

Bromeliads as biodiversity amplifiers and habitat segregation of spider communities in a Neotropical rainforest

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Abstract. Although bromeliads can be important in the organization of invertebrate communities in Neotropical forests, few studies support this assumption. Bromeliads possess a three-dimensional architecture and rosette grouped leaves that provide associated animals with a good place for foraging, reproduction and egg laying, as well as shelter against desiccation and natural enemies. We collected spiders from an area of the Atlantic Rainforest, southeastern Brazil, through manual inspection in bromeliads, beating trays in herbaceous+shrubby vegetation and pitfall traps in the soil, to test if: 1) species subsets that make up the Neotropical forest spider community are compartmentalized into different habitat types (i.e., bromeliads, vegetation and ground), and 2) bromeliads are important elements that structure spider communities because they generate different patterns of abundance distributions and species composition, and thus amplify spider beta diversity. Subsets of spider species were compartmentalized into three habitat types. The presence of bromeliads represented 41% of the increase in total spider richness, and contributed most to explaining the high beta diversity values among habitats. Patterns of abundance distribution of the spider community differed among habitats. These results indicate that bromeliads are key elements in structuring the spider community and highlight the importance of Bromeliaceae as biodiversity amplifiers in Neotropical ecosystems.

Keywords: Alpha and beta diversity, Atlantic rainforest, bromeliad-dwelling spiders, community structure, habitat type

Habitat structural complexity (i.e., physiognomic diversity) plays an important role in population dynamics and in the distribution and organization of animal communities in natural systems (Lawton 1983; Langellotto & Denno 2004; Srivastava 2006). Structurally more complex habitats can increase food availability, provide more shelter against predators and climatic harshness and supply alternative resources (Langellotto & Denno 2004).

Several studies have shown that habitat complexity (architecture) is a key factor determining spider species richness and composition (Robinson 1981; Greenstone 1984; Wise 1993; Halaj et al. 2000; Langellotto & Denno 2004; Beals 2006). For example, using an artificial structure made of wood and wire, Robinson (1981) showed that spiders with different foraging strategies use habitats according to their architectural characteristics, which end up segregating the spiders into species subsets. If this experiment foretells the real spider distribution in natural communities, structurally different habitats will be represented by non-random species subsets with lower percentages of shared species as habitat dissimilarity increases. Indeed, habitat structure is an important predictor of the spider communities in several natural ecosystems (e.g., Halaj et al. 2000).

Considering that most of the animals associated with the plant family Bromeliaceae are habitat specialists (Greeney 2001; Romero 2006; Balke et al. 2008; Omena & Romero 2008), different habitat architectures could generate differentiated subsets of spider communities. Bromeliads occur almost exclusively in Neotropical regions (with the exception of an African species: Benzing 2000) and represent an excellent study system to investigate compartmentalization phenomena. Bromeliads are a good example of complex structures because

they have leaves organized in a rosette, which usually form a tank that accumulates rainwater and nutrient-rich debris (Benzing 2000). Such characteristics result in a great variety of microhabitats for terrestrial (Romero & Vasconcellos-Neto 2005a, b; Romero 2006; Omena & Romero 2008) and aquatic animals (Greeney 2001; Srivastava 2006; Balke et al. 2008), which generally use bromeliads for foraging, reproduction, egg laying, nursery, and shelter against desiccation and natural enemies (Romero & Vasconcellos-Neto 2005a). For these reasons, bromeliads were considered to be biodiversity amplifiers (sensu Rocha et al. 2000). However, although various studies have suggested several advantages of bromeliads for the fauna of Neotropical forests (Benzing 2000; Greeney 2001; Romero 2006), to our knowledge there is no study showing that these plants are important in structuring spider communities and as amplifiers of total richness and beta diversity (i.e., species turnover among habitats: Tuomisto & Ruokolainen 2006; Novotny et al. 2007).

Our hypothesis is that bromeliads are key elements of spider community structure and that they contribute to amplifying the diversity of these arthropods in Neotropical ecosystems. To evaluate this hypothesis, we compared species abundance distribution patterns (dominance curves) and species composition (beta diversity) of spiders in bromeliads, herbaceous+shrubby vegetation and ground habitats to test whether 1) species subsets that make up the spider Neotropical forest community are compartmentalized in different habitat types (i.e., bromeliads, vegetation and ground) and 2) whether bromeliads are important elements that structure spider communities because they generate different patterns of abundance distributions and species composition, and thus amplify spider beta diversity. In this study, we consider total richness as the total number of spider species from the three habitat types (bromeliads, herbaceous and shrubby vegetation

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and ground), and beta diversity as the difference in the spider species composition between habitats.

METHODS

Study site.—This work was done at the Santa Lúcia Biological Station (SLBS) (19°57'S, 40°31'W, 600–900 m asl), an area of 440 ha in Santa Teresa County, Espírito Santo State, southeast Brazil. The vegetation of SLBS is characterized as primary Atlantic Rainforest. The region has an average rainfall of 1868 mm with November being the wettest month, with an average rainfall of 268.8 mm and June the driest of the year with 58.9 mm (for more details see Mendes & Padovan 2000).

At SLBS, the Bromeliaceae family is of great importance in the physiognomy of the vegetation, dominating various stretches of forest understory, generally making up large agglomerates of multispecific patches that occur naturally between forests and rocky outcrops on shallow and structurally poor ground (hereafter named “bromeliad patches”: Wendt et al. 2008). Small patches vary from 0.005 to 0.14 ha and large ones from 0.43 to 0.93 ha (see Wendt et al. 2008). The forest vegetation, with a not-well-defined canopy stratification, is predominated by members of the family Myrtaceae (e.g., genus *Eugenia*), followed by species of *Ocotea* (Lauraceae), *Pouteria* (Sapotaceae) and some Rubiaceae, Melastomataceae, Fabaceae and Areaceae (see Thomaz & Monteiro 1997).

