

Spider guilds in the tree-shrub strata of riparian forests in southern Brazil

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Abstract. We evaluated spider guild abundance and vegetation complexity in riparian forests in southern Brazil in four distinct river basins over 2 yr. We compared spider guild abundance among rivers, habitats (edges vs. forest interior), and against vegetation complexity. We also compared spider assemblages between juvenile and adults in terms of guilds. Of 42,057 spiders sampled, 79% were juveniles and 21% were adults. Space-web weaving was the most abundant guild whereas cursorial hunters was the least abundant one. Weaving spiders dominated over hunters (59% vs 40.58%, respectively). Thirty-four families were recorded; ambush hunters totaled 11 families; space web sheet builders and hunting runners had eight families each and there were seven families for orbicular web builders. Space web sheet builders dominated on all levels: among rivers and habitats (edges and forest interior). Unexpectedly, spider guilds did not seem to be influenced by environmental complexity, given the variables measured, under a Canonical Correspondence Analysis. There was an interaction between guild relative abundance and ontogeny, since the proportion of the space web sheet builders guild among adult spiders was larger than the proportion among juveniles, with a decrease in proportion of adults especially for hunting runners.

Keywords: Guild composition, diversity, beating tray, habitats, vegetation complexity

Spider guilds are usually classified based on hunting strategies and predation habits (Uetz 1991; Silva 1996; Uetz et al. 1999; Höfer & Brescovit 2001). According to Simberloff & Dayan (1991), a guild is defined as a group of species exploiting the same environmental resource classes in a similar fashion.

In Brazil, Höfer & Brescovit (2001) analyzed spiders and their guilds in Ducke Reserve, Manaus, in the Brazilian Amazon, across several years. Given the high diversity of tropical spider assemblages and the lack of knowledge on species' biology, they recognized future guild classifications can potentially be distinct from the present ones.

Other studies in Brazil (Battirola et al. 2004; Oliveira-Alves et al. 2005; Peres et al. 2007; Souza-Alves et al. 2007; Rodrigues et al. 2009; Dias et al. 2010), South America (Silva 1996; Silva & Coddington 1996; Flórez 1999; Avalos et al. 2007; Benavides & Flórez 2007; Rubio et al. 2008) and elsewhere in the world (Jennings & Hilburn 1988; Uetz et al. 1999; Toti et al. 2000; Whitmore et al. 2002; Chen & Tso 2004; Sørensen 2004; Laeser et al. 2005; Loeser et al. 2006; Hore & Uniyal 2008), focused in various aspects of spider guilds, especially their differential occurrence in distinct environments, plant strata and capturability by different collection methods.

Even though spiders are recognized as being very important ecologically (Simó et al. 1994), especially as essential components of forest ecosystems (Moulder & Reichle 1972), studies exploring this taxon as an indicator of habitat disturbance (Cardoso et al. 2010) and the effects of its predatory function in the ecosystem are still incipient for many regions, markedly tropical and subtropical ones. Although the literature on spider guilds has focused in habitat use and occupancy, many environments and vegetation physiognomies

are still understudied, and among those stand the riparian forests.

Riparian forests are those kinds of vegetation associated to water courses (Ab'Saber 2000). In Brazil they are legally protected (Brazilian Forest Code, law 477/1965) and considered permanent preservation areas, but that has not prevented them from being degraded. This is clearly a case of bad management of natural resources (Kilca 2002), with important societal ramifications ranging from lower food production, lost opportunities for ecotourism and unknown levels of biodiversity loss (Malavasi et al. 2004).

Several studies demonstrate that changes in vegetation surrounding rivers, streams and brooks affect the associated invertebrate fauna (Nakano & Murakami 2001; Kato et al. 2003; Baxter et al. 2005). The resident fauna of riparian forest edges is also affected (Laeser et al. 2005). Riparian forests can work as corridors for spider dispersal between distant ecosystems (Raizer et al. 2005). However, human disturbance on these forests can affect this flow or even halt it. Hence, there is an urgent need to know and characterize the spider fauna associated with riparian forests in Brazil. The aim of this research was to compare the abundance of spiders guilds occurring in different riparian forests (drainage basins), among forest habitats (edges and forest interior), and differences found among guilds for adult and juvenile spiders. Distinct methods for measuring forest structure and complexity and how the latter influence spider guilds were also evaluated.

METHODS

Study areas.—Samples were taken from riparian forests in four different drainage basins in southern Brazil, state of Rio Grande do Sul (Fig. 1).



Figure 1.—Schematic map of Brazil and Rio Grande do Sul State. State map shows the studies riparian forests. See Methods for abbreviations.

1. *Piratini river (PR)*: Sampling area is on the North bank of the lower Piratini, in the southern region of the Coastal Plain in Arroio Grande municipality ($31^{\circ}54'06.47''\text{S}$, $52^{\circ}39'08.29''\text{W}$). The selected forest section is approximately 14 m a.s.l. and 39 km long down the valley, having 4,000 ha of riparian forest, representing the largest native continuous forest in this region currently. Temperatures are on average 18.2°C with February the hottest (23.4°C) and July the coldest month (10.2°C); annual rainfall reaches 1,283 mm, with August the rainiest month (123 mm) and January the drier (48 mm) (Oliveira & Ribeiro 1986). According to Teixeira et al. (1986) the Piratini river vegetation on its lower course has areas with Pioneer Formations with riverine and marine influences. Typical plant species include *Allophylus edulis* (Sapindaceae), *Eugenia uruguayensis* (Myrtaceae), *Trichilia clausenii* (Meliaceae), *Banara tomentosa* (Salicaceae), *Gymnanthes concolor* (Euphorbiaceae) and *Chrysophyllum marginatum* (Sapotaceae) (Kilca 2002).

