a better behavior compared with other methods such as Mantel and MRPP because it is less affected by heterogeneous dispersion (Anderson and Walsh 2013). All data analyses were conducted in software R 3.3.1 (R Development Core Team, 2016), using cati (Taudiere & Violle, 2016) and vegan packages (Oksanen et al., 2016).

Results

Overall, our database comprises 305 spiders from 68 species associated with 19 bromeliad species (256 individuals). Bromeliad leaf length, leaf width and number of leaves varied from 16 to 208 cm (mean = 52.1, SD = 20.9), 2 to 18 cm (mean = 6.4, SD = 3.1), and 3 to 54 leaves (mean = 18.2, SD = 8.2), respectively. Spider prosoma height, width, length and opisthosoma length varied from 0.39 to 6.38 cm (mean = 1.04, SD = 0.86), 0.44 to 7.9 cm (mean = 1.17, SD = 1.06), 0.44 to 10.1 cm (mean = 1.49, SD = 1.3), and 0.62 to 10.84 cm (mean = 1.85, SD = 1.46), respectively.

After partitioning spider trait variance, morphological traits at the population level varied less than expected by change. Specifically, there was less variation of prosoma height ($T_{IP/IC}$ = 0.039, P < 0.05), prosoma width ($T_{IP/IC}$ = 0.036, P < 0.05), prosoma length ($T_{IP/IC}$ = 0.029, P < 0.05) and opisthosoma length ($T_{IP/IC}$ = 0.034, P < 0.05) within species than compared to the whole community within the same plot (Fig. 1). This result indicates there

are density dependent processes acting as internal filtering. Conversely, we did not find any significant pattern at the community ($T_{IC/IR}$) and regional ($T_{PC/PR}$) levels to all measured traits ($P > 0.05$). The observed values of $T_{IC/IR}$ and $T_{PC/PR}$ were not different from the null distribution (Fig.1). Taken together, these results agree with our premise that morphological variation among spider species is more important than within species. Importantly, it is strongest at the plot level, where spider populations from different species compete for host plants.

The relative importance of inter and intraspecific morphological variability between and within bromeliad species varied from highly dominated by intra ($\rightarrow$ -1) to highly dominated by interspecific variability ($\rightarrow$+1). Specifically, we found that the BW of bromeliad leaf length varied from -0.54 to 0.97, whereas the BW of leaf width varied from -0.96 to 0.95, and of number of leaves from -0.89 to 0.99. We found that plots with higher interspecific variability of leaf length had higher spider functional beta diversity ($R_2 = 0.359$, $F = 9.10$, $P = 0.040$), but it did not affect taxonomic beta diversity (PERMANOVA $R_2 = 0.117$, $F = 2.15$, $P = 0.141$). However, neither BW of leaf width nor number of leaves affected functional (PERMANOVA $R_2 = 0.071$, $P = 0.287$) and taxonomic beta diversity (PERMANOVA $R_2 = -0.007$, $P = 0.941$). In addition, spider morphological traits varied between patches and they were concentrated in three clumped peaks (Fig. 2).

We decomposed trait diversity across the nodes of bromeliad phylogeny and found that higher percentages of leaf length variability are coming from the root (Ro test = 0.832, P = 0.001). However, there is no significant variation explained by a single (SN test = 0.256, P = 0.712) or few nodes (FN test = 0.565, P = 0.198) (Fig. 3). In addition, the variation of leaf width and the number of leaves were random throughout the phylogeny ($P > 0.05$ for all Ro, SN and FN statistics). These results suggest that an ancient split between the subfamilies Bromelioideae and Tillandsioideae dictates most of the variability between the leaf length of bromeliad species. Besides the root node, four nodes represented by the clade Bromelioideae explained 43.2% of the whole bromeliad leaf length variability (Fig. 3).