Data surveying.—We sampled spiders from bromeliads, herbaceous and shrubby vegetation (hereafter called vegetation) and ground in nine bromeliad patches 125 to 1031 m apart. Surveying was done in 24 permanent plots during ten sampling periods between February 2006 and September 2007, in one-month intervals. Numbers of plots per patch and plot size were weighed according to the area of each patch. Plot size was 7 × 3 m ($n = 6$) for small patches and 20 × 3 m ($n = 18$) for large patches of bromeliad and ground samples. In bromeliad patches with at least two plots ($n = 5$ patches), each plot was 21 m from the nearest. We sampled terrestrial and epiphytic bromeliads (up to 1.5 m high) in all plot areas and manually collected spiders on all the plant foliage surfaces (dead and live leaves), in the interior of the rosette and between the leaf axils of 1110 bromeliads of 32 species. Bromeliaceae sampling was done using non-destructive methods. We kept collected spiders in 75% ethanol for later identification.

In contrast to the bromeliads, the vegetation is usually less dense; thus we had to increase sampling effort (plot size). We used plots of 20 × 20 m ($n = 18$) in large patches, and of 20 × 7 m ($n = 6$) in small patches. Each plot was 1 m apart; although this distance might not distinguish between two vegetation communities, plots at a distance of more than 1 m could include fauna outside the bromeliad patch. The number of plots per bromeliad patch varied from one to five depending on the size of the patch. For example, in the smallest bromeliad patch (0.005 ha) we made a single 7 × 3 m plot, while for a larger one (0.93 ha) we made five 20 × 3 m plots. To avoid temporal discrepancies in comparative analysis, the three habitat types were concomitantly sampled in each sampling period. We used beating trays to sample twenty herbaceous-shrubby plants from each plot of the large patches ($n = 18$) and ten plants from each plot of the small patches ($n = 6$), for a total of 420 sampled plants. Chosen plants were not

higher than 3 m, and the distance between them varied from 1 to 3 m. Beating trays were made up of a 1 × 1 m square wooden beam frame holding a 1m² cotton cloth; these trays were placed under the shrub to be sampled and, with the help of a stick, we beat the shrub 20 times so that the spiders would fall onto the cloth. After this procedure, we preserved the spiders in 75% ethanol.

We collected ground spiders in 195 pitfall traps distributed in 24 plots; the pitfall traps were set up inside each bromeliad plot. Each trap was 2 m (large plots) to 1.5 m (small plots) apart. The number of traps in each bromeliad patch varied according to the size of the patch; ten and five ground traps were set up in large and small patches, respectively. Those plots in rocky outcrops ($n = 3$) did not receive pitfalls. The traps were made of plastic (500 ml) and contained approximately 400 ml water, 10 ml detergent and 10 g thick salt. Each trap had a slab of polystyrene as a roof to avoid capturing leaves and rainwater. Traps remained active in the field for seven days only during the sampling period, after which the material was collected, sorted in a laboratory and the spiders stored in 75% ethanol. Voucher specimens were deposited in the Instituto Butantan (IBSP, Brazil).

We used different sampling methods for each habitat type to maximize spider collection. Each method used here is the most appropriate for the purpose of this study (Santos 1999; Romero & Vasconcellos-Neto 2005a, b).

Statistical analyses.—We ran an individual-based rarefaction to control for variation in sampling effort among habitats using the software EstimateS 8.0 (Cowell 2006); we used confidence intervals of 95% for the three habitats. This method allowed comparisons among unbalanced samples or with samples having different patterns of species distribution (Gotelli & Colwell 2001). To test whether spider communities were organized in subsets of compartmentalized species in each habitat type, and whether bromeliads amplify the beta diversity of spider communities, we used Bray-Curtis, Chao-Jaccard and Chao-Sorensen quantitative similarity indexes. The Bray-Curtis index is positively biased toward unbalanced samples, while Chao-Jaccard and Chao-Sorensen indexes are generally resistant to undersampling (Chao et al. 2005, 2006). The indices proposed by Chao et al. (2005, 2006) are particularly important for our work, since our samples are not balanced and include many rare species. We calculated the three index values and the variances with bootstrap methods ($n = 200$ iterations) using SPADE (Chao & Shen 2003). We also calculated the estimated relative abundance values of the shared species (\hat{U} and \hat{V}) between two separate communities, in which \hat{U} is the estimated relative abundance of the shared species of community 1, while \hat{V} is that of community 2 (Chao et al. 2005, 2006). With \hat{U} and \hat{V} values we could infer whether dominant spiders were bromeliad specialists (i.e., lower values of relative abundance). The three index values varied from 0 (maximally dissimilar communities, with no shared species) to 1 (identical communities; Chao et al. 2006) and represent, respectively, high rate of change in species composition (high beta diversity) and low rate of change in species composition (low beta diversity: Novotny et al. 2007).

We repeated the similarity index calculations with the ten most dominant spider species in each type of habitat, because rare species could be responsible for a high dissimilarity

between these habitats (Brown 1984). Additionally we estimated the similarity of the two most common spider families, Salticidae and Theridiidae, among habitats. If these spider families represent very different guilds (Romero & Vasconcellos-Neto 2007), they could respond differentially to habitat structure. We also applied a Non-metric Multidimensional Scaling (NMDS) analysis to Bray-Curtis dissimilarity matrices using Primer 6.0 software (Clarke & Gorley 2006) to represent species composition graphically. Values of stress < 0.05 are considered indicative of an excellent representation of the data, while stress < 0.1 indicates a good scaling with a low tendency to error, and stress > 0.3 is typical of points that are arbitrarily disposed in a two-dimensional classification (Clarke & Gorley 2006).

