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

PAULO H. P. GUSMÃO, PEDRO H. A. SENA, TIA GONÇALVES, LILIAN S. OUÇHI-MELO and THIAGO GONÇALVES-SOUZA

Abstract. 1. Non-trophic interactions between plants and animals can affect community structure and species trait composition. However, it is unclear how changes in intraspecific and interspecific morphological traits of plant species affect non-trophic interactions at a metacommunity scale. Additionally, whether plant evolutionary history determines taxonomic and functional diversity of plant-dwelling predators is an open question.

2. To address these gaps, this study used a published dataset with spiders dwelling exclusively on bromeliads to investigate if: (i) intra- and interspecific variability in host plant morphological traits affects spider taxonomic and functional diversity; and (ii) bromeliad trait evolution determines present-day patterns of spider trait diversity.

3. Spider and bromeliad traits were measured, and a new statistical framework was used to quantify the response of spider beta diversity to intra- and interspecific variation in bromeliad traits. In addition, bromeliad traits were decomposed across its phylogenetic tree to check whether the current variation in morphological traits of bromeliads is a result of either ancestral or recent diversification.

4. Bromeliad intraspecific variation did not affect spiders, but leaf length variation between bromeliad species had a positive effect on spider functional beta diversity. Interestingly, the most ancestral split between two subfamilies explained most of the variation in bromeliad species, which suggests that spider functional diversity could represent an outcome of bromeliad evolutionary history.

5. Overall, the results of this study suggest that interactions between plants and organisms that do not feed directly on their tissues could be shaped by plant evolutionary history, which in turn suggests that non-trophic interactions can be maintained over time.

Key words. Arthropods, biotic filter, bromeliads, evolutionary history, non-trophic interactions.
Introduction

Ecological and evolutionary processes can drive species distribution as well as their functional traits through space and time, dictating community assembly processes. In 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 the ecological role of species, affecting their persistence and coexistence in ecological communities (Mcgill et al., 2006; Violle et al., 2007). For instance, 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 on how morphological changes in plants might affect coexisting species that are associated with these plants.

In general, animals are labile organisms, which allows them to respond to, or adapt to, new environmental conditions (DeWitt et al., 1998). From an adaptive perspective, selective pressures imposed by the environment could be expressed as physiological, behavioural, or morphological changes over successive generations (Mcgill et al., 2006). The physical environment can influence patterns of community structure as much as species intra- and interspecific interactions. When animals forage and breed in or on other organisms, such as plants, selection pressures imposed on either organisms could possibly affect the associated biota. For instance, plants with open flowers can be pollinated by visitors with large bodies and short mouthparts, whereas these same visitors cannot pollinate flowers with narrow, tubular morphologies (Garibaldi et al., 2015). Therefore, spatial variation in plant species and their traits could influence the distribution of traits in cooccurring interactors.

Accordingly, ancient changes in plant morphology and present-day ecological processes could interactively determine the trait diversity of plant-dwelling species. This effect can be stronger in plant families with distinct morphological structures or architectures, such as domatium-bearing plants (Chomnick & Renner, 2015) and the Bromeliaceae family (Romero et al., 2006). Some plants, such as bromeliads, are widely known by their water accumulation in a central tank, which creates an important ecosystem for invertebrates, bacteria, zooplankton, etc. (Srivastava et al., 2004; Romero & Vasconcellos-Neto, 2005). These organisms provide nutrients for plants and are thus crucial for their survivorship (Romero et al., 2006). Bromeliads, in turn, might protect spiders against disturbance regimes (e.g. 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 on present-day, bromeliad-dwelling communities.

In the Neotropics, associations between spiders and bromeliads are very common (Romero, 2006), which opens a fruitful and wide field for investigations on how associations throughout evolutionary time could cause shifts in spider traits, such as affecting body compression and 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 as plant morphology has favoured the selection of specific morphological types (Podgaiski et al., 2013; Gonçalves-Souza et al., 2014). In addition, the arrangement of bromeliad leaves could favour species able to forage in tight spaces, such as spiders with compressed bodies. Therefore, bromeliads have a very distinctive architecture compared with the surrounding vegetation, thus favouring specialization (de Omena & Romero, 2010). Trait variation exists among bromeliad taxa, which suggests that interspecific variation in bromeliads plays a role in shaping spider distribution. Furthermore, spiders can respond to bromeliad morphological variation because of their dependence on plant traits for web attachment, conduction of vibrational signals, and foraging, as suggested in other spider–plant systems (Riechert and Gillespie, 1986; Uetz, 1991). As a result, interspecific variation in bromeliad traits can affect both spider taxonomic and functional diversity.