Discussion

Taken together, our results suggest that spider morphological diversity can arise from interspecific variability of plant traits regarding two complementary mechanisms: (i) long term evolutionary history, with two different subfamilies division (estimated to occur from 9 to 14 Mya: Givnish et al., 2011) triggers most of the morphological variation between bromeliad species, which led to evolutionary changes in spider morphology; (ii) fine scale (<

60 m2) variability of bromeliad leaf length acts as an internal environmental filter determining density-dependent interactions, which ultimately regulates spider morphology at local scales. Consequently, and confirming our first hypothesis, bromeliad interspecific traits variation, rather than intraspecific, is driving changes in spider functional beta diversity. So, the outcome of higher interspecific variability in bromeliad leaf length found for some patches, is an increasing in the morphological diversity of spiders. This creates a strong morphological gradient where is evident how the spider-bromeliad association have been evolving together in the past 14 Mya years, since the biggest split between Bromelioideae and Tillandsioideae. Furthermore, because plant interspecific variability did not explain spider taxonomic diversity, our findings suggest that associations of spiders with bromeliads is driving morphological adaptations (analogous to the so called "trait-matching", common in mutualistic networks: Dehling et al., 2014) without the influence of species identity and the regional pool.

By integrating results of bromeliad traits patterns of evolutionary variation and their effects on spider trait diversity, we were able to identify that adaptive radiations of plants can generate adaptive responses of predators that do not feed directly on plant tissues, as previously suggested for mutualistic networks (Dehling et al., 2014). Previous studies indicate that niche and habitat selection theories could explain the evolution of traits of predatory arthropods living on plants (e.g. Gonçalves-Souza et al., 2014; Gibb et al., 2015). First, the increasing in bromeliad trait variability (independent of species identity) expand the niche availability for spiders, which may favor specialization through niche partitioning. For example, Schirmel et al. (2012) demonstrated that increasing habitat heterogeneity through successional stages favored both taxonomic and functional diversity of spiders and beetles. Moreover, specialization may be reinforced by habitat selection, because those arthropod species that recognize plants with important morphological structures might improve their fitness. Consequently, the evolution of habitat specialization improves the ability of certain species to find suitable sites for feeding and reproducing (Romero & Vasconcellos-Neto, 2005). In fact, de Omena & Romero (2008, 2010) demonstrated that a spider species that live and reproduce exclusively on bromeliads use visual cues to differentiate leaf morphology and the architecture of their host plants. These results and our findings reinforce the expectation that habitat selection is driven by a trait-based mechanism in spider-bromeliad systems. Furthermore, we found that spiders traits were organized in clumps (Fig. 3), which suggested that competition and niche availability allow self-organized size distributions and a lumpy coexistence, as demonstrated by theoretical (Schefer & van Nes, 2006) and computational models (Sakavara et al., 2018).

Several studies have shown that arthropods interact with their abiotic habitat and consequently might suffer environmental pressures driving a non-random trait variation (Lambeets et al., 2008; Schirmel et al., 2012). Our results suggest that previous evidence concerning spider response to abiotic conditions (e.g. Lapinski et al., 2015) is also generalized to non-trophic relationships between spiders and host plants, as this mutual interaction might molt both organism traits, through evolutionary processes. In fact, most spiders use bromeliads for courtship, shelter, oviposition, hunting or web attachment (Romero et al., 2006; Gonçalves-Souza et al., 2010; de Omena et al., 2018). By hunting and reproducing within plant leaves, spiders may benefit bromeliad, because they could deter herbivores. Also, spiders are important agents to improve bromeliad growth (Romero et al., 2006; Gonçalves et al., 2011).

As argued before (e.g. Pavoine et al., 2010; Gerhold et al., 2015), including phylogenetic information to untangle trait diversity improves our understanding about the link between local ecological processes and species evolutionary history. Across the 39 bromeliad species studied here, the split between subfamilies Bromelioideae and Tillandsioideae (from 9 to 14 Mya, Givnish et al., 2011) concentrated most of the present-day trait variability among all plants. This is especially remarkable because we found that much of the variance in spider functional diversity was indeed explained by differences between bromeliad species. Consequently, it suggests the association between spiders and bromeliads may be older than previously thought. Although rarely reported, trait-mediated selection of host plants by spiders was found in two-species systems, such as between Salticidae and Bromeliaceae (morphology-based selection: de Omena & Romero, 2008, 2010) and Thomisidae and Asteraceae (odor-based selection: Heiling et al., 2004). Thus, we posit that species-specific interactions between spiders and plants might be scaled up to metacommunities mediated by trait-specific association which, in turn, depends on plant evolutionary history.