2. *Camaquã river (CR)*: Study area is on the North bank of the lower Camaquã ($31^{\circ}01'01.7''\text{S}$, $51^{\circ}56'42.0''\text{W}$), on the centre-south portion of the Coastal Plain in Cristal municipality. It is

also approximately 14 m a.s.l. and suffers frequent seasonal flooding. The area is in a good conservation state, with forest continuity over an alluvial plain and low indication of human disturbance (Marchi 2005), although the forest is not particularly tall. Average annual temperatures are 18.9°C , with July colder (13.3°C) and January/February warmer (24.3°C). Average annual rainfall is 1,234 mm, with September the rainiest month (135 mm) and November the driest (65 mm) (IPAGRO 1989). Marchi (2005) mentions the largest trees in the region being *Luehea divaricata* (Malvaceae), *Salix humboldtiana* (Salicaceae) and *Vitex megapotamica* (Lamiaceae), also with shrub components *Psychotria carthagenensis* (Rubiaceae) and *Ruellia angustiflora* (Acanthaceae). Amongst the most abundant trees in Camaquã river there are *Sebastiania commersoniana* (Euphorbiaceae), *Eugenia verticillata* (Myrtaceae), *Allophylus edulis*, *Cupania vernalis* (Sapindaceae) and *Gymnanthes concolor*.

3. *Sinos river (SR)*: The study area is in Parobé, South bank of the river ($29^{\circ}41'06.94''\text{S}$, $50^{\circ}51'05.98''\text{W}$), altitudes between 6–10 m a.s.l. (Daniel 1991). The forest is not continuous, with fragmentation along the river, but the chosen sampling spot includes the largest patch of forest in the region. On the North

bank there is a beach used by locals (Daniel 1991), but on the South bank the forest is taller, surrounded by flooding grasslands, wetlands and, further on, enclosed pastures. The highest monthly average temperatures reach 22° C and the coldest are 3–18° C. Sinos river rainfall is 1,200–1,750 mm annually (Daniel 1991; Diesel 1991), with monthly averages between 90 (drier) and 190 mm (rainiest), and rains more common in winter months (Oliveira & Ribeiro 1986), leading to higher river levels. In the study area large deciduous trees like *Luehea divaricata* and *Anadenanthera macrocarpa* (Fabaceae) can be found, in winter leaf loss occurs quickly revealing the semideciduous character of such forests (Daniel 1991). Shrubs are uniformly distributed in the area, especially *Psychotria leiocarpa*, *P. myriantha* (both Rubiaceae), and *Justicia brasiliana* (Acanthaceae) (Diesel 1991).

4. Maquiné river (MR): This study area is in a forest fragment on the East bank of Maquiné river (29°40'47.99"S, 50°11'20.03"W), of which the whole valley covers 622 km², within the Serra Geral slopes region adjacent to the Coastal Plain (Sevegnani & Baptista 1995). This region is part of the UNESCO Atlantic Forest Biosphere Reserve since 1992. Within Maquiné's drainage basin there is a conservation unit (Reserva Biológica da Serra Geral), comprising 4,845 ha. The region is considered of extreme importance to the conservation of the Brazilian Atlantic forest (Conservation International do Brasil et al. 2000), for its high biodiversity but also fragility to anthropization. Average temperatures for the coldest month are 13–15° C and for the warmest month are 23–25° C; annual rainfall ranges from 1,400 to 1,800 mm, with elevated frequency of rainy days throughout the year (Oliveira & Ribeiro 1986). Natural vegetation in the valley, although mainly represented by dense humid forest, is a biogeographic transition with elements of the semideciduous seasonal forest. Land cover is extremely heterogeneous, a mosaic of primary and secondary vegetation at various stages of development along with agriculture areas (Sevegnani & Baptista 1995).

Sampling.—Sampling occurred across 2 yr (01 August 2007–06 June 2009), with two samples per season on each of the four regions studied. In the subtropical region this study was undertaken, there are four distinct seasons in terms of temperature, with rainfall evenly distributed or with a slight predominance of rains during winter. In each riparian forest, parallel transects were established in three habitats within the forest: the closest possible to the edge of the forest with the river; the closest possible to the edge of the forest with the adjoining grassland/pasture and the forest interior as far as possible from either edge. These three transects constituted a set; the minimum distance between transects within a set was 20 m. Two sets of transects were established per riparian forest. Each transect was a straight line approximately 50 m long; sampling never exceeded 2 m on each side of this line. Overall, 24 transects were sampled per sampling date among all areas.

Spiders in the tree-shrub layer were sampled with a beating tray during 45 min on each transect, totaling 288 h of sampling. Beating was employed on vegetation between 0.5 and 1.5 m. This method is efficient in sampling spiders living on small and medium sized shrubs, tall herbs, woody lianas, small trees and shoots of larger trees (Coddington et al. 1996; Sørensen et al. 2002). The beating tray was a wood structure

mounted as a cross (70 × 70 cm) covered by a white nylon sheet. Spiders were transferred to 80% ethanol on the spot.

Spiders were deposited in the Museu de Ciências Naturais de Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (MCN/FZB, curator: Erica H. Buckup).