The association between spiders and bromeliads constitutes a good system to understand effects of habitat heterogeneity (measured as morphological variation within and between plant species) on beta diversity components, due to their close relationship (de Omena & Romero, 2008, 2010). However, even though spiders are not restricted to this type of habitat, previous studies have already shown that spider diversity tends to respond positively to habitat heterogeneity (Podgaiski et al., 2013). On the other hand, bromeliads can also be positively affected (e.g. increasing in size) by spiders, as the latter control herbivore pressure and may increase nutrient provisioning (Romero et al., 2006; Goncalves et al., 2011). However, how spiders respond to these changes in plants and how evolutionary changes in plant and spider morphologies are affecting each other are still unclear and may highlight the processes that have led them to the current association.

Therefore, we combined phylogenetic and functional beta diversity to compare how spatial and temporal variation in bromeliads could be associated with spider trait diversity. By doing so, we were able to analyse how different bromeliad lineages might explain spider and trait diversity (Leprieur et al., 2012). In addition, spatial variation in bromeliad functional traits might affect spider communities and traits (Villéger et al., 2013). For instance, previous studies have demonstrated that changes in plant morphology affect spider trait variation, as sites with higher plant diversity were also sites with higher spider trait diversity (Podgaiski et al., 2013). However, how these changes in plant morphology affect spider morphological traits and phylogenetic structure remains an unanswered question.

In the present study, we aimed to demonstrate how intra- and interspecific variations in bromeliad morphological traits affect functional traits of bromeliad-dwelling spiders, and whether there is a pattern of bromeliad trait distribution across their phylogeny, explaining spider functional diversity. We tested the following hypotheses:

1 Non-trophic relationships between spiders and host plants change spider traits through evolutionary processes. We predicted that spider traits would respond positively to variation in bromeliad traits, with higher functional beta diversity in areas where bromeliad traits exhibit higher interspecific variation (scenario 1 in Fig. 1a,b). As a result, bromeliad traits affect both spider functional and taxonomic diversity.
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Fig. 1. Schematic representation of the two scenarios hypothesised as drivers of spider taxonomic and functional diversities. Spiders and bromeliads with different colours represent distinct species. Geometrical shapes in spider opisthosoma represent different morphological traits. Each local patch represents a local assembly of bromeliads with varying traits that affect spider taxonomic and trait diversity differently (according to each scenario). Bars below each bromeliad patch indicate the amount of trait variation explained by intra- (grey) or interspecific (yellow) variation. [Colour figure can be viewed at wileyonlinelibrary.com].

2 Intraspecific variation in plant morphology is associated with shifts in spider morphology. Thus, we expected that any morphological variation in bromeliad traits over ecological timescales (e.g. plasticity, phenology) would increase spider taxonomic and functional diversity (scenario 2 in Fig. 1c,d). This indicates that changes at a shorter timescale (e.g. variation in bromeliad leaf size in response to droughts or phenological changes) might affect spider community structure and functional diversity.

To analyse successfully whether intra- or interspecific trait differences in 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 were able to provide a more in-depth investigation of historical and contemporary processes driving trait-to-trait responses in non-trophic interactions.

Materials and methods

Study area

We used the data collected by Gonçalves-Souza et al. (2011) at Estação Biológica Santa Lúcia (EBSL), a Neotropical rainforest area located in the municipality of Santa Teresa, Espírito Santo, Brazil (19°57’S, 40°31’W). The EBSL covers an area of 440 ha with elevations ranging from 600 to 900 m on a highly undulated topography with abundant rocky outcrops. The average annual rainfall is 1868 mm, with the highest precipitation events in November and the lowest in June (Mendes and Padovan, 2000). As described by Gonçalves-Souza et al. (2011), bromeliads dominate the understory of this area and generally grow in multispecies clusters, 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). Rainforest bromeliad species richness is one of the highest in the Neotropics (n = 75 species; Wendt et al., 2008). In some areas, a single patch can have several bromeliad genera, each one with variations in morphological traits (such as plant shape, number of leaves, leaf width, and leaf length). The genera with the highest species richness in the Bromeliaceae family 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 analyses.

