

DOES THE STRUCTURAL COMPLEXITY OF AQUATIC MACROPHYTES EXPLAIN THE DIVERSITY OF ASSOCIATED SPIDER ASSEMBLAGES?

Josué Raizer and Maria Eugênia C. Amaral: Departamento de Biologia, Centro de Ciências biológicas e da Saúde, Universidade Federal de Mato Grosso do Sul, C.P. 549, Campo Grande, MS 79070-900 Brazil

ABSTRACT. Differences in species richness and species composition of spiders associated with aquatic macrophytes of different structural complexities were examined in the Pantanal floodplain of Mato Grosso do Sul, Brazil. The plants studied were *Nymphaea amazonum* (Nymphaeaceae), *Salvinia auriculata* (Salviniaceae), *Echinodorus paniculatus* (Alismataceae) and *Eichhornia azurea* (Pontederiaceae), whose classes of complexity were determined based on their leaf and branch densities, vertical structure, and height. Data were collected from 62 monospecific plant patches in temporary lentic environments. A total of 235 spiders of 33 species in 13 families was collected. *Nymphaea amazonum*, the plant with the lowest complexity class, did not provide adequate sites for the establishment of spiders, and only four individuals of four spider species were found on its patches. *Salvinia auriculata* and *E. paniculatus* shared the intermediate class of complexity, but showed statistically significant differences in composition and richness of spider species. In *E. paniculatus*, greater height and lower leaf and branch densities favored the establishment of web weavers, whereas the smaller height and higher density of *S. auriculata* promoted the occurrence of wandering spiders. *Eichhornia azurea*, the plant with the highest complexity class, presented the greatest number of unique spider species, differing from the other plants in spider species composition. Results indicate that richness and composition of spider species associated with aquatic macrophytes in the study site are influenced by the structural complexity of these plants.

Keywords: Araneae, community structure, South Pantanal, species composition, species richness

Habitat structural complexity can affect species diversity (Pianka 1978; Robinson 1981; Gunnarson 1988; Cornell & Lawton 1992; Shorrocks & Sevenster 1995; Balfour & Rypstra 1998). This hypothesis has been supported by studies focusing on different animal species in several environments (Pianka 1966, 1967; Murdock et al. 1972; Uetz 1975, 1977; Hatley & MacMahon 1980; Dueser & Porter 1986; Dean & Connell 1987; Pearsons et al. 1992). It has been shown, for example, that the vertical structure of vegetation in North American temperate forests is a better indicator of bird diversity than the diversity of plant species with which the birds are associated (MacArthur & MacArthur 1961).

Spatial and architectural features of habitat structure can determine diversity, density, and distribution of spider species (Hatley & MacMahon 1980; Balfour & Rypstra 1998). Similarly, environmental physiognomy (for instance, open or closed forest; dense or sparse litter layer) and physical structure can significantly influence spider habitat prefer-

ence (Jennings et al. 1988; Uetz 1991). Number and dominance of spider species tend therefore to be highly related to the structure of the plant community on which they occur (Gunnarsson 1990; Uetz 1991; Baur et al. 1996). These relationships among plant and spider communities appear to be determined primarily by the structural complexity of the plant, which can provide, for example, a variety of retreats and attachment sites for webs, as well as favorable microclimatic conditions (Hatley & MacMahon 1980; Pulz 1987).

Few are the studies performed on the association of spiders and aquatic macrophytes, and on the effects of the structural complexity of aquatic macrophytes on the community structure of associated spider species. Even these studies, however, have been limited to reporting the occurrence of spiders on those plants (e.g., Merck 1988; Heckman 1994) or to describing new species (Brescovit et al. 2000).

The present work examined the influence of plant structural complexity on spider com-

munities associated with aquatic macrophytes in the southern Pantanal, Brazil, by evaluating the variation of spider species composition and richness on four plant species.

METHODS

Study site.—The Pantanal is a floodplain of ca. 140,000 km² located in central South America, mainly within Brazil. This area is, in fact, an assemblage of diverse landscapes occupying the hydrographic sub-basins of the Paraguay watershed. Each of these sub-basins has its characteristic hydrologic regimes, soil types, and geologies, which affect fauna and flora distribution (Boggiani & Coimbra 1996).