Environmental complexity.—Vegetation structure was evaluated with four different methods. For vegetation density four transects were established in the same areas where spiders were sampled. Each transect was determined as a 25 m long line held 1 m above the ground, from which vegetation touches to the line were counted. At the starting point of each transect the vegetation vertical structure was evaluated, with a 2 m long, 20 mm diameter rod. The rod was held upright and the number of vegetation touches to the rod was counted. At this same point, vegetation height was measured to an approximation with the help of a 3 m long rod hold high by one of the sampling crew, observed by another sampler from a fixed (10 m) distance. Vegetation cover was sampled at the same point in the transect from a printed (20 × 20 cm) photograph taken up at a fixed height (1 m); a transparent grid (10 × 10 mm) was placed on the photograph and the number of squares with more than 50% of its area covered was counted. All measures are modified from Raizer (2004) and Raizer et al. (2006).

Guild membership.—As a basis for guild separation we used Silva (1996), Uetz et al. (1999), Höfer & Brescovit (2001) and Rodrigues et al. (2009). All spiders, separated by families, were grouped in one of the following guilds: a) web spinners: 1. orb weavers (construct bidimensional webs) and 2. space web sheet builders (construct tridimensional webs); b) hunters: 1. hunting runners (search and hunt their prey actively) and 2. ambushers/stalkers (do not build webs but sit-and-wait for their prey).

Data analysis.—Three factors of interest were tested: river basins (four levels: Piratini, Camaquã, Sinos and Maquiné); habitats (three levels: river edge, forest interior and grassland edge); and spider maturity (two levels: juvenile and adult). A MANOVA (multivariate analysis of variance) was employed to compare guild abundance proportions (arcsine transformed) with factor levels, implemented in PASW (SPSS®) 18.0. To test for vegetation structure effects and habitats on the relative proportion of spider guilds a MANCOVA (multivariate analysis of covariance) was employed with habitat as the single factor and four quantitative vegetation variables (vegetation density, structure, height and cover) as covariates. In both cases Pillai's Trace was the chosen statistic. To illustrate the effect of vegetation structure and habitats on proportional abundance of the spider guilds, an ordination was developed (Canonical Correspondence Analysis, CCA, Ter Braak 1986). The CCA was implemented in PAST (Paleontological Statistics 1.87b) (Hammer and Harper 2008).

RESULTS

Overall 42,057 spiders were obtained, juveniles more abundant than adults (79% and 21%, respectively); family richness reached 34 (Table 1). Web builders were prevalent ($n = 24,992$; 59.4%) over hunters (17,065; 40.6%). The most abundant guild was space web sheet builders ($n = 16,308$ individuals, eight families) (Fig. 2) dominated by Theridiidae (77.4%) and Linyphiidae (19%). The least abundant guild was

Table 1.—Spider guilds (juvenile and adults) and respective families in different riparian forests of southern Rio Grande do Sul, Brazil.

Guilds/Families	Riparian forests				Total	%
	Piratini	Camaquã	Sinos	Maquiné		
Orb weavers						
Araneidae	1,900	1,357	749	1,016	5,022	11.941
Tetragnathidae	399	385	246	280	1,310	3.115
Theridiosomatidae	421	357	203	203	1,184	2.815
Uloboridae	237	168	391	208	1,004	2.387
Nephilidae	21	22	43	5	91	0.216
Deinopidae	10	19	15	17	61	0.145
Mysmenidae	3	7	2	-	12	0.029
Space web sheet builders						
Theridiidae	4,356	3,423	2,348	2,491	12,618	30.002
Linyphiidae	284	258	300	2,253	3,095	7.359
Pholcidae	1	115	98	163	377	0.896
Hahniidae	-	-	1	95	96	0.228
Scytodidae	-	11	3	58	72	0.171
Amaurobiidae	6	5	2	9	22	0.052
Dictynidae	1	-	14	6	21	0.050
Synotaxidae	-	-	-	7	7	0.017
Ambushers/stalkers						
Thomisidae	1,242	1,439	823	697	4,201	9.989
Salticidae	719	1,042	1,129	983	3,873	9.209
Mimetidae	115	328	145	63	651	1.548
Pisauridae	46	85	127	271	529	1.258
Sparassidae	-	85	103	73	261	0.621
Philodromidae	1	3	77	79	160	0.380
Senoculidae	51	15	23	38	127	0.302
Oxyopidae	6	11	72	2	91	0.216
Ctenidae	-	-	-	17	17	0.040
Hersiliidae	-	-	1	-	1	0.002
Idiopidae	-	-	-	1	1	0.002
Hunting runners						
Anyphaenidae	1,933	1,954	1,701	1,210	6,798	16.164
Corinnidae	87	26	16	37	166	0.395
Oonopidae	22	25	6	32	85	0.202
Miturgidae	26	9	11	28	74	0.176
Lycosidae	4	1	8	3	16	0.038
Gnaphosidae	-	3	4	3	10	0.024
Clubionidae	-	-	-	3	3	0.007
Segestriidae	-	-	-	1	1	0.002
Total	11,891	11,153	8,661	10,352	42,057	100
Families	24	26	29	32	34	
Exclusive Families	0	0	1	5		

hunting runners (7,153 individuals, eight families), dominated by Anyphaenidae (95%) and Corinnidae (2.3%). For ambushers there were 9,912 individuals in 11 families with Thomisidae (42.4%) and Salticidae (39.1%) most abundant. Among orb weavers there were 8,684 individuals in seven families, being Araneidae (57.8%) and Tetragnathidae (15.1%) the most abundant families.