To test whether bromeliads increased spider beta diversity, we partitioned the total diversity (measured as species richness) into average alpha diversity (within habitat types) and beta diversity (among habitat types) following Crist et al. (2003). Since the sampling unit was habitat type, we considered plots nested inside habitats and habitats nested inside patches to perform the partitioning procedure. We ran the analysis and tested the significance of the alpha and beta values with 10,000 randomizations (individual-based procedure) using the program PARTITION (Veech & Crist 2007). This randomization generates a null distribution of each alpha and beta diversity estimated, which was compared with the observed alpha and beta values (Summerville et al. 2006). In addition, to test how much each habitat contributed to the total beta diversity, we performed four different partitioning analyses: 1) total, including all habitat types, 2) excluding bromeliad data, 3) excluding vegetation data, and 4) excluding ground data. The explanation percentage for beta diversity obtained in the first analysis was used as a standard to calculate whether exclusion of data of one habitat diminished the percentage of explanation of beta diversity.

Species abundance distribution (diversity dominance curves) is one of the most used approaches to describe community structure, because it is possible to compare communities with few or no species in common (McGill et al. 2007). This characteristic is especially important in the case of the community we are studying, since the three habitat types have few species in common (see results). To be able to compare the communities of the three habitats and to verify whether bromeliads have distinct patterns of spider abundance, we drew dominance curves for each habitat with a ranking-abundance diagram (RAD), in which the y axis represents species abundance and the x axis the species rank (organized from the most to the least abundant species on a logarithmic scale) (Magurran 2004; Fattorini 2005). A number of theoretical distributions have been proposed to model observed RAD, the most commonly used being the broken stick model (BS), the lognormal model (LN), the log series (LS), and the geometric series (GS). To assess which model best fit the data, we calculated the expected frequencies under each model and compared these expected frequencies with the observed frequencies, using χ^2 tests calculated by the program PAST (Hammer et al. 2001). When observed data did not differ significantly (i.e., $P > 0.05$) from the expected frequencies calculated under a given model, the model was considered to fit the data well (Magurran 2004).

When more than one model adjusted an observed distribution, we made a linear regression to choose the model that better fit the data (Fattorini 2005). This was the case for the BS distribution and GS model, because some data did not show distributions statistically different from these models. In such circumstances, the goodness-of-fit of regression was evaluated considering a fit index (FI: an alternative R^2 which can be used to compare models based on different transformation), standard error of estimate in actual units (S_e) and the coefficient of variation (CV), and Akaike's Information Criterion (AIC) (see Fattorini 2005 for details). Values of S_e calculated for the GS models can be compared with $S_{y,x}$ values of BS models (Fattorini 2005). We did not analyze data with linear regression using the LS model because this model is mathematically similar to the geometric series (May 1975) and because the LS model has a statistical origin and little use with ecological data (May 1975, Fattorini 2005).

RESULTS

Species richness of spider communities.—We collected 617 adult spiders belonging to 155 morphospecies and 33 families in the three habitats (Appendix 1). On the bromeliads, we found 348 adult spiders belonging to 75 morphospecies and 22 families. In the vegetation we collected 220 individuals belonging to 95 morphospecies and 16 families. Finally, on the ground we collected 49 individuals belonging to 25 morphospecies and 16 families. Whereas in the vegetation the most speciose groups were Theridiidae ($n = 25$ species) and Salticidae ($n = 19$), on the ground the most speciose families were Salticidae ($n = 5$) and Linyphiidae ($n = 4$) (Appendix 1). The most speciose families on the bromeliads were Salticidae and Theridiidae, with 16 and 11 species, respectively. Based on a smaller sample ($n = 45$ individuals), a rarefaction procedure detected that the vegetation habitat had the highest richness, followed by ground and bromeliad habitats (Fig. 1). However, the presence of Bromeliaceae was responsible for a 41% increase in the total spiders' species richness, because this habitat possessed an exclusive spider fauna (see below). Without taking the bromeliad samples into account the number of spider species in SLBS was 110, but including the bromeliad fauna the number of spider species increased to 155. Likewise, the vegetation sampling was responsible for a 74% increase in spider richness.

Beta diversity.—Similarity values of spider community composition in the three habitats were low (Table 1). None of the three indices gave similarity values larger than 0.5 for any habitat comparison. Similarity values were even lower when we used only the ten most abundant species of each habitat in the analysis (Table 1). The similarity of the species composition of the two most common families (i.e., Salticidae and Theridiidae) among the three types of habitat was also low (Fig. 2, Table 1). The low stress values in Figs. 2A–C indicate good scaling with little possibility of data being inadequately interpreted. Although the Bray-Curtis index appears biased positively due to unbalanced samples, we consider our results conservative to bias, indicating that the spider communities were compartmentalized.