The present study was carried out in a Pantanal sub-region known as “Pantanal do Miranda e Abobral” (*sensu* Adámoli 1982), located in Mato Grosso do Sul state, southwestern Brazil (19°22′–19°33′S; 57°2′–57°3′W). The climate is characterized by a wet season extending from December–May and a dry one from June–November. All samples were collected from temporary lentic environments located in the vicinity of a 25 km stretch of the MS-184 road. These lentic environments are formed by depressions in the terrain that remain inundated by nearby rivers or filled with rainwater for most of the wet season, resulting in temporary ponds. When rains end and rivers start to recede, the water level in these ponds begins to fall, and they eventually disappear during the dry season. Because of this cycle, data collection had to be limited to the period when water was not entirely depleted.

Aquatic macrophytes.—The plants investigated were *Nymphaea amazonum* Mart. & Zucc. (Nymphaeaceae), *Salvinia auriculata* Aublet (Salviniaceae), *Echinodorus paniculatus* Mich. (Alismataceae), and *Eichhornia azurea* (Sw.) Kunth (Pontederiaceae), which are illustrated in Fig. 1. The floating leaves of *N. amazonum* have glabrous, membranous, orbicular, laminate limbs and lie flat on the water surface, forming a discontinuous, thin, flat carpet. Patches of *S. auriculata* resemble a continuous, thick, curly carpet formed by upright chains of smaller, floating leaves. This is a herbaceous plant with short petioles and pilose, oval limbs. *Echinodorus paniculatus*, another herbaceous plant, has long triangular petioles and leaves that emerge vertically or obliquely. Limbs are glabrous, coriaceous and

lanceolate. *Eichhornia azurea*, also herbaceous, has leaves that emerge vertically or obliquely; but its petioles are cylindrical, shorter than those of *E. paniculatus* and have a sheath. Limbs are glabrous, fleshy and obovate.

Quantification of the structural complexity of aquatic macrophytes.—The structural complexity of monospecific patches of those four aquatic macrophytes was quantified by measuring plant density, height and vertical structure above the water surface, based on the methodology of Balfour & Rypstra (1998). Ten patches of each plant were sampled, employing a 1 m² floating PVC frame whose sides were numbered at 10 cm intervals, thus defining an orthogonal grid. Numbering ran from 0–10 on one of the sides, then proceeded from 11–21 on the adjacent side (with numbers 10 and 11 coinciding on the corner edge). On the remaining two sides, these integer sequences (0–10, 11–20) were repeated so as to mirror those parallel to them.

In order to measure plant density in each sample, an integer from 0–21 was drawn. A horizontal line was then positioned connecting the same two integers lying on opposite sides of the frame, and the number of branches and leaves touching this line was recorded.

For measuring the vertical structure of the plants, two integers were drawn, one of them from 0–10 and the other from 11–21. Two horizontal lines were thus determined, at whose intersection a third, vertical line was positioned. The number of leaves and branches touching this vertical line was recorded. Plant height was considered as the highest point at which the plant touched this vertical line.

To determine the structural complexity classes of the plant patches, the differences among the variables considered were tested by analysis of variance (ANOVA) and Tukey test ($\alpha = 0.05$). Three possible arbitrary values were then assigned to the means of those variables: value 0 to the smallest mean, 1 to the intermediate, and 2 to the greatest mean.

Data sampling.—Data were collected from 13 ponds from November 1994 to April 1997. A total of 62 monospecific patches was sampled, namely, 12 of *N. amazonum*, 18 of *S. auriculata*, 10 of *E. paniculatus*, and 22 of *E. azurea*. Patch area was estimated and subdivided in numbered sub-areas of 1 m², and one