Spider guilds and rivers.—In all river sites more web building spiders were found than hunters. There were significant differences in guild proportion among rivers (MANOVA: orb web, $F = 17.37$, $P < 0.001$; space web, $F = 39.65$, $P < 0.001$; hunting runners, $F = 8.59$, $P < 0.001$; ambushers, $F =$

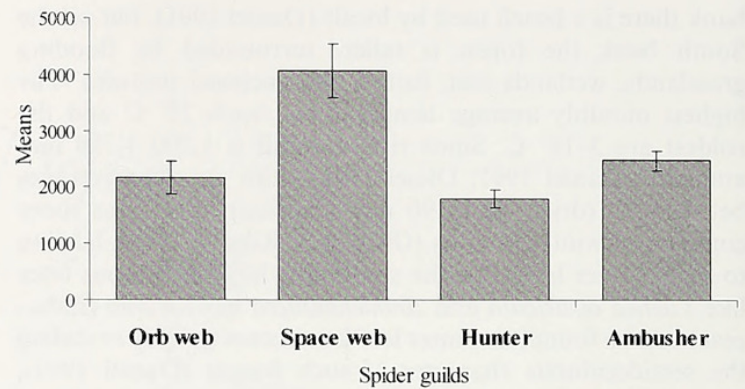


Figure 2.—Spider abundance (average over four rivers \pm SE) among guilds in riparian forests of Rio Grande do Sul, Brazil.

30.26, $P < 0.001$). The most prevalent guild was space web sheet builders (Piratini = 4,648; Camaquã = 3,813; Sinos = 2,767; Maquiné = 5,082), followed by ambushers (Piratini = 2,180; Camaquã = 3,008; Sinos = 2,500; Maquiné = 2,224) on all rivers (Fig. 3) but Piratini, having orb weavers as the second most abundant guild ($n = 2,991$); on all rivers the least abundant guild was hunting runners (Piratini = 2,072; Camaquã = 2,018; Sinos = 1,746; Maquiné = 1,317) (Fig. 3).

The Synotaxidae family (spacers web sheet build) was exclusive to Maquiné river, as were Clubionidae and Segestriidae (hunting runners), Ctenidae and Idiopidae (ambushers), the latter being the sole Mygalomorphae family recorded here (Table 1). Sinos river had a single exclusive family (Hersiliidae-ambushers).

Spider guilds and forest habitats.—A larger spider abundance was found for the forest interior ($n = 16,281$; 38.7%), then for the grassland edge (13,121; 31.2%) and the smaller abundance occurred in the river edge (12,655; 30.1%). Guild proportions differed significantly among all habitats (MANOVA: orb web, $F = 28.39$, $P < 0.001$; space web, $F = 6.79$, $P < 0.005$; hunting runners, $F = 7.51$, $P < 0.003$; ambushers, $F = 36.61$, $P < 0.001$). The dominant guild is still space web sheet builders; the least abundant guild was hunting runners in the river edge and forest interior, and orb weavers for the grassland edge (Fig. 4). Hunters occurred more on edges; hunting runners in the grassland edge ($n = 2,627$), ambushers on the river edge ($n = 3,605$). Weaving spiders were more abundant in the forest interior, for both space web sheet builders ($n = 6,943$) and orb weavers ($n = 4,013$) (Fig. 4).

Family richness resulted in 30 recorded in the river edge (one exclusive family – Idiopidae: ambushers), 32 in the forest interior (one exclusive – Segestriidae: hunting runners) and 30 in the grassland edge (one exclusive – Hersiliidae: ambushers).

Spider guilds and vegetation structure.—CCA results are shown on Figure 5. The eigenvalues for the two first axes were: 0.049 (axis 1) and 0.010 (axis 2). The permutation test did not return significant values for axes 1 and 2 ($P = 0.42$ and 0.24, respectively), indicating the guilds are not significantly correlated to the environmental complexity variables evaluated. The triplot (Fig. 5) demonstrates the first axis to be related to vegetation structure variables (positively) and to vegetation density (negatively). The second axis appears positively related to cover and height. Habitats occur around the origin, being indifferent to the evaluated variables, except forest interior in Maquiné, tending to

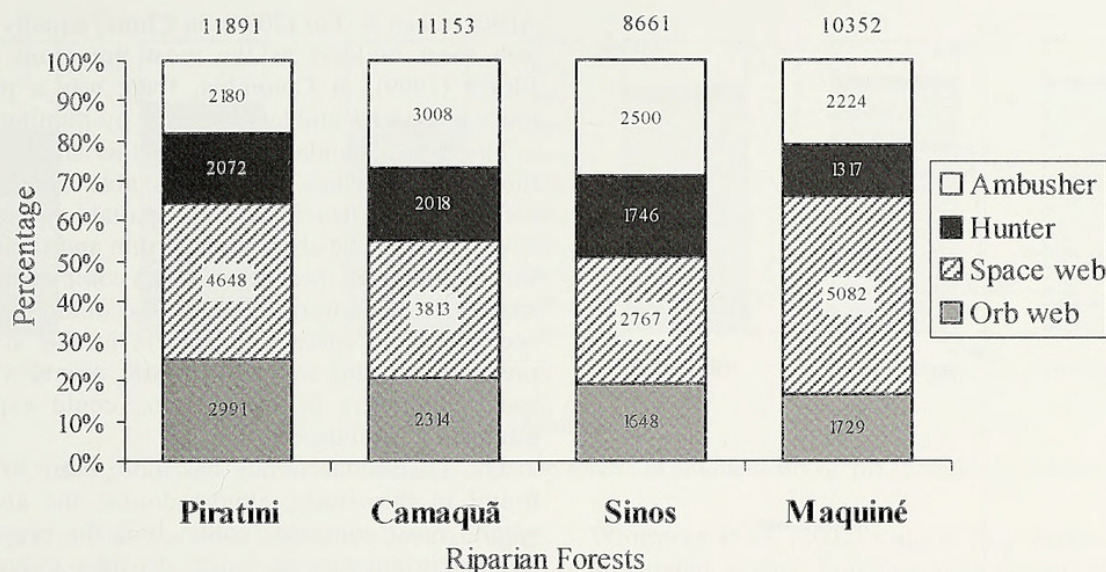


Figure 3.—Spider abundance (juvenile and adults) among guilds in riparian forests of southern Brazil.