Some spider families were restricted to a specific habitat type: nine were exclusive to bromeliads, seven to the ground and four to the vegetation (Appendix 1). Families found only

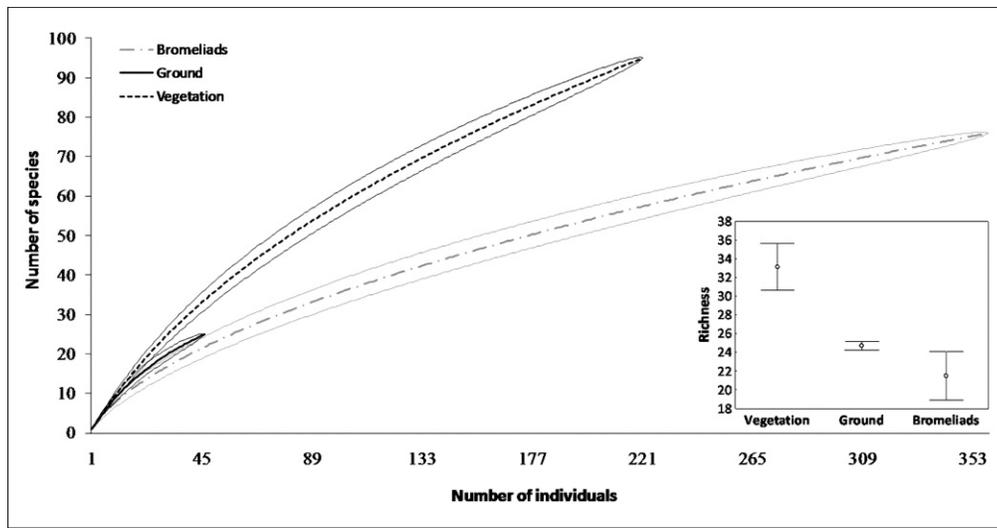


Figure 1.—Individual-based rarefaction and 95% ellipsoid confidence intervals (CI 95%) for the three habitat types. In detail (inferior right) we show the comparison of the three habitats rarefied to the smaller sample (ground habitat, $n = 45$ individuals). The bars in the detailed graph also represent the CI 95%.

in the bromeliad habitat were Ctenidae, Hahniidae [although one occasional individual (i.e., 0.86% of all individual from this family) was found in vegetation], Miturgidae, Mysmenidae, Ochyroceratidae, Pisauridae, Scytodidae, Segestriidae, Sparassidae and Trechaleidae (Appendix 1). Sixty percent of the bromeliad spider species occurred only on bromeliads ($n = 45$ species), 69.5% of the vegetation species were exclusive to this habitat ($n = 66$ species) and 40% of ground spiders were exclusively associated with the ground ($n = 10$ species). When bromeliads were excluded from the partition analysis, the percentage explained by observed beta diversity (comparing with total diversity) decreased by 11%. In contrast, when vegetation and ground data were removed, the percentage

explained by observed beta diversity decreased only by 2.4% and 1%, respectively. In all calculations of partitioned diversity, the value of beta diversity was higher than expected by chance ($P < 0.0001$: Table 2). Thus, bromeliad habitat contributed to the increase in beta diversity by intensifying the species turnover among habitats.

Most of the species shared between bromeliads and other habitats were rare species, as shown by the low relative abundance of the species in common between bromeliads and vegetation ($\hat{U} = 0.287$) and between bromeliads and ground ($\hat{U} = 0.112$: Table 1). The five most abundant spider species on bromeliads were exclusively associated with these plants and represented 59% of all individuals found in this habitat.

Table 1.—Bray-Curtis, Chao-Jaccard and Chao-Sorensen (\pm SE) similarity index values comparing all spider species (total), the ten most abundant species and the two most common families (Salticidae and Theridiidae). \hat{U} (\pm SE) represents the estimated relative abundance of shared species in community 1 and \hat{V} (\pm SE) the estimated relative abundance of shared species in community 2. Compared habitats were bromeliad (Br), vegetation (Veg) and ground (Gr).

	Bray-Curtis index	Chao-Jaccard index	Chao-Sorensen index	\hat{U}	\hat{V}
Total					
Br ¹ × Veg ²	0.130±0.02	0.225±0.04	0.367±0.06	0.287±0.09	0.509±0.14
Br ¹ × Gr ²	0.071±0.01	0.104±0.02	0.188±0.04	0.112±0.03	0.591±0.18
Veg ¹ × Gr ²	0.089±0.02	0.268±0.04	0.422±0.07	0.267±0.07	1.000±0.15
Ten most abundant species					
Br ¹ × Veg ²	0	0	0	0	0
Br ¹ × Gr ²	0	0	0	0	0
Veg ¹ × Gr ²	0.035±0.02	0.038±0.02	0.074±0.03	0.066±0.04	0.083±0.05
Salticidae					
Br ¹ × Veg ²	0.104±0.04	0.131±0.04	0.232±0.07	0.145±0.05	0.570±0.24
Br ¹ × Gr ²	0.076±0.05	0.101±0.04	0.184±0.08	0.113±0.05	0.498±0.29
Veg ¹ × Gr ²	0.113±0.04	0.138±0.05	0.242±0.09	0.138±0.06	1.000±0.326
Theridiidae					
Br ¹ × Veg ²	0.193±0.05	0.245±0.07	0.393±0.10	0.724±0.21	0.270±0.09
Br ¹ × Gr ²	0	0	0	0	0
Veg ¹ × Gr ²	0.05±0.03	0.027±0.02	0.053±0.04	0.027±0.02	1.000±0.39