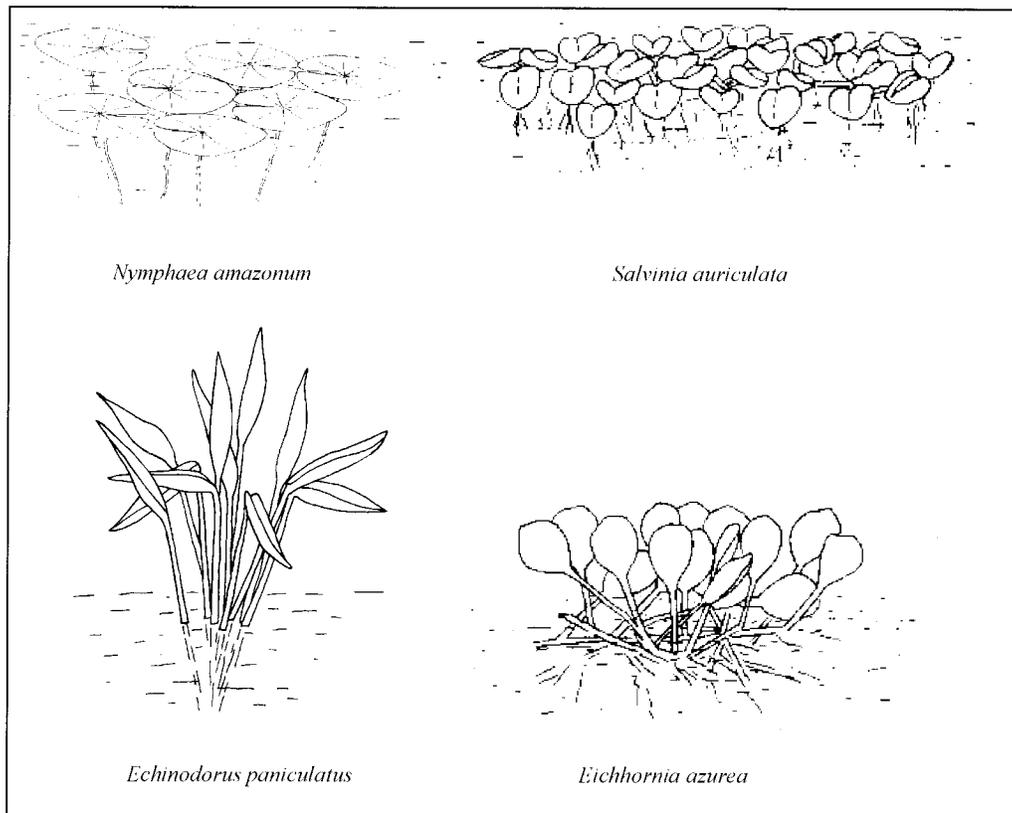


Figure 1.—Schematic depiction of the four aquatic macrophyte species investigated. *Nymphaea amazonum* forms a thin mat that lies flat on the water surface. *Salvinia auriculata* forms a mat that is rich in recesses and projections. *Echinodorus paniculatus* has stems that emerge vertically or obliquely without ever forming a mat. The carpet formed by *Eichhornia azurea* is also rich in recesses and projections, but has a series of vertical and oblique emerging stems.

of them was randomly chosen as the sampling point for that patch. This sampling area was delimited with the help of a 1 m² floating PVC frame whose sides were fitted with a 15 cm high nylon-mesh screen to prevent spiders from escaping. At all sampling points, plant species richness had value 1. All spiders visually located were collected for identification, and their voucher specimens are deposited in the Museum of Instituto Butantan, São Paulo.

Spider species composition and richness.—In order to compare spider species richness among the plant species, the smallest sample size (number of individuals collected associated with one of the plant species) was considered, since species richness is dependent on the number of individuals sampled. Spider species richness was then estimated for

each plant species by rarefaction, using the software RAREFACT (Krebs 1989). The expected number of species and the standard deviation for each complexity class were thus obtained. Species richness was considered to differ among complexity classes if no overlap occurred between the intervals generated by the standard deviation of species richness for each sample. The mean numbers of spider species per sample were statistically compared among the plant species by analysis of variance. The mean number of spider species and the number of individuals, both grouped by guild (web or wandering spiders), were also analyzed (ANOVA, Tukey test, and χ^2 test of independence, $\alpha = 0.05$).

RESULTS

Quantification of plant structural complexity.—Results obtained for the structural

complexity of the monospecific patches of aquatic macrophytes are shown in Table 1. Complexity class was lowest for *N. amazonum* (class 0) and highest for *E. azurea* (class 4). No plant species fitted classes 1 or 2. *Salvinia auriculata* and *E. paniculatus* shared the same complexity class (class 3), despite differences found in the variables involved in its determination: *S. auriculata* presented greater density and smaller height, whereas for *E. paniculatus* density was smaller and height was greater. *Eichhornia azurea* provided the greatest value for vertical structure, but its values for plant density and height were intermediate. *Nymphaea amazonum* did not show any variation in either height or vertical structure (both at value 0), and its density never exceeded three leaves per meter.