There are a few caveats in the present study. The high frequency of rare species (especially those represented by single individuals: singletons) in tropical arthropods may overemphasize the variability between-species, because intraspecific changes could be only calculated in species with more than two individuals. However, previous studies have demonstrated that some spider functional traits (such as size and habits) do not explain singleton frequency (Coddington et al., 2009), which suggests that undersampling do not necessarily affect our conclusions. In addition, the absence of a time-calibrated phylogeny for both bromeliads and spiders prevent us to track lineage-specific co-adaptations. For example, the ancient colonization of diving beetles (Dysticidae) on bromeliads (12-23 Mya) originated

by allopatric speciation a morphologically distinct lineage that contributed to the origin of a specialized lifestyle (Balke et al., 2008).

Conclusion

Here we provided a combined approach integrating intra and interspecific trait variability of interacting species into a phylogenetic context to analyze present-day patterns of spider diversity in an Atlantic Rainforest threatened environment. Our results support interspecific variability among bromeliads as the main driver of spider trait variation. Most of the variation comes from the root of bromeliad phylogeny suggesting that evolutionary forces are pushing spider morphological traits into greater variability. When studying the association of top-predators such as spiders and plants, we can now expect that these relationships might be mediated by host plant traits, which in turn can have great ecological and evolutionary relevance. For example, previous studies demonstrated that top predators are more sensitive to climate stability, habitat size and complexity (e.g. Ledger et al., 2013; Romero et al., 2016). Thus, by underlining the traits mediating spiders-bromeliads association we are able to provide information about how habitat specialization and resource acquisition have been occurring in the Atlantic Rainforest hotspot and also help decision makers improve public politics for habitat management and conservation.

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Contribution of authors

T.G-S. designed the study, collected the data (with help from T.N.B), and conducted all analyses, all authors discussed the theoretical background and study hypothesis, P.H.P.G. wrote the first version of the manuscript, T.G.-S., P.H.A.S., T.N.B. and L.S.O.-M contributed substantially to manuscript writing.

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Graphical abstract (highlights)

• Whether plant trait variation and its evolutionary history determine taxonomic and functional diversity of plant-living predators is an open question.

• Spatial variation in bromeliad leaf length variation between species has a positive effect on spider functional beta diversity. This spatial signature generates a lumpy distribution of spider body sizes.