remain close to vegetation density (densveg) and forest interior in Piratini, close to vegetation structure (struveg). The MANCOVA did not reveal any significant differences in guild proportions for any of the environmental complexity variables, except space web sheet builders having a significant influence of vegetation cover ($F=8.17$; $p=0.03$) and vegetation density ($F=7.03$; $p=0.04$).

Ontogenetical changes in spider assemblages.—Comparing adult and juvenile spider assemblages, strong shift can be found regarding guild abundance. Among the juveniles, 47% are hunters and 53% weavers; among adults, only 17% are hunters and 83% weavers.

There are large statistical differences among guild proportions contrasting adult and juvenile spiders (MANOVA: orb weavers, $F=173.67$, $P < 0.0001$; space web sheet builders, $F=1837.56$, $P < 0.0001$; hunting runners, $F=879.60$, $P < 0.0001$; ambushers, $F=375.34$, $P < 0.0001$). Juvenile spiders have more homogeneous abundances among guilds, whilst adults have a large difference between space web sheet builders and

the other guilds. There is an especially large decrease in the proportion of hunting runners in the passage to the adult stage (Figs. 6, 7).

Among different rivers, juvenile spiders (Fig. 6a) show consistent abundance patterns among guilds, with higher abundances for space web sheet builders in riparian forests of Piratini and Maquiné rivers and more ambushers in Camaquã and Sinos rivers. In terms of adults (Fig. 6b), there is a decrease, especially in hunting runners, and a strong increase in the proportion of space web sheet builders for all rivers (significant interaction: orb web, $F=6.74$, $P < 0.002$; space web, $F=14.85$, $P < 0.0001$; hunting runners, $F=5.45$, $P < 0.005$; ambushers, $F=11.01$, $P < 0.0001$).

There is an increase in the proportion of space web sheet builders for adults also for habitats (Fig. 7) (MANOVA: space web, $F=17.49$, $P=0.0002$) with the other guilds also differing significantly among habitats, except orb weavers ($F=1.37$, $P=0.27$). For hunting runners, juvenile cursorials (Fig. 7a) have a higher proportion compared to adults (Fig. 7b).

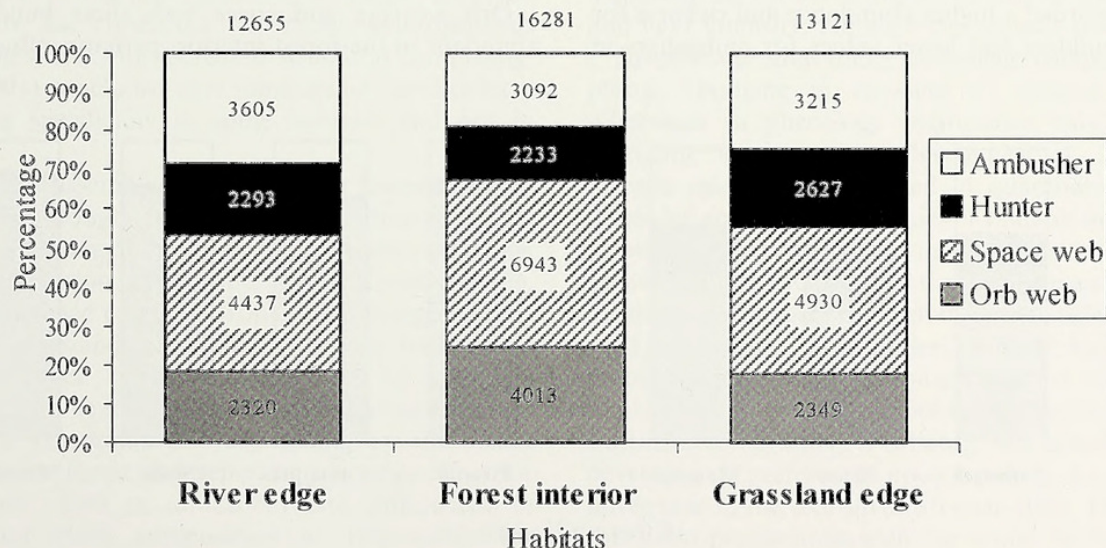


Figure 4.—Spider guild abundance (juvenile and adults) in the three habitats of riparian forests of southern.