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Database

The database used in this study derived from Gonçalves-Souza et al. (2011). In this study, the authors aimed to understand how plant architectural complexity affects spider abundance and richness. They found that the number of bromeliad leaves affects species richness by increasing spider abundance. Spiders were sampled in nine bromeliad patches located 125–1031 m apart from each other, in 24 permanent plots within the patches. Samplings were performed seven times between February 2006 and July 2007. Thus, different patches were sampled once, at different times. As patches vary greatly in size, they adjusted plot size and used six plots of size 7 × 3 m for small patches (varying from 0.005 to 0.14 ha) and 18 plots of size 20 × 3 m 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. Spiders were manually collected from all foliage surfaces (live and dead leaves), rosette interiors, and leaf axils in up to 10 bromeliad individuals (maximum height at vegetation 1.5 m) in each plot, totalling 1110 bromeliads belonging to 39 species. They sampled bromeliads using non-destructive methods. In each plot where bromeliads exceeded 10 individuals, they sampled the 10 individuals that were more spatially widespread in that plot. This spatial division of hyperabundant species was performed to circumvent the problem of sampling ramets. Therefore, a maximum of 10 individual bromeliads were considered per species per plot due to the high abundances of some species (e.g., N. procerum and A. lamarchei) and to the increased probability of sampling ramets. However, they removed bromeliad species with less than five individuals to calculate intra-versus interspecific variation (see analysis in the following). Spiders were fixed in 75% alcohol, and voucher species were deposited at the Instituto Butantan (IBSP; curator: A.D. Brescovit).

Bromeliad and spider morphological traits

We chose bromeliad effect traits [defined as traits that have an impact on ecosystem functioning sensu Violle et al. (2007)] that affect spider response traits (Gonçalves-Souza et al., 2014). We thus attempted to choose some spider traits that could reflect their association with bromeliad traits, such as body compression and size. Gonçalves-Souza et al. (2014) showed that spiders with more compressed bodies were associated with bromeliads with greater leaf length. Number of leaves might be one of the most distinguishable traits, as spiders such as Salticidae can select their host plant using 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 & Vascancellos 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. The selected spider traits are important for several aspects of spider ecology. For instance, spiders with a larger prosoma have advantages in their competition against rivals, which, in turn, provides benefits in feeding or reproduction (Taylor et al., 2001; Uetz et al., 2002; Persons & Uetz, 2005). All spiders collected were photographed and measured (mm) using a stereoscopic microscope (Leica MZ 16, Wetzlar, Germany). Bromeliads were measured with a tapeline (cm) during the fieldwork conducted by Gonçalves-Souza et al. (2011).

Decomposition of bromeliad trait diversity on bromeliad phylogeny

We manually produced a consensus tree topology using the MESQUITE 3.2 software (Maddison & Maddison, 2017), describing phylogenetic relationships among 39 bromeliad species based on the phylogenetic hypothesis proposed by Givnish et al. (2011), who used eight plastid regions (atpB-rbcL, matK, ndhF, psbA-trnH, rpl32-trnL, rps16, trnL intron, trnL-trnF). 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 relative to trait diversity among clades descending from it. By decomposing trait variation across nodes, the sum of the values of all internal nodes will represent the total trait diversity of the clade. The total trait diversity is first calculated without considering the phylogenetic structure; thus, total diversity represents trait distances among species. This approach allowed us to find out whether some bromeliad nodes contribute disproportionately to their morphological variation (Pavoine et al., 2010). If there is a random variation in trait diversity across 11 nodes of a 12-species phylogeny, for example, the average node contribution should be close to 9%. Consequently, this method tests whether one or a few nodes explain more variation than expected by chance. Specifically, it uses 999 permutations to evaluate if trait diversity is concentrated: (i) on phylogenetic root (Ro test: root/tips skewness); (ii) on a single node (SN test: single-node skewness test), (iii) or on a few nodes (FN test: few-nodes skewness test) (for more detail, see Pavoine et al. (2010)). This is an auxiliary analysis to improve our understanding 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

To find out whether bromeliad traits influenced spider trait distribution, we decomposed both bromeliad and spider intraspecific and interspecific variability to determine which mechanism (trait turnover of bromeliad species or intraspecific bromeliad variation) was responsible for spider trait variation in the community (see Lepš et al. (2011)).