Spider species composition and richness.—A total of 235 spiders belonging to 33 species was found (Table 2). Because some of the individuals collected were juvenile, they could only be taxonomically identified down to family or genus level. Only four individuals—and each of these of a different species—were found on *N. amazonum*. Their occurrence was regarded as fortuitous, and the corresponding data were excluded from the composition and richness analyses. As for the other three plants, 15 spider species (63 individuals) were found on *S. auriculata*, 14 species (54 individuals) on *E. paniculatus*, and 24 species (114 individuals) on *E. azurea*. Four species of spiders were common to these three plant species. Regarding composition, *E. azurea* presented the greatest number of unique spider species (9 species; 37.5%), followed by *S. auriculata* (5 species; 33.33%) and *E. paniculatus* (3 species; 21.43%). The smallest overlap in species composition occurred between *S. auriculata* and *E. paniculatus*, with only 5 common species (ca. 35%). Four of these five species were also common to *E. azurea*, accounting for 39.15% of the overall total of individuals collected.

Overall, wandering spiders outnumbered web weavers, both in the number of species and of individuals (Table 2). Wandering individuals accounted for 66.23% of the total collected (Fig. 2). When only those animals collected from *E. paniculatus* are considered, the proportion of wandering individuals falls to ca. 37% (Fig. 2). The proportions between wandering and web spiders differed signifi-

cantly among the three plants analyzed ($\chi^2 = 8.05$, $df = 2$, $P < 0.02$, Fig. 2). The proportion of individuals between guilds was higher for wandering spiders on both *S. auriculata* and *E. azurea*, but higher for web spiders on *E. paniculatus*.

As to richness, the expected number of spider species arrived at by employing the rarefaction method differed among plant species. By applying this method to the 54 individuals found on *E. paniculatus* (the smallest number of spiders found on any of the three plants analyzed), the number of spider species could be estimated at 18.89 (SD \pm 1.56) for *E. azurea*, 14.10 (SD \pm 0.84) for *S. auriculata*, and 14 for *E. paniculatus* (Table 2). Taking into account the intervals generated by the standard deviation of the expected number of species, *E. azurea* presented the greatest richness, whereas *S. auriculata* and *E. paniculatus* did not differ from each other. Statistical analysis of the data on spider species number per sample for each plant species did not reveal any significant differences among the three plants analyzed (ANOVA, $F = 0.598$, $df = 2$, $P = 0.545$). However, when the numbers of spider species per guild were compared among the plants, *E. paniculatus* showed the greatest richness of web spiders and the smallest one of wandering spiders, whereas *S. auriculata* and *E. azurea* did not differ significantly from each other (Table 3).

DISCUSSION

Nymphaea amazonum, the plant with the lowest structural complexity, had the lowest richness of spiders, with four species but only one individual of each (Table 2). The occurrence of these was regarded as fortuitous, since the same four species were abundantly found on all the other macrophytes (Raizer 1997). This is indicative that *N. amazonum* does not favor the establishment of a community of associated spiders. In fact, because its leaves are smooth and lie flat on the water surface, this plant does not provide microsites for oviposition, molting, or construction of any kind of web or retreat. Spiders living on these leaves would also be directly exposed to solar radiation, which favors dehydration (Pulz 1987). Furthermore, potential prey (such as diptera and orthoptera) are rarely found on *N. amazonum* (Raizer pers. obs.).

Spider species composition varied not only

Table 1.—Structural complexity of monospecific patches of aquatic macrophytes in southern Pantanal, calculated from the following variables: plant density (leaves and branches per meter), vertical structure of the plant (number of branches and leaves), and plant height (in centimeters). Values for the same variable that are followed by the same letter do not differ statistically (Tukey test, $\alpha = 0.05$). For each variable, complexity was assigned values 0, 1, or 2, depending on statistical differences or similarities (a = 0; b = 1; c = 2). For each plant species, the structural complexity class is the sum of the complexities of each variable.