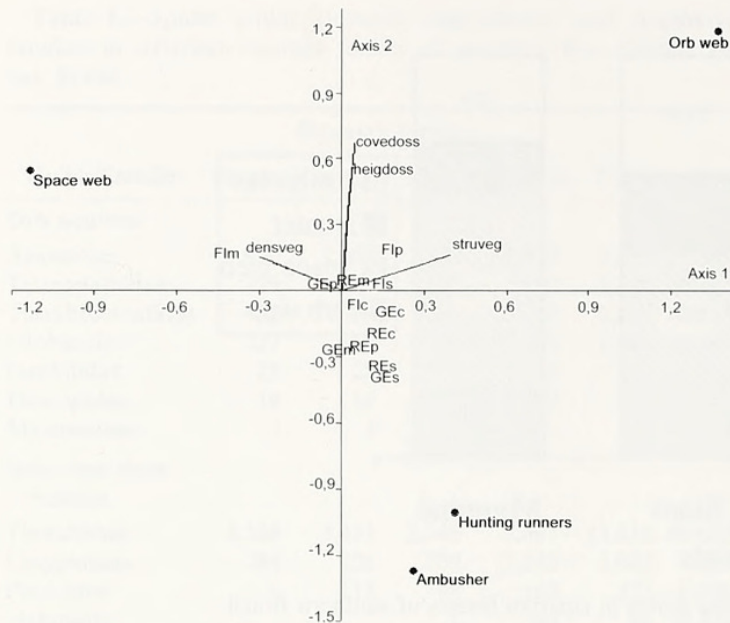


Figure 5.—Canonical correspondence analysis for spider guild abundance (juvenile and adults) response to environmental complexity variables evaluated among habitats in riparian forests in southern Brazil (RE: river edge, FI: forest interior, GE: grassland edge; p: Piratini river; c: Camaquã river; s: Sinos river; m: Maquiné river; covedoss: canopy cover; heigdoss: canopy height; densveg: vegetation density; struveg: vegetation structure).

DISCUSSION

The variation in guild proportions for the different rivers evaluated demonstrates that vegetation physiognomy influences the functional relationship between spiders and their environment. However, there is a degree of homogeneity among rivers in spider guild proportions that suggests a model for the tree-shrub strata of riparian forests of south Brazil: a large abundance of spiders in the space web sheet builders guild and a lower representation for hunting runners. This distinguishes the tree-shrub strata fauna functionally from other habitats occupied by spiders within a forest, such as the underground or topsoil, where hunting spiders usually dominate (Höfer 1997; Loeser et al. 2006; Peres et al. 2007).

This model has been reported from other parts of the world. Sørensen (2004) recorded a higher abundance and richness for space web sheet builders and lower values for ambushers in

Africa. Chen & Tso (2004), in China, equally point out space web sheet builders as the most numerous guild. Also for Flórez (1999), in Colombia, there was a predominance of space web sheet builders followed by hunting runners.

The most abundant guilds in this environment are likely those with families and species able to adequately occupy niches, given structural and spatial characteristics of the environment. The abundance of thin and ramified branches in shrubs and small trees generating a complex three-dimensional spatial structure in riparian forests could possibly explain this occupation of space web spiders in this strata. A lack of preferred hunting and sit-and-wait points within the forest, such as flowers or open spots, could explain the lower numbers of ambushers.

The Theridiidae family has more than 30% of all spiders found in this study, almost double the abundance of the second most common family. It is the prevalent family for various inventories in South America (Silva 1996; Silva & Coddington 1996; Flórez 1999; Benavides & Flórez 2007; Avalos et al. 2007). Theridiidae, along with Linyphiidae, were responsible for the space web sheet builders guild being dominant in riparian forests. The higher abundance of space web, overall, suffers a strong influence of the high numbers of individuals in Maquiné river, and a lower influence from Sinos river. Linyphiidae really determined the higher space web sheet builders abundance in Maquiné river (73% of the spiders were in this family).

In the Samiria river riparian forest of Peru, Silva (1996) recorded a higher abundance of hunting runners and a lower number of ambushers. As they sampled different vegetation strata, guild composition was distinct from what we found, indicating a variability in the fauna probably according to vegetation height. In Colombia, Benavides and Flórez (2007), sampled the Igapó forest influenced by the Taraira river, where cursorials dominated, whilst in the *terra firme* forest, irregular web builders dominated. The seasonal inundation regime is thus a factor that seems to affect the araneofauna composition in Igapó forests. We recorded higher abundances for hunters on forest edges; the river edge had more spiders among ambushers. This environment is usually subject to strong winds and can be influenced by floods, which could have lead to lower abundances for the other guilds.

Orb weavers and space web sheet builders were more abundant in the forest interior, perhaps influenced by abiotic