We combined two different approaches to test whether trait variation between bromeliad species increases spider functional beta diversity. The first one is a premise test and the second compares relationships between bromeliads and spiders. First, it is necessary to evaluate the variation in spider traits within and between species and plots. Thus, we decomposed the variance in spider traits across different organisational levels: (i) population ($T_{IP/IC}$: trait variance in individuals within the same
species relative to the variance in the community within plots); (ii) community (\(T_{\text{ICMR}}\): 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 (\(T_{\text{PCMR}}\): 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 calculate ratios of variances (both intra- and interspecific) across different scales. These authors suggested that \(T\)-statistics could be used to infer two types of process acting at two spatial scales: the external filter that operates at large spatial scales (e.g., climate, soil) and the internal filters, which represent processes working at fine spatial scales, such as competition, parasitism, and micro-environmental heterogeneity (Violle et al., 2012). More specifically, \(T_{\text{IPRC}}\) is a measure of niche packing representing an 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. Violle et al. (2012) argued that the observed value of \(T_{\text{IPRC}}\) statistics allows comparison of internal filters affecting individual differences and species coexistence. In our study, if \(T_{\text{IPRC}}\) was relevant, we could infer that density-dependent processes (e.g., competition) and variation in microhabitat heterogeneity (e.g., host plant morphology) played a role in spider trait diversity. \(T_{\text{ICMR}}\), on the other hand, quantifies whether external filtering (e.g., climatic or soil differences between plots) affects population variance (regardless of species identity), assessing the community-wide variance relative to the variance in the regional pool. Finally, \(T_{\text{PCMR}}\) compares species averages against all traits in the region and can thus be used to test how external filtering affects differences between species (details in Violle et al., 2012). Hence, we expect that internal filters (density-dependent processes and microhabitat heterogeneity, such as shifts in host plant morphology) should be more important than external filters such as climate. This premise means that spider populations co-occurring in host plants within the same patch are morphologically similar compared with spiders from the entire region.

The second approach was organised in four steps. First, we quantified the amount of bromeliad trait variance explained by intraspecific variability (\(W\)), the variation due to species turnover (interspecific) (\(B\)) and their covariance (Lepš et al., 2011), and used the proportional contribution of each part (\(W\) and \(B\)) as predictor variables of spider functional and taxonomic diversity. This method uses the 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 variation, and specific averages) using plot as a sampling unit. As a result, by summing each term we obtained the total variance (100\%), and an individual term contribution, which represents the percentage explained by intra- (\(W\)) versus 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 a predictor variable of spider (functional and taxonomic) beta diversity. To visualise the relative importance of between- and within-species bromeliad variation in spider beta diversity, we created a statistical test referred to as \(BW\)-statistics, which subtracts \(W\) from \(BW\) ranges from \(-1\) (when total variance is explained solely by within-species variance) to \(+1\) (total variance totally explained by between-species variance) (Fig. 1a–d). Each bar below the bromeliads shows the total variance in patches dominated by inter- or intraspecific variability. Third, we used spider beta diversity (taxonomic or functional) as the dependent variable (\(y\)-axis) and \(BW\) as the independent variable (\(x\)-axis) in the following analysis. We predicted that increasing \(BW\) (\(\rightarrow\) +1) would increase spider functional beta diversity (hypothesis 1; scenario 1 in Fig. 1).