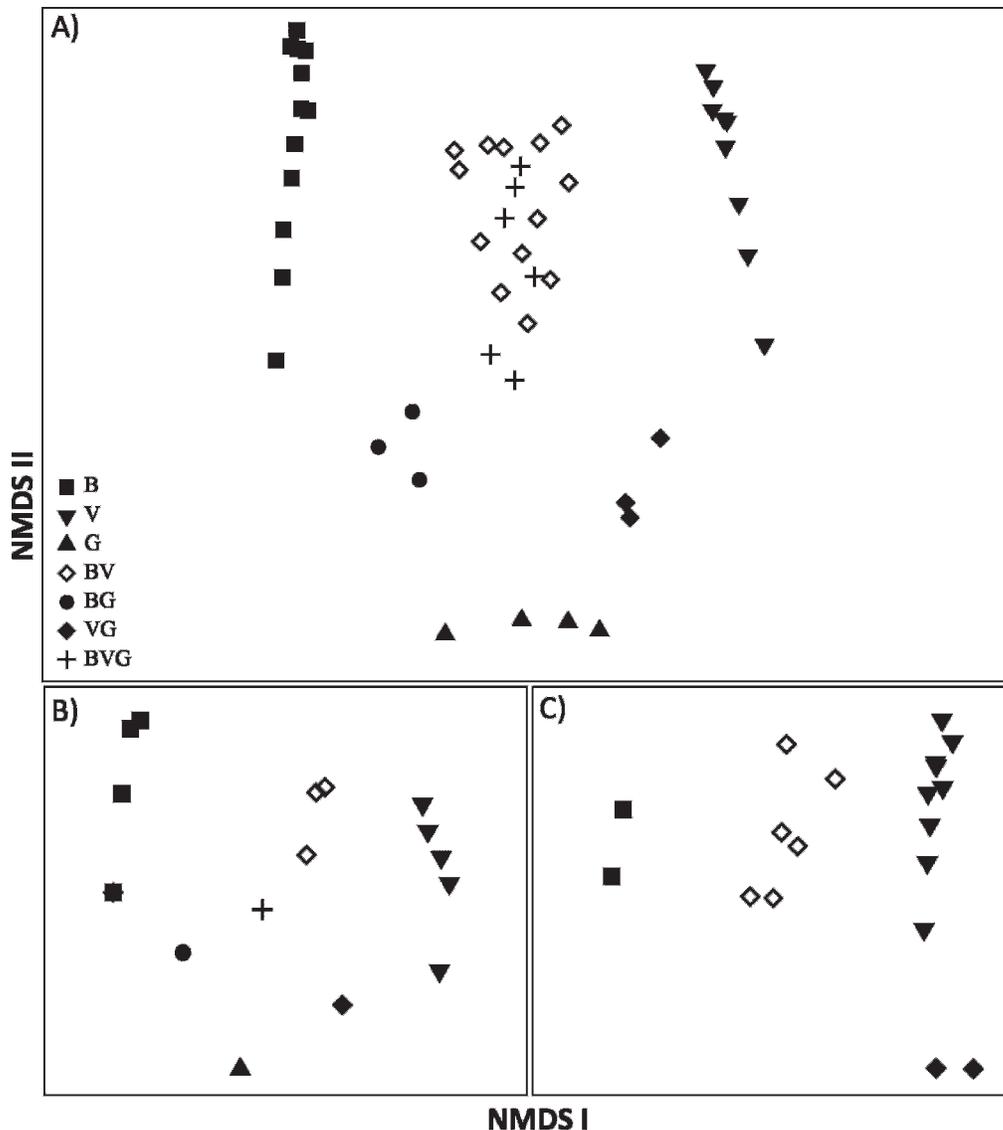


Figure 2.—Result of non-metric multidimensional scaling (NMDS) analysis showing segregation of whole spider communities among the three habitat types (A: 2D stress = 0.07), as well as for community of Salticidae (B: 2D stress = 0.04) and Theridiidae (C: 2D stress = 0.05). The symbols represent spider species that were exclusively associated with one habitat type; i.e., bromeliad (B), vegetation (V), ground (G), and species that occur in two [bromeliad and vegetation (BV), bromeliad and ground (BG), and vegetation and ground (VG)] or three habitats (BVG).

Species abundance distributions.—The abundance distribution pattern of bromeliad-living spiders did not deviate from a LN distribution (Fig. 3, Table 3), with few dominant species and many intermediate and rare ones (42 singletons and 13 doubletons). Abundance distribution of spiders in the vegetation habitat was better modeled by BS ($y = 11.288 - 5.752x$, $S_e = 0.788$, $CV [\%] = 33.450$, $FI = 0.899$) than by the GS model ($y = 0.696 - 0.001x$, $S_e = 1.487$, $CV [\%] = 68.502$, $FI = 0.634$). Abundance distributions of ground spiders were better modeled by BS ($y = 4.825 - 3.018x$, $S_e = 0.431$, $CV [\%] = 23.489$, $FI = 0.870$) than GS ($y = 0.577 - 0.031x$, $S_e = 0.465$, $CV [\%] = 25.686$, $FI = 0.848$). According to the values of the AIC, the abundance distribution of spiders in these two habitats is actually better explained by the BS model (vegetation: $\Delta AIC = 122.981$, ground: $\Delta AIC = 3.689$;

Fig. 3, Table 3), which suggests an equitable abundance distribution among species.

DISCUSSION

Our results show that spider communities are compartmentalized according to the habitat type. Formation of compartments in the interactions between animals and plants is commonly observed between phytophagous insects and their host plants (e.g., Prado & Lewinsohn 2004) because of chemical and/or physical restrictions determined by the plants (Schoonhoven et al. 2005). Compartmentalizing was also found in mutualistic networks of ants and myrmecophytic plants (Guimarães et al. 2007), probably due to limited space in the colonies and olfactory restrictions that make it impossible for the queen to find other non-hosting plant

Table 2.—Partitioning of species diversity in three habitat types into alpha and beta components. We performed the partitioning in alpha and beta diversity considering all habitat types, excluding vegetation, ground and bromeliad from the analysis. The expected value (mean, maximum, minimum) was assessed with 10,000 randomizations. In all comparisons the *P*-value was < 0.0001.

Habitat type	Species richness			
	Observed	Mean	Expected Maximum	Minimum
Within habitat (alpha diversity)				
Total (three habitat types)	12.1	16.9	18.2	15.4
Without vegetation	9.3	11.6	12.7	10.6
Without ground	12.5	17	18.5	15.6
Without bromeliad	18.6	25.1	28.5	22
Between habitat (beta diversity)				
Total (three habitat types)	134.9	130.1	131.6	128.8
Without vegetation	79.7	77.4	78.4	76.3
Without ground	125.5	121	119.5	122.4
Without bromeliad	82.4	75.9	79	72.5

species. In contrast to this, spiders do not usually feed on plants, and few species have a mutualistic association with their host plants (see Romero & Vasconcellos-Neto 2007; Romero et al. 2008).