	<i>Nymphaea amazonum</i>	<i>Salvinia auriculata</i>	<i>Echinodorus paniculatus</i>	<i>Eichhornia azurea</i>	ANOVA results
Plant density (mean \pm SD)	2.60 \pm 0.52a	95.10 \pm 17.38c	6.30 \pm 5.17a	35.40 \pm 4.55b	$F = 209.252$, $df = 3, P < 0.001$
Plant vertical structure (mean \pm SD)	0.00 \pm 0.00a	2.80 \pm 1.23b	3.30 \pm 1.70b	6.90 \pm 2.13c	$F = 35.866$, $df = 3, P < 0.001$
Plant height (mean \pm SD)	0.00 \pm 0.00a	1.81 \pm 1.15a	80.30 \pm 29.02c	54.95 \pm 11.55b	$F = 65.175$, $df = 3, P < 0.001$
Value of plant density complexity	0	2	0	1	—
Value of plant vertical structure complexity	0	1	1	2	—
Value of plant height complexity	0	0	2	1	—
Plant structural complexity class (sum of the previous values)	0	3	3	4	—

Table 2.—Abundance of spider species collected from monospecific patches of four species of aquatic macrophytes in southern Pantanal. (Plants: NA = *Nymphaea amazonum*, SA = *Salvinia auriculata*, EP = *Echinodorus paniculatus*, EA = *Eichhornia azurea*. Spider guilds: WAN = wandering spiders, WEB = web spiders.) Number of samples, mean number of spider species, and richness obtained by rarefaction are also indicated.

Spiders	Number of individuals sampled per plant species						Guilds		
	NA	SA	EP	EA	WAN	WEB	WAN	WEB	
Anyphaenidae									
<i>Osoiriela rhodonota</i> Mello-Leitão	0	0	0	2	X				
<i>Otoniela</i> sp.	0	0	1	4	X				
Araneidae									
<i>Actinosoma pentacanthum</i> (Walckenaer)	0	10	0	1				X	
<i>Alpaida veniliae</i> (Keyserling)	0	0	7	1				X	
<i>Araneus guttatus</i> (Keyserling)	0	1	0	1				X	
<i>Eustala</i> sp.	0	0	0	1				X	
<i>Metazygia gregalis</i> (O. P.-Cambridge)	0	2	16	5				X	
sp1 (not identified)	0	0	0	6				X	
Ctenidae									
<i>Neoctenus comosus</i> Simon	0	0	0	2			X		
Dictynidae									
sp1 (not identified)	0	0	0	1			X		
Linyphiidae									
sp1 (not identified)	0	0	0	2					X
Lycosidae									
<i>Hogna</i> sp	1	18	2	13			X		
<i>Lycosa nycthemera</i> Bertkau	0	5	0	12			X		
sp1 (not identified)	0	4	1	7			X		
sp2 (not identified)	0	7	0	0			X		
sp3 (not identified)	0	0	0	1			X		
Pisauridae									
<i>Ancylometes concolor</i> (Perty)	0	6	0	9			X		
sp1 (not identified)	0	1	1	0			X		
Salticidae									
<i>Beata</i> sp.	0	1	0	7			X		
<i>Chira</i> sp1	0	2	0	0			X		

Table 2.—Continued.

Spiders	Number of individuals sampled per plant species						Guilds		
	NA	SA	EP	EA	WAN	WEB			
<i>Chira</i> sp2	0	0	0	7	X				
sp1 (not identified)	0	0	1	0	X				
sp2 (not identified)	0	0	1	0	X				
sp3 (not identified)	0	1	0	0	X				
sp4 (not identified)	0	1	0	0	X				
sp5 (not identified)	0	1	0	0	X				
Tetragnathidae									
<i>Leucauge</i> sp.	0	0	4	6		X			
<i>Tetragnatha</i> sp.	1	0	6	3		X			
Theridiidae									
sp1 (not identified)	0	0	0	2		X			
Theridiosomatidae									
<i>Argyrodes</i> sp.	0	0	1	1		X			
Thomisidae									
<i>Misumenops</i> sp.	0	0	1	0	X				
Trechaleidae									
<i>Paradosenus corumba</i> Brescovit & Raizer	1	0	2	9	X				
<i>Thaumasia</i> sp.	1	3	10	11	X				
Total individuals	4	63	54	114	158	77			
Total species	4	15	14	24	22	11			
Number of samples	12	18	10	21	—	—			
Mean number of species ± SD	0.33 ± 0.65	3.50 ± 2.31	5.40 ± 4.30	5.43 ± 5.80	—	—			
Species richness by rarefaction from 54 individuals ± SD	—	14.10 ± 0.84	14.00 ± 0.00	18.89 ± 1.56	—	—			