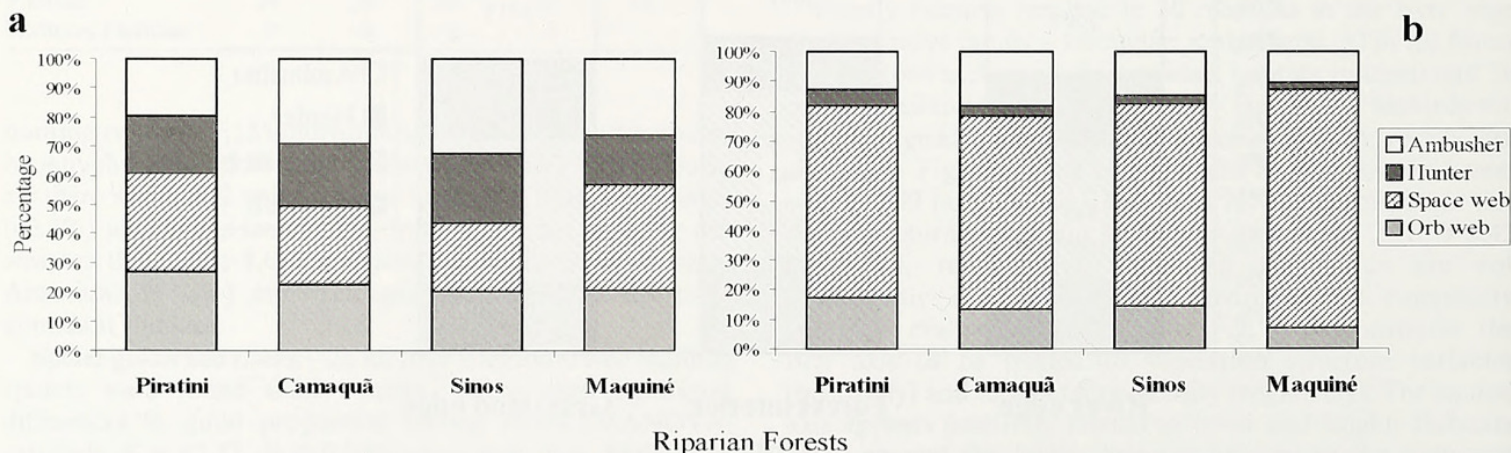


Figure 6.—Spider guilds in riparian forests of southern Brazil. (a) Juvenile. (b) Adults.

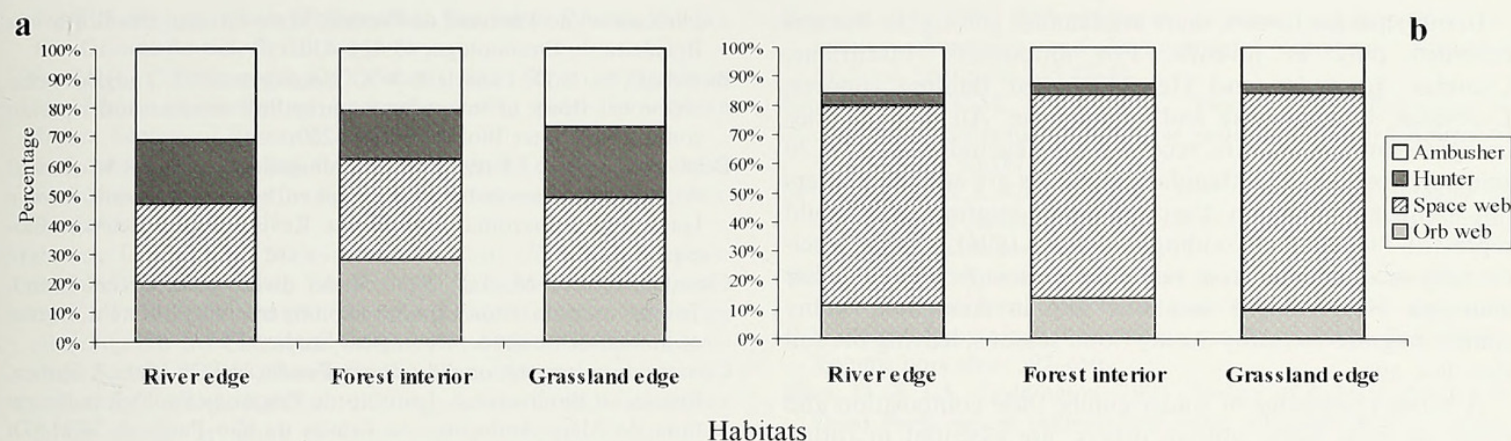


Figure 7.—Spider guilds and habitats in riparian forests of southern Brazil. (a) Juvenile. (b) Adults.

factors on the edges, as floods at river edges, as above, or light and wind intensity at the grassland edge. Among hunters, abundances were homogeneous among habitats, with more individuals on the edges, perhaps related to a hunting strategy independent of web type. According to Baldissera et al. (2004), web distribution and occurrence can be influenced by a forest/edge gradient, because changes in microclimate created by the border can cause thermal tension and damage webs due to the winds.

The forest border is a place where species from different environments can establish and then disperse to the interior of the fragment, creating a flow of immigrants faced by species inhabiting the forest interior. Oliveira-Alves et al. (2005) suggest that the edge effect acts like a natural barrier, impeding the flow of spiders among the environments; these authors found a higher richness for the edge compared to the forest interior.

The lower abundance of orbicular web spinners on edges can be a consequence of the lack of proper habitat and/or wind exposure, being more open, compared to the riparian forest interior, a pattern similar to what is found by Hore & Uniyal (2008). Souza-Alves et al. (2007) recorded more weavers in the forest and more hunters in the grassland; Oliveira-Alves et al. (2005) observed that the hunter guild dominates on the edge and web builders in the forest centre; similar to what was found here. Rubio et al. (2008) observed web builders to be connected to more heterogeneous environments and those with increased structural complexity. Goetze et al. (2001) concluded that some spider families have species occurring specifically in some habitats and not in others.

Studies on spider assemblages suggest that faunal composition tends to be strongly related to environmental spatial heterogeneity as determined by the plant community on which spiders live (Gunnarsson 1990; Uetz 1991; Rypstra 1986). Possibly, the occurrence of plants from neighboring environments, such as grasslands, introduces distinct habitats to riparian forests edges. These habitats can be occupied differentially by the spider guilds, some species perhaps coming from the grasslands as well, mixing up the spider fauna of the riparian forest and generating an edge effect for guild composition. Toti et al. (2000) cite differences in physiognomy and plant composition as responsible for differences in guild composition in spider assemblages.

Whitmore et al. (2002) suggest that similar kinds of habitats are similar in their familial spider composition and that there is an influence of habitat structural complexity on guild composition.