Fourth, we calculated spider functional and taxonomic beta diversities within each plot using the methodology proposed by de Bello et al. (2011). It quantifies beta diversity values using the Rao quadratic index (Rao, 1982). This method uses functional (Euclidean index) and taxonomic (Simpson index) distances within and between plots to decompose \(\gamma\)-diversity into alpha and beta components. We used Jost’s correction to control for differences in alpha diversity between plots and to reduce the potential negative effect of plot size on beta diversity. It converts the biased Simpson index to its equivalent numbers by dividing \((1/1 – a)\) and \((1/1 – \gamma)\) obtaining \(\alpha_{\text{Eqv}}\) and \(\gamma_{\text{Eqv}}\), respectively. Then, the unbiased beta diversity (\(\beta_{\text{Eqv}}\)) is calculated by the following formula: \(\alpha_{\text{Eqv}}/\gamma_{\text{Eqv}}\). Thus, the produced distance matrix uses \(\beta_{\text{Eqv}}\) to get functional (or taxonomic) beta diversity between plots, which is not affected by alpha diversity (de Bello et al., 2010). 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 using the ‘adonis’ function of the vegan package in \(R\) (Oksanen et al., 2016). We constrained permutations in PERMANOVA within patch/month to control for non-independence between plots of the same patch or samples collected in the same month.

In addition, we used the BETADISPER method to compare plots where intraspecific (or interspecific) variation is higher than interspecific (or intraspecific) variation; thus, we compared two groups representing those plots where \(BW\) is lower (\(BW \rightarrow -1\)) or higher than \(0\) (\(BW \rightarrow +1\)). Significant group comparisons (i.e., \(P < 0.05\)) in BETADISPER indicate that one group has higher heterogeneity in dispersion, which can be interpreted as a measure of functional beta diversity (Anderson & Walsh, 2013), and thus large heterogeneity indicates higher beta diversity. Previous studies have advocated that PERMANOVA had better power than other methods such as Analysis of Similarities (ANOSIM), Mantel, and Multi-response Permutation Procedures (MRPP) as it is less affected by heterogeneous dispersion (Anderson & Walsh, 2013).

As we sampled a different number of plots among patches and due to different sized patches, we have also used the functional rarefaction method to evaluate if the sampling effort could affect our analyses. Ricota et al. (2012) created a sample-based functional rarefaction method using species abundance and functional distances between samples. To account for the different sampling size/effort between patches, we calculated the expected functional diversity per patch considering the same effort. In this case, we obtained the rarefied functional diversity per patch and correlated this value with the number of plots in

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that patch. If plot size/quantity affects the number of sampled traits, this correlation must be significant ($P < 0.05$). All data analyses were conducted with R v.3.3.1 (R Development Core Team, 2016), using the 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 three 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 chance. More specifically, there was less variation of prosoma height ($T_{IPIC} = 0.039$, $P < 0.05$), prosoma width ($T_{IPIC} = 0.036$, $P < 0.05$), prosoma length ($T_{IPIC} = 0.029$, $P < 0.05$), and opisthosoma length ($T_{IPIC} = 0.034$, $P < 0.05$) within species compared with the entire community within the same plot (Fig. 2). Conversely, we did not find any significant pattern at the community ($T_{ICCR}$) and regional ($T_{PCPR}$) levels for all measured traits ($P > 0.05$), as the observed values were not different from the null distribution (Fig. 2). When analysed together, the results obtained from the $T$-statistics corroborated our premise that trait morphology variation is higher between species than variation within a single species. Importantly, morphological variation was higher at the plot level than at the species level. Furthermore, the number of plots did not affect the expected functional diversity (obtained with functional rarefaction) among patches ($r = -0.0359$, $P = 0.484$).

The relative importance of inter- and intraspecific morphological variation between and within bromeliad species varied from highly dominated by intraspecific variability ($\rightarrow -1$) to highly dominated by interspecific variability ($\rightarrow +1$). More 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 the value associated with the number of leaves varied from $-0.89$ to $0.99$. We found that plots with higher interspecific variability in leaf length had higher spider functional beta diversity ($R^2 = 0.359$, $F = 9.11$, $P = 0.035$), yet it did not affect taxonomic beta diversity ($PERMANOVA$, $R^2 = 0.117$, $F = 2.16$, $P = 0.11$). Indeed, we found there is higher functional beta diversity in plots dominated by interspecific variation than in those with higher intraspecific variation ($BETADISPER$, $F = 8.59$, $P = 0.008$; Fig. 3a,b). The average distance to the centroid was 2.8-fold higher in plots dominated by interspecific variation. However, neither $BW$ of leaf width ($PERMANOVA$, $R^2 = 0.002$, $P = 0.62$) nor number of leaves affected functional ($PERMANOVA$, $R^2 = 0.05$, $P = 0.309$) and taxonomic beta diversity (leaf width: $PERMANOVA$, $R^2 = 0.07$, $P = 0.437$; number of leaves: $PERMANOVA$, $R^2 = 0.007$, $P = 0.95$). Moreover, spider morphological traits varied between patches and they were concentrated in three clumped peaks (Fig. 4).