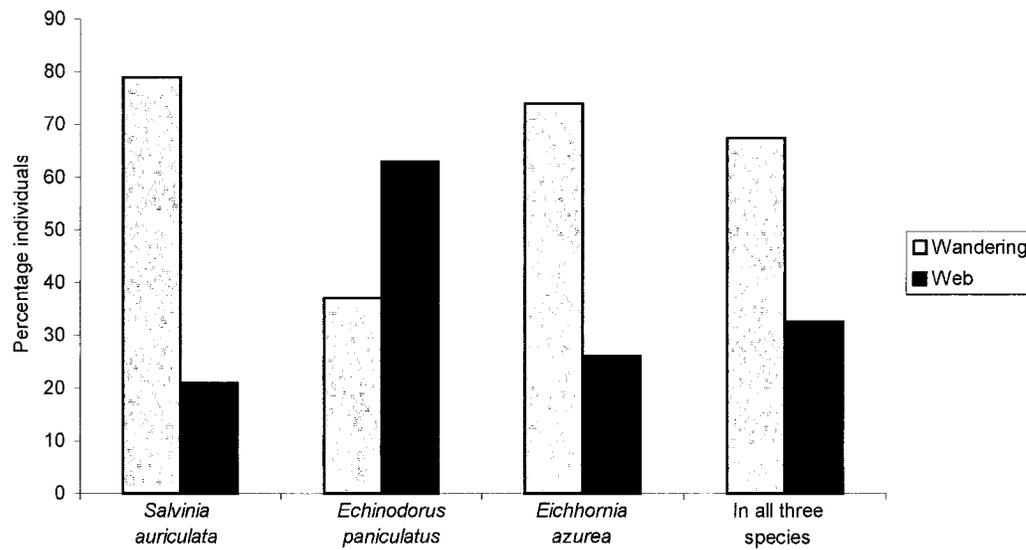


Figure 2.—Percentages of the numbers of individuals of each spider guild (wandering and web spiders) for the aquatic macrophytes analyzed (*Salvinia auriculata*, *Echinodorus paniculatus* and *Eichhornia azurea*).

among plants of different structural complexity classes, but also between those of the same class (*S. auriculata* and *E. paniculatus*). Differences between these two class-3 plants can be explained by the differences in height and density of their emerged parts. *Salvinia auriculata*, having high leaf density and small height above the water surface, favored the establishment of wandering spiders, which hunt and build their retreats on the leaves. Among the few web-weaving species found on this plant, only one, *Actinosoma pentacanthum* (Walckenaer, 1837), builds webs that are parallel to the water surface (Raizer 1997). This was actually the only spider seen employing the leaf mat of *S. auriculata* to attach a web with such orientation. On the other

hand, *E. paniculatus*, the macrophyte with the lowest leaf density and greatest height, favored the establishment of spiders that weave large-sized webs—such as those of the families Araneidae and Tetragnathidae. Similar results were found by Döbel et al. (1990) in a study on a community of spiders associated with the grass *Spartina alterniflora* Loes. This intertidal salt marsh plant presents three distinct habits: short, intermediate, and tall forms. The short form favors the occurrence of wandering spiders, while the intermediate one, with an architecture similar to that of *E. paniculatus*, enables the establishment of web-weaving species.

The variation in species composition among *E. azurea* (complexity class 4), *S. auriculata*

Table 3.—Mean proportion of spider species number per guild (web and wandering spiders) on *S. auriculata*, *E. paniculatus*, and *E. azurea*. Analysis of variance (ANOVA) was performed for the arc sine of the square root of the proportions of spider species per sample. On each line, values followed by the same letter do not differ significantly (Tukey test, $\alpha = 0.05$).