So, what process is responsible for spiders forming compartmentalized communities? According to Uetz (1991), spiders use tactile and vibratory clues to select a habitat, and choose substrates that are the best conductors of these stimuli. Spiders specialized to live on bromeliads can benefit from the three-dimensional structure of these plants, being favored not only by conductors of tactile and vibratory stimuli but also by visual stimuli, which are fundamental for foraging and mating

(e.g., Barth et al. 1988). Moreover, the characteristic structure of bromeliads makes it easier to construct webs for various spider guilds and provide protection against natural enemies and climatic conditions (Romero & Vasconcellos-Neto 2005a; Romero 2006). Therefore, the specialization of individuals for specific plant or substrate structural characteristics could be responsible for spiders and other organisms compartmentalizing communities. However, this specialization may prevent species from using other habitats (Rosenzweig 1987; Morris 1987, 2003). Community compartmentation could also be seen for Salticidae and Theridiidae, two families belonging to distinct functional groups (Romero & Vasconcellos-Neto

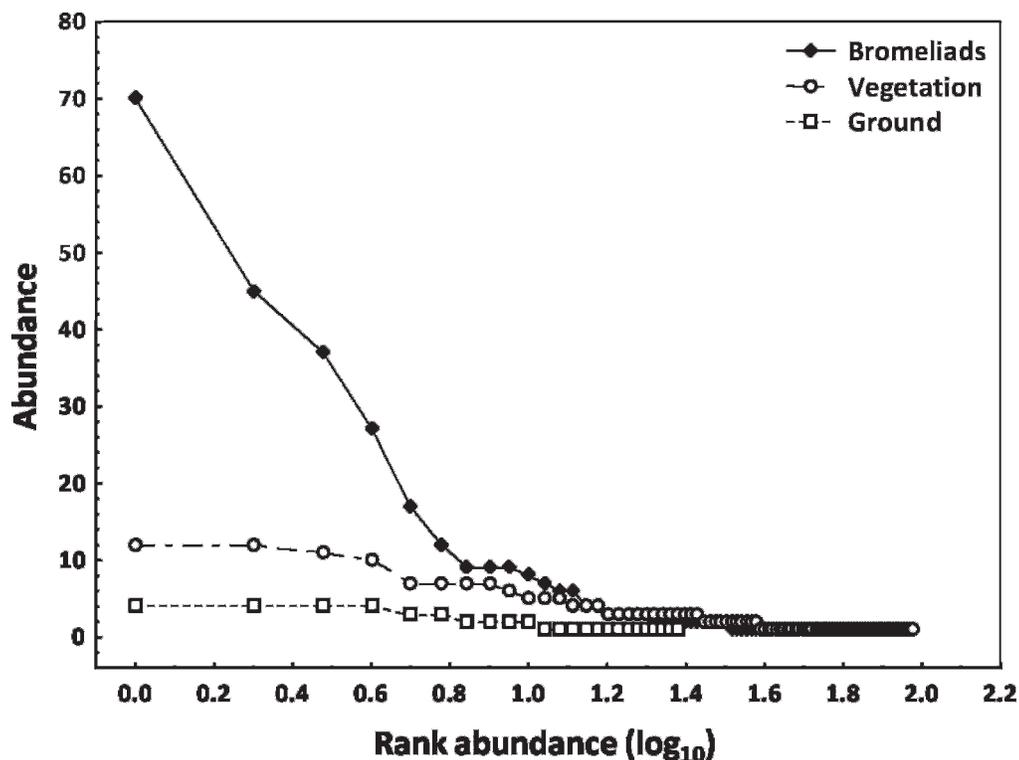


Figure 3.—Abundance ranking diagram (dominance curve) showing a lognormal distribution of bromeliad spiders, and broken stick distribution of non-bromeliad vegetation and ground. We found 75 species in the bromeliads, 95 species in the vegetation and 24 on the ground.

Table 3.—Comparisons between observed and expected values of species abundance in spiders that occur in bromeliads, vegetation and on the ground. The asterisk indicates that the data do not fit/deviate from to the model ($P < 0.05$).

Model	Habitat type					
	Bromeliad		Vegetation		Ground	
	χ^2	P	χ^2	P	χ^2	P
Broken stick (BS)	237.5	<0.0001*	6.5	1	1.6	0.977
Lognormal	4.8	0.183	7.2	0.028*	0	0
Logseries	126.3	<0.0001*	3.4	1	1.1	0.955
Geometric Series (GS)	812.7	<0.0001*	47.8	0.132	1.2	0.976

2007). This pattern reinforces the role of habitat structure on the organization of different organisms in a community.

Although bromeliads have the smaller rarefied richness, plants of the Bromeliaceae family create a habitat that amplifies total richness and beta diversity of spider communities, possibly because of their specific fauna. The variety of spatial niches available in bromeliads (e.g., foliar axils, foliar blades, space between leaves, dry and green leaves, central and peripheral tanks) could be responsible not only for the specialization of various arthropod groups in bromeliads [e.g., aquatic beetle (Balke et al. 2008), some jumping spiders (Romero 2006; Romero & Vasconcelos-Neto 2007)], but also for the increase in total spider species richness. A larger number of niches makes specialization easier and reduces competition through spatial segregation (Cramer & Willig 2005), which usually increases biological diversity (habitat heterogeneity hypothesis: MacArthur & MacArthur 1961). Despite not having sampled forest areas without bromeliads, we believe that our results are robust enough to infer that the Bromeliaceae amplify spider diversity, because the spiders that specialize on bromeliads (i.e., the subset of bromeliad spider species) do not occur in association with other types of substrates (e.g., Romero 2006; Omena & Romero 2008).