We decomposed trait diversity across bromeliad phylogeny nodes and found that higher percentages of leaf length variation derive from the root ($Ro test = 0.832$, $P = 0.001$). However, there is no significant variation explained by a single node (SN...
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**Fig. 3.** (a) Ordination based on a principal coordinates analysis (PCoA) comparing plots where interspecific variation was higher than intraspecific variation (red, ‘interspecific’) and plots where intraspecific variation was higher than interspecific variation (blue, ‘intraspecific’). This plot was produced using the function ‘vegan::plot.betadisper’. (b) Boxplots summarising the mean distance between plots to the centroid of each group. The higher the hull area (a) and distance (b) to the centroid, the higher the spider functional beta diversity. [Colour figure can be viewed at wileyonlinelibrary.com].

**Fig. 4.** Density plots showing the variation of prosoma height, width, and length, and opisthosoma length combining spiders found in all plots (grey area) and the variation within each plot (coloured lines). The arrows indicate three peaks of species with similar sizes, which is known as a lumpy distribution. [Colour figure can be viewed at wileyonlinelibrary.com].

Fig. 5. Decomposition of bromeliad trait diversity (leaf length) across the nodes of the bromeliad phylogenetic tree. This decomposition identifies those nodes contributing disproportionately to bromeliad trait diversity. Each circle represents the percentage of interspecific leaf length variation accounted for by each node. The variation coming from the root (16%) explained most of the variation between bromeliad species (see the text for details). [Colour figure can be viewed at wileyonlinelibrary.com].

test = 0.256, P = 0.712) or by a few nodes (FN test = 0.565, P = 0.198) (Fig. 5). In addition, the variation in 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 variation in leaf length among bromeliad species. Aside from the root node, four nodes represented by the clade Bromelioideae explained 43.2% of the leaf length variation of the entire bromeliad community (Fig. 5).

Discussion

Taken together, our results suggest that spider morphological diversity can arise from interspecific variability in plant traits regarding two complementary mechanisms. First, the morphological variation between two subfamilies [which probably occurred from 9 to 14 million years ago (Ma); Givnish et al., 2011] is associated with shifts in spider morphology, which suggests that plant evolutionary history could explain spider trait diversity. Second, the spatial distribution of bromeliads from different species at the local scale (< 60 m²) and their varying leaf length act as an internal environmental filter determining density-dependent interactions, which could ultimately explain trait diversity. Consequently, and supporting our first hypothesis, variation in bromeliad interspecific traits is driving changes in spider functional beta diversity rather than variation in intraspecific traits (as expected from Scenario 1, Fig. 1). Therefore, the outcome of higher interspecific variability in bromeliad leaf length found for some patches is an increase in the morphological diversity of spiders. Furthermore, plant interspecific variation did not explain spider taxonomic diversity. Our findings suggest that interspecific variation in bromeliad functional traits affect spider trait diversity. This positive effect of plant traits on spider functional diversity is similar to those patterns found in other plant–animal interactions, such as mutualistic networks (Dehling et al., 2014).

By integrating results of bromeliad trait patterns of evolutionary variation and their effects on spider trait diversity, we found some indications that adaptive radiations of plants could generate adaptive responses from 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 trait evolution of predatory, plant-dwelling arthropods (e.g. Gonçalves-Souza et al., 2014; Gibb et al., 2015). First, the increase in bromeliad trait variability (a microenvironmental heterogeneity) broadens niche availability for spiders, which may favour specialisation through niche partitioning. In fact, because there is less variation among individuals within the same species when compared with other coexisting species from the same plot, this result reinforces the idea that density-dependent processes and microenvironmental heterogeneity act as internal filters. Previous studies have demonstrated that increased habitat heterogeneity through successional stages favoured both taxonomic and functional diversity of spiders and beetles (Schirmel et al., 2012). Moreover, specialisation may be reinforced by habitat selection, as arthropod species that recognise plants with important morphological structures might improve their fitness. Consequently, the evolution of habitat specialisation 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 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 spider traits are organised in clumps (Fig. 3), which suggested that competition and niche availability allow self-organised size distributions and a lumpy coexistence, as demonstrated by theoretical (Scheffer & van Nes, 2006) and computational models (Sakavara et al., 2018). These authors argued that groups of species with similar traits ("species clumps") emerge from a combination of neutral and niche processes and that the presence of different clumps (similar to a multimodal distribution) reduce competition and favour coexistence (Scheffer & van Nes, 2006).