Guild	<i>Salvinia auriculata</i> (mean \pm SD)	<i>Echinodorus paniculatus</i> (mean \pm SD)	<i>Eichhornia azurea</i> (mean \pm SD)	ANOVA results
web spiders	0.19 \pm 0.22a	0.54 \pm 0.31b	0.24 \pm 0.26a	$F = 4.525$, $df = 2$, $P = 0.017$
wandering spiders	0.81 \pm 0.22a	0.46 \pm 0.31b	0.76 \pm 0.26a	$F = 4.525$, $df = 2$, $P = 0.017$

and *E. paniculatus* (both of class 3) is possibly due to the number of spider species that are unique to *E. azurea* and to the small overlap of species composition between this plant and *E. paniculatus* (3 species in common) or *S. auriculata* (5 species in common). In addition, the proportion of web weavers occurring on *E. paniculatus* was higher than that of wandering spiders, whereas the opposite was observed for *S. auriculata* and *E. azurea* (Fig. 2). These data corroborate the results obtained by Hatley & MacMahon (1980) when comparing spider species compositions for bushes with differing leaf and branch densities. According to their findings, spider species that constructed large-sized webs were found in less structurally complex bushes with lower leaf and branch densities, but not in high-density plants. Our findings support the hypothesis that plants of different structural complexities favor distinct associations of spider species, thus influencing the species composition of such communities, as also found in other studies (e.g., Hatley & MacMahon 1980; Döbel et al. 1990, and Balfour & Rypstra 1998).

The expected number of spider species, as determined by rarefaction, varied among plant species. The greatest richness was the one recorded for the plant with the highest complexity class (*E. azurea*). However, no significant statistical difference was evidenced when richness was assessed by the mean number of spider species per sample, among plants.

Nonetheless, in a third analysis, when richness was assessed separately for each guild, the mean proportions between species numbers varied significantly (Table 3). *Echinodorus paniculatus* presented the highest proportion of web spider species, probably due to the dependence of such spiders on this plant's architecture, characterized by its high density and great height of leaves. On the other hand, the proportion of web spider species on *E. azurea* did not differ from that found for *S. auriculata*. This can be explained on the basis that orb-webs are usually anchored to open sites, which facilitate the capture of flying prey (insects). This feature would render the high leaf density of *E. azurea* unfavorable to the construction of such webs, which are mainly built on the edges of the patches formed by this plant (Raizer 1997). Nor does

S. auriculata offer suitable sites for the attachment of orb-webs, except those parallel to the water surface.

When wandering spiders alone were considered, *E. paniculatus* showed the smallest species richness, whereas *S. auriculata* and *E. azurea* did not differ from each other. As with web weavers, plant architecture can explain such results: *E. paniculatus* lacks a suitable architecture for the establishment of various species of wandering spiders since it never forms a mat on the water surface; *S. auriculata* and *E. azurea*, in turn, with their high leaf and branch densities, do form continuous mats that are rich in recesses and projections that favor wandering spiders.

The number of species of a given guild is thus influenced by variables of the structural complexity, such as the density and height of leaves and branches. In the present study, tall plants with low leaf densities displayed a larger number of web spider species, whereas a greater richness of wandering spiders was found for short plants with high leaf densities.

Our results support the hypothesis that structural complexity of plants also influences spider species richness, and corroborate other studies on the influence of habitat structure on species richness and species composition of spider assemblages (Hatley & MacMahon 1980; Greenstone 1984; Jennings & Hilburn 1988; Uetz 1991; Baur et al. 1996).

Habitat structural complexity is in fact one of the main factors used to explain species diversity (e.g., MacArthur & MacArthur 1961; Pianka 1978; Hatley & MacMahon 1980; Dean & Connell 1987; Shorrocks & Sevenster 1995). Magurran (1988) stated that habitats with high microsite diversity have greater species richness, since different microsites can have characteristic species associated with them. Other studies testing the relationship between structural complexity and species diversity have demonstrated that greater microsite diversity leads to a greater number of niches and can minimize interspecific competition (e.g., Pianka 1978; Hatley & MacMahon 1980; Shorrocks & Sevenster 1995). The present study has revealed that structurally dissimilar habitats may show similar spider species richnesses while differing in species composition. These findings support the suggestions of Jennings et al. (1988) and Baur et al. (1996) that communities of

spiders or other invertebrates are mainly organized as a function of the structural complexity of the environments.

Variations in species composition can be explained by habitat preferences resulting from behavioral and morphological characteristics of the spiders (Johnson 1995; Richman 1995).

Since richness of aquatic macrophyte species did not vary in the present investigation, remaining at value 1, it can be concluded that structural complexity is an important factor for the organization of spider communities on these plants, a factor that can affect richness and, even more strongly, composition of the spider species associated with them.

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