The species abundance distribution patterns in the three habitat types also support the hypothesis that bromeliads are important elements in structuring spider communities. Even though species abundance related to vegetation and ground was equitable (broken-stick model), the bromeliads were dominated by a few common species and many intermediate and rare spiders (lognormal model). It is possible that the high dominance of certain spider species in bromeliads is related to interspecific interactions in which competitively superior spiders win or even feed on smaller spiders (Wise 1993). A monopolization of better sites or resources by competitively superior animals was reported for other animals (e.g., birds: Fretwell & Lucas 1970; salmon: Hendry et al. 2001), and in the case of spiders such disputes could be related to the benefits that bromeliads provide to resident animals. Indeed, the body size (measured as prosoma length) of bromeliad spiders was 16% greater than in the vegetation spiders (t -test = 2.26, $P = 0.024$). This may suggest that large-sized spiders are superior competitors, which, because of their larger dimensions, are able to drive off or catch smaller species. It is also possible that bromeliads support larger numbers of prey, relative to other habitats, thus allowing the persistence of larger spiders, which in other habitats cannot find adequate prey for their higher energetic needs. These two mechanisms are not mutually

exclusive, and possibly they combined to produce a concentration of spiders on the bromeliads.

In conclusion, we have shown that spiders form subsets of communities compartmentalized according to the habitat type and that bromeliads represent an important habitat that influences the structure of these communities. As far as we know, this is the first work to show the formation of between-habitat compartments in spider-plant interactions. Our data reinforce the importance of habitat structure in determining community structure and diversity patterns in spiders (e.g., Robinson 1981; Greenstone 1984). Plants of the Bromeliaceae family seem to provide essential habitats for some taxonomic groups of spiders (this study, also see Romero 2006) and for other animals in Neotropical regions (e.g., Greeney 2001; Balke et al. 2008) because they are able to support a larger number of individuals and species and, consequently, amplify the total richness and beta diversity of the animals they host. These plants possibly represent a fundamental structural component for the arrangement of biological communities and can be used as model organisms in studies concerning animal-plant interactions. However, experimental studies manipulating vegetation structures are necessary to understand the causal factors related to the influence of architecture/complexity of the habitat on the spider communities.

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Appendix 1.—List of families and spider morphospecies and their abundances in each habitat type.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Amaurobiidae			2
Amaurobiidae gen.n.1			2
Anyphaenidae	2	9	
<i>Aysha</i> gr. <i>helvola</i>		1	
<i>Bromelina oliola</i> Brescovit, 1993	1		
<i>Iguarima censoria</i> (Keyserling, 1891)		1	
<i>Katissa</i> sp.1		1	
<i>Macrophyes jundiai</i> Brescovit, 1993		2	
<i>Osoriella rubella</i> (Keyserling, 1891)		1	
<i>Osoriella</i> sp.1	1	1	
<i>Teudis</i> sp.1		1	
<i>Wulfilopsis leopoldina</i> Brescovit, 1997		1	
Araneidae	4	16	
<i>Alpaida atomaria</i> Simon, 1895		1	
<i>Alpaida</i> sp.1		1	
<i>Araneus stabilis</i> (Keyserling, 1892)		1	
<i>Araneus</i> sp.1		1	
<i>Cyclosa fililineata</i> Hingston, 1932		3	
<i>Eustala</i> sp.1		1	
<i>Hypognatha</i> sp.1		1	
<i>Mangora aripeba</i>		2	
<i>Mangora</i> sp.1	1	1	
<i>Metazygia</i> sp.1	2		
<i>Micrathena acuta</i> (Walckenaer, 1842)	1		
<i>Micrathena clypeata</i> (Walckenaer, 1805)			1
<i>Micrathena</i> sp.1		1	
<i>Ocrepeira gnomo</i> Mello-Leitão, 1943		1	
<i>Testudinaria</i> sp.1		2	
Barychelidae			4
<i>Neodiplothele</i> sp.1			4
Corinnidae	8	3	3
<i>Castianeira</i> sp.1	3	3	2
<i>Corinna</i> gr. <i>rubripes</i> C.L. Koch, 1841	1		
<i>Corinna</i> sp.1			1
<i>Corinna</i> sp.2	1		
<i>Corinna</i> sp.3	1		
<i>Corinna</i> sp.4	1		
<i>Corinna</i> sp.5	1		

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
Ctenidae			4
<i>Ctenus</i> aff. <i>ornatus</i>			1
<i>Enoploctenus cyclothorax</i> (Bertkau, 1880)		1	
<i>Isoctenus</i> sp.1		2	
Dictynidae			1
<i>Dictyna</i> sp.1			1
Hahniidae	116		1
Hahniidae sp.1		70	
Hahniidae sp.2		37	
Hahniidae sp.3		9	1
Linyphiidae	52	29	5
<i>Anodoration claviferum</i> (Millidge, 1991)			4
<i>Dubiaranea</i> sp.1	4		1
<i>Dubiaranea</i> sp.2		1	
<i>Eurymorion insigne</i> Millidge, 1991		2	
<i>Fissiscapus pusillus</i> Millidge, 1991	27		
Linyphiidae sp.1	3	12	1
Linyphiidae sp.2		2	
Linyphiidae sp.3		9	1
Linyphiidae sp.4		1	1
<i>Meioneta</i> sp.1		1	1
<i>Sphecozone</i> sp.1		3	7
<i>Sphecozone</i> sp.2		1	1
Lycosidae			4
<i>Allocosa</i> sp.1			4
Mimetidae			1
<i>Ero</i> sp.1		2	1
Miturgidae		1	1
<i>Radulphius laticeps</i> Keyserling, 1891		1	1
Mysmenidae		1	
Mysmenidae sp.1		1	
Nemesiidae			2
<i>Stenoterommata</i> sp.1			2
Ochyroceratidae		1	
<i>Ochyrocera</i> sp.1		1	
Oonopidae		8	
<i>Oonops</i> sp.1		8	2
Palpimanidae			3
<i>Otiotrops</i> sp.1			3
Philodromidae			1