• Plant evolutionary history dictates most of the present-day morphological variability among bromeliad species which, in turn, affect spider trait variation.
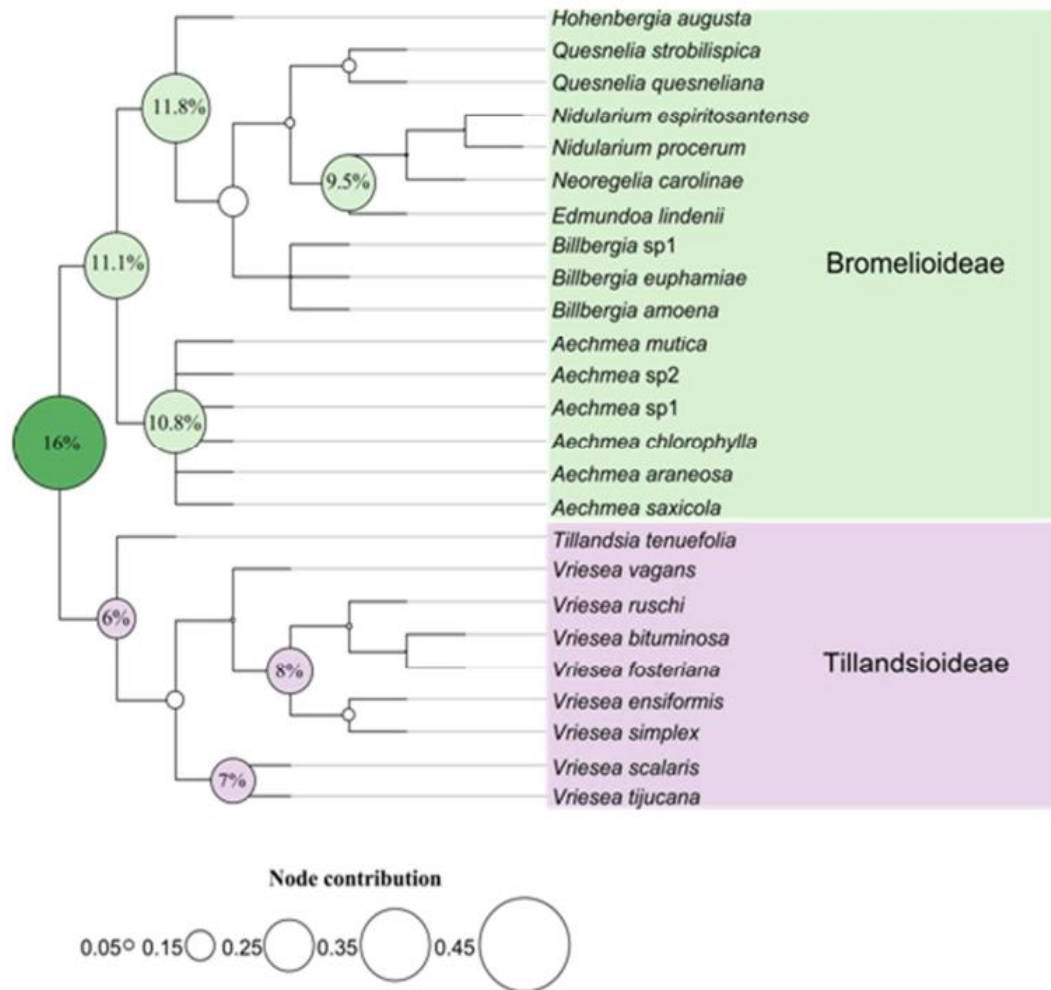
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