Many studies have shown that arthropods interact with their abiotic habitat, and consequently, might suffer environmental pressures that drive 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) might also be generalised to non-trophic relationships between spiders and host plants. We hereby suggest that living on plants might cause shifts in spider traits and that plant evolutionary history could cause this difference. In fact, many spiders use bromeliads for courtship, shelter, oviposition, hunting, or web attachment, which reinforces the possibility of a long-term association between spiders and bromeliads (Romero et al., 2006; Gonçalves-Souza et al., 2010; de Omena et al., 2018). Furthermore, by hunting and reproducing on plant leaves, spiders may be beneficial to bromeliads because they could deter herbivores and improve bromeliad growth (Romero et al., 2006; Gonçalves et al., 2011).

As argued before (e.g. Pavoine et al., 2010; Gerhold et al., 2015), the inclusion of phylogenetic information in order to untangle trait diversity improves our understanding of 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 Ma; Givnish et al., 2011) concentrated most of the present-day trait variation 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 (mostly leaf length). Consequently, it could indicate that the association between spiders and bromeliads is 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 (odour-based selection; Heiling et al., 2004). Thus, we postulate that the current knowledge showing some species-specific interactions between spiders and plants might be more widespread in spider communities, which, in turn, could depend on plant evolutionary history.

There are a few caveats in the present study. First, caution should be taken when inferring eco-evolutionary dynamics from different groups of organisms over time, as many mechanisms could generate similar patterns (e.g. Li et al., 2018). For example, neutral evolution or other pressures such as canopy height, microclimate, etc., could interact with bromeliads to affect the evolutionary history of spiders. Alternatively, the wide spectrum of plant species may represent ‘habitats’ of varying quality favouring spiders from different sizes (Halaj et al., 2000). Thus, because spider body size is a good predictor of competitive ability (Wells, 1988; Schuck-Paim, 2000), resource apportionment could explain the way in which plant interspecific variation affects spider functional diversity. The high frequency of rare species (especially those represented by single individuals: singletons) in tropical arthropods may overemphasise between-species variation, because intraspecific changes could only be 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 does not necessarily affect our conclusions. In addition, the absence of a time-calibrated phylogeny for both bromeliads and spiders prevents us from tracing lineage-specific co-adaptations. For instance, the ancient colonisation of diving beetles (Dysticidae) on bromeliads (12–23 Ma) originated a morphologically distinct lineage by allopatric speciation, which contributed to the origin of a specialised lifestyle (Balke et al., 2008).

**Conclusion**

We provided a combined approach integrating intra- and interspecific trait variation of interacting species into a phylogenetic context to analyse present-day patterns of spider diversity in a threatened Atlantic rainforest environment. Our results support interspecific variability among bromeliads as the main driver of spider trait variation. Most of the variation stems from the root of bromeliad phylogeny, which could indicate that evolutionary forces might drive spider morphological traits into higher variation. 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 could be of great ecological and evolutionary relevance. Previous studies have demonstrated that top predators are more sensitive to climate stability, habitat size, and complexity (Ledger et al., 2013; Romero et al., 2016, 2018). Thus, by underlining the trait-mediating spider–bromeliad association, we can provide information on how habitat specialisation and resource acquisition have been occurring in the Atlantic rainforest biodiversity hotspot.

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Author contributions

TG-S designed the study, collected the data (with help from TNB), and conducted all analyses. All authors discussed the theoretical background and study hypothesis. PHPG wrote the first version of the manuscript, and TG-S, PHAS, TNB and LSO-M contributed substantially to the manuscript writing.

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