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
<i>Berlandiella</i> sp.1			1
Pholcidae	50	6	2
<i>Carapoia ubatuba</i> Huber, 2005	1		2
<i>Mesabolivar</i> sp.1		3	
<i>Metagonia</i> sp.1		1	
<i>Metagonia</i> sp.2		1	
<i>Psilochorus</i> sp.1	45		
<i>Tupigea nadleri</i> Huber, 2000		1	
<i>Tupigea</i> sp.1	4		
Pisauridae	2		
<i>Architis</i> sp.1	2		
Salticidae	49	36	5
<i>Alcmena</i> sp.1		1	
<i>Arnoliseus</i> sp.1	1	2	
<i>Beata</i> sp.1		4	
<i>Chira micans</i> (Simon, 1902)		1	
<i>Chirothecia</i> sp.1		1	
<i>Consingis</i> sp.1	1	1	
<i>Coryphasia</i> sp.1	12		
<i>Cotinusa</i> sp.1		5	
<i>Cotinusa</i> sp.2		2	
<i>Cylistella</i> sp.1		3	
<i>Erica</i> sp.1		1	
Euophryinae sp.1		1	1
Euophryinae sp.2	2	1	1
Euophryinae sp.3	2	7	
Euophryinae sp.4			1
Euophryinae sp.5	1		1
Euophryinae sp.6		1	
Euophryinae sp.7		1	
Euophryinae sp.8	1		
Salticidae			
Euophryinae sp.9	1		
<i>Fluda</i> sp.1	6		
<i>Lyssomanes</i> sp.1		1	
<i>Lyssomanes</i> sp.2		1	
<i>Martella</i> sp.1	3		
<i>Myrmarachne</i> sp.1	1		
<i>Noegus</i> sp.1	1		
<i>Psecas</i> sp.1	6		
<i>Sarinda</i> sp.1	1		
<i>Vimius</i> sp.1	9		
<i>Zuniga</i> sp.1		1	
Salticidae sp.1		1	1
Salticidae sp.2	1		
Scytodidae			
<i>Scytodes</i> sp.1	1	3	
Segestriidae			
<i>Ariadna</i> sp.1	2		
Sparassidae			
<i>Olios</i> sp.1	3		
Symphytognathidae		1	
<i>Symphytognatha</i> sp.1		1	
Synotaxidae		2	
<i>Synotaxus</i> sp.1		2	
Tetragnathidae	4	8	
<i>Chrysometa</i> sp.1	1	1	

Appendix 1.—Continued.

Family/species	Habitat type		
	Bromeliad	Vegetation	Ground
<i>Chrysometa</i> sp.2			3
<i>Homalometa</i> sp.1	2		
<i>Leucauge</i> sp.1			1
<i>Leucauge</i> sp.2	1		
<i>Tetragnatha</i> sp.1			3
Theridiidae	18	74	7
<i>Achaearana</i> sp.1			1
<i>Argyrodes</i> sp.1			1
<i>Audifia</i> sp.1	1		
<i>Chryso</i> sp.1			10
<i>Chryso</i> sp.2			2
Theridiidae			
<i>Dipoena woytkowskii</i> Levi, 1963			1
<i>Dipoena</i> sp.1			7
<i>Dipoena</i> sp.2			1
<i>Dipoena</i> sp.3			5
<i>Dipoena</i> sp.4			1
<i>Echinotheridion</i> sp.1			1
<i>Episinus</i> sp.1			1
<i>Episinus</i> sp.2			1
<i>Euryopsis</i> sp.1	1		1
<i>Faiditus</i> sp.1			1
<i>Platnickina mneon</i> Bösenberg & Strand, 1906			4
<i>Phycosoma altum</i> (Keyserling, 1886)			6
<i>Rhomphae</i> sp.1	2		
<i>Spintharus gracilis</i> Keyserling, 1886			3
<i>Tekellina</i> sp.1	7		1
<i>Theridion</i> sp.1			3
<i>Theridion</i> sp.2			12
<i>Theridion</i> sp.3			1
<i>Theridion</i> sp.4	1		5
<i>Theridion</i> sp.5	1		
<i>Theridion</i> sp.6	1		
<i>Thwaitesia affinis</i> O. Pickard-Cambridge, 1882			1
<i>Thwaitesia</i> sp.1	1		2
<i>Thymoites</i> sp.1	1		2
<i>Thymoites</i> sp.2	1		
<i>Thymoites</i> sp.3	1		
Theridiosomatidae	2		8
<i>Chthonos</i> sp.1			7
<i>Ogulnius</i> sp.1			1
<i>Naatlo</i> sp.1	2		
Thomisidae	4		7
<i>Acentroscelus</i> sp.1			1
<i>Epicadus</i> sp.1	1		3
<i>Strophius</i> sp.1	1		
<i>Tmarus</i> sp.1	2		3
Trechaleidae	17		
<i>Barrisca</i> sp.1	17		
Uloboridae			3
<i>Miagrammopes</i> sp.1			3
Zodariidae			4
<i>Tenedos</i> sp.1			4
Families total	22	16	16
Species total	75	95	25
Specimens total	348	220	49