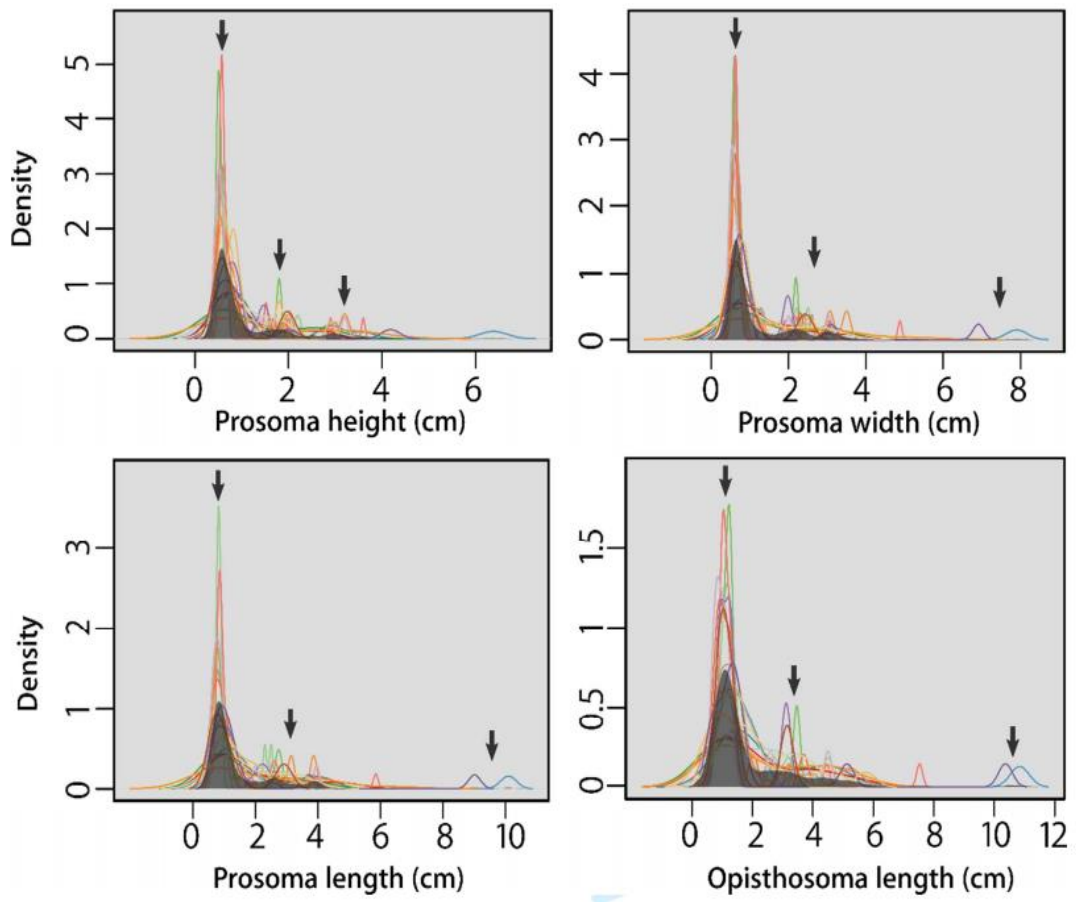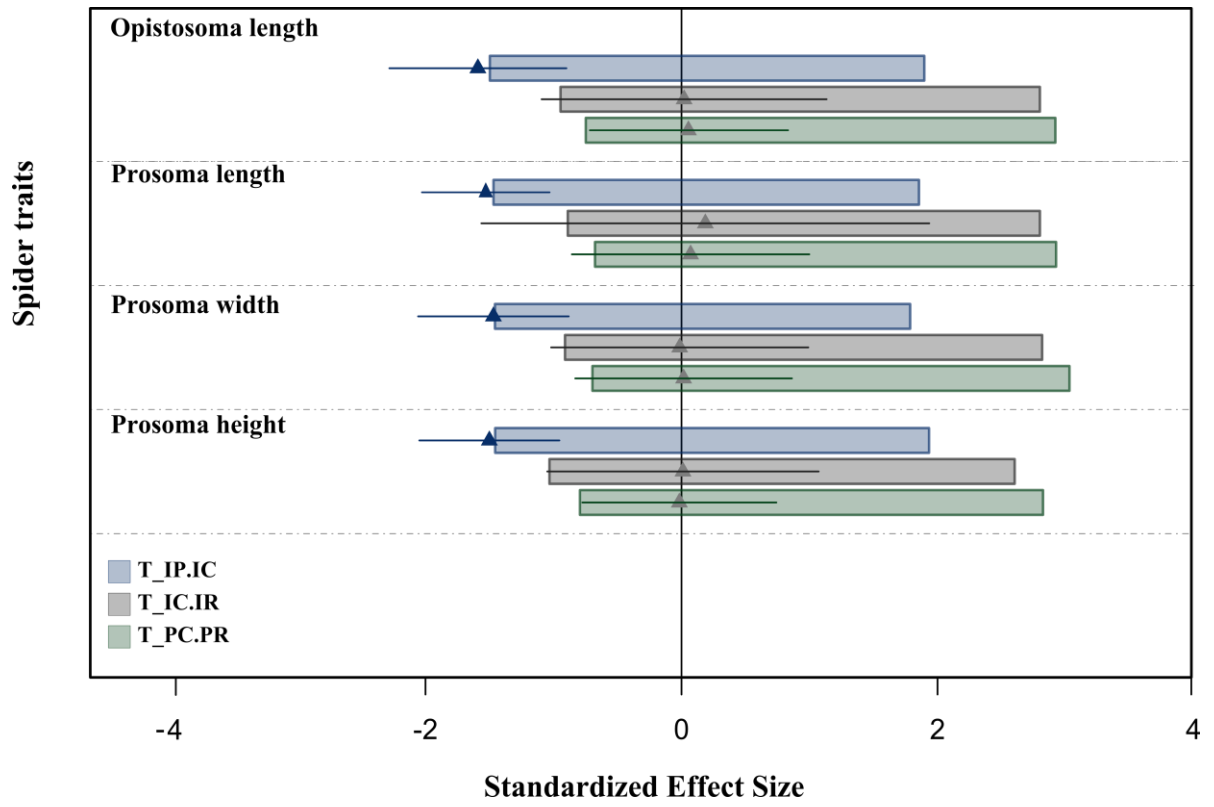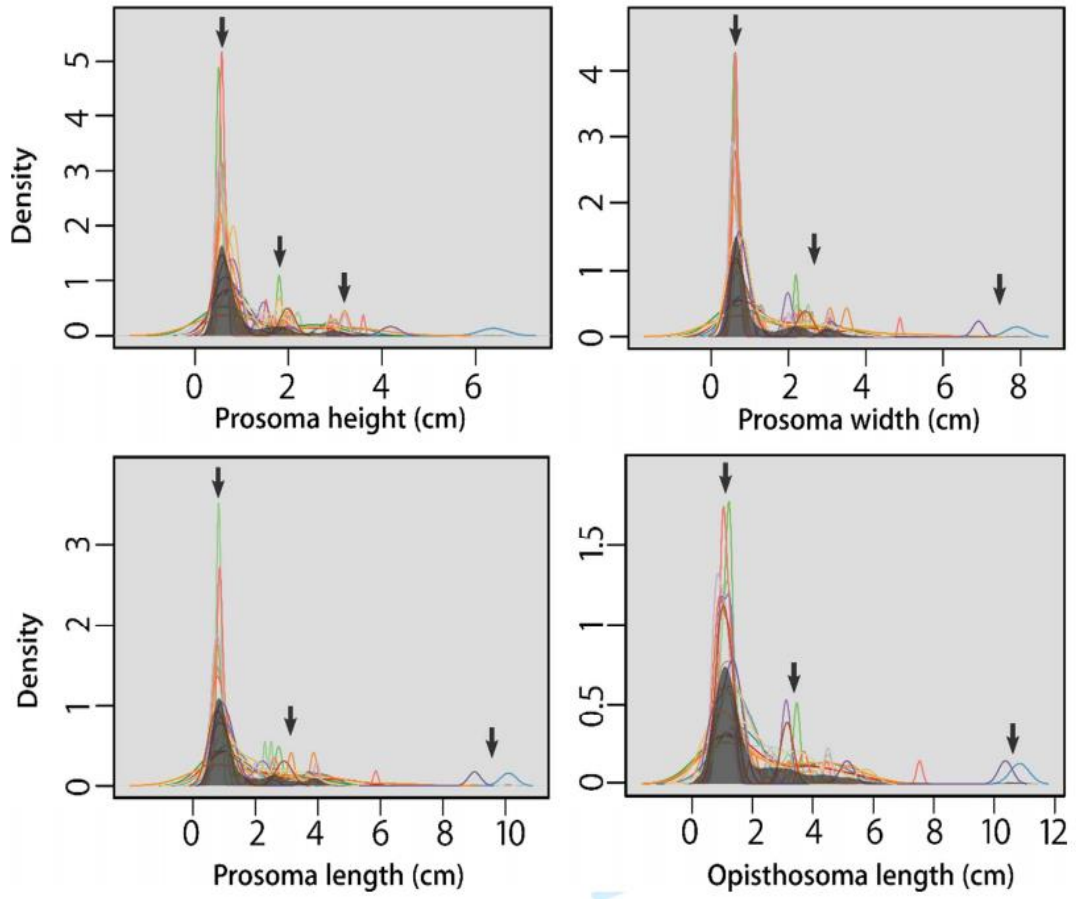
Figure 3. Trait diversity (leaf length) decomposition across the nodes of bromeliads phylogeny. The circles represent the percentage of interspecific leaf length variability accounted by each node. The variability coming from the root, explained most of the variation between bromeliad species (see main text).

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4 **ANEXOS**

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