Despite considering a suite of factors that can determine riparian forest structure (Ab'Saber 2000), we have failed to find those structural factors that affect spider guilds. Although there are clear effects of habitat on the spider guilds, these guilds were not influenced by the differences found in plant structure and environmental complexity of riparian forests. There are at least two possibilities to explain this: a question of scale and of variation among sampling units. First, the scale at which the environment was evaluated might not be relevant for spiders. The methods are employed and planned by humans and adequate for human perception of the environment, at the scale of meters. Spiders might respond at a smaller scale, that of centimeters or even millimeters. Secondly, riparian forests may present low variation in vegetation structure so as to not affect spider guilds – for spiders with different hunting strategies, such forests are effectively homogeneous. Structural variation must thus be very large to lead to significant changes in abundances, reflecting the opportunistic and generalist character of spiders ecologically (Nentwig 1986; Uetz 1991). Abundance changes in spider guilds of the tree-shrub strata can be more strongly associated to abiotic changes mentioned above, such as wind and light intensity, among other aspects not evaluated here.

Juvenile and adult spider assemblage composition can be more plastic, changing in response to various factors, such as differences in phenology (maturation time) and differential mortality, among others (Sackett et al. 2008). Frequently, juvenile spiders are not used in quantitative analyses, being discarded and with them a series of valuable information: here we identified a large difference in the pattern of guild abundance between adults and juvenile, that is, the maturation process has distinct consequences for each different spider guild.

Many papers cite hunters (either hunting runners or ambushers) as more abundant on the soil surface (Peres et al. 2007; Loeser et al. 2006) or in the canopy (Silva 1996; Battistola et al. 2004). Probably, the species in these guilds develop such preferences upon reaching the adult stage, being infrequent in the tree-shrub stratum then. Thus, the change in this guild proportions with age could be the consequence of this active vertical selectivity on the part of the spiders.

In our riparian forests, there are families among the hunters recorded only as juvenile. For ambushers: Pisauridae, Ctenidae, Idiopidae and Hersiliidae; for hunting runners: Lycosidae, Gnaphosidae and Segestriidae. All such families except Pisauridae are rare, recorded as a few individuals (< 20 spiders). Possibly, low abundance families are actually spiders not frequently seen in the tree-shrub stratum and could represent "tourists" (Coddington et al. 1996), present accidentally or *en marche* from one environment (soil) to another (canopy). Höfer (1997) mentions that in Amazonia, many spiders migrate vertically during flood seasons, leaving the soil they live on.

A better knowledge of spider guilds, their composition and effect on food webs, among others, are essential in future studies. More abundant guilds can have a fundamental role in the environment, resulting in functional information similar to that of a taxonomic bioindicator. Nowadays, given the scarce knowledge of life history and behavior of most Neotropical species (Höfer & Brescovit 2001; Dias et al. 2010), "higher taxa", such as families for spiders, are increasingly being used in recent studies. According to Uetz et al. (1999) the ideal situation so as to reflect the reality of spider guilds, would be to know the natural history of each species, however this is still far off for most families. Additionally, different classifications are used for the same taxa and groups depending on the authors, which makes comparison among studies difficult. We hope the increasing amount of information on Neotropical spiders being produced will allow us nevertheless to paint a picture of the functional relationships of the guilds, fostering the understanding of the ecosystems they live in as well.

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LITERATURE CITED

- Ab'Saber, A.N. 2000. O suporte geológico das florestas beiradeiras (ciliares). Pp. 15–25. In *Matas Ciliares: Conservação e Recuperação*. (P.R. Rodrigues & H.F. Leitão Filho, eds.). EDUSP/FAPESP, São Paulo.
- Avalos, G., G.D. Rubio, M.E. Bar & A. González. 2007. Arañas (Arachnida: Araneae) asociadas a dos bosques degradados Del Chaco húmedo en Corrientes, Argentina. *Revista de Biología Tropical* 55:899–909.
- Baldissera, R., G. Ganade & S.B. Fontoura. 2004. Web spider community response along an edge between pasture and *Araucaria* Forest. *Biological Conservation* 118:403–409.
- Battistola, L.D., M.I. Marques, J. Adis & A.D. Brescovit. 2004. Aspectos ecológicos da comunidade de Araneae (Arthropoda, Arachnida) em copas da palmeira *Attalea phareolata* Mart. (Arecaceae) no Pantanal de Poconé, Mato Grosso, Brasil. *Revista Brasileira de Entomologia* 48:421–430.
- Baxter, C.V., K.D. Fausch & W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrates prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Benavides, L. & E. Flórez. 2007. Comunidades de arañas (Arachnida: Araneae) en microhábitats de dosel en bosques de tierra firme e Igapó de la Amazonía Colombiana. *Revista Ibérica de Aracnología* 14:49–62.
- Chen, K.-C. & I.-M. Tso. 2004. Spider diversity on Orchid Island, Taiwan: a comparison between habitats receiving different degrees of human disturbance. *Zoological Studies* 43:598–611.
- Conservation International do Brasil, Fundação SOS Mata Atlântica, Fundação Biodiversitas, Instituto de Pesquisas Ecológicas, Secretaria do Meio Ambiente do Estado de São Paulo & SEMAD/ Instituto Estadual de Florestas MG. 2000. Avaliações e Ações Prioritárias para a Conservação da Biodiversidade da Mata Atlântica e Campos Sulinos. Ministério do Meio Ambiente, Brasília.
- Cardoso, P., M.A. Arnedo, K.A. Triantis & P.A.V. Borges. 2010. Drivers of diversity in Macaronesian spiders and the role of species extinctions. *Journal of Biogeography* 37:1034–1046.
- Coddington, J.A., L.H. Young & F.A. Coyle. 1996. Estimating spider species richness in a Southern Appalachian cove hardwood forest. *Journal of Arachnology* 24:111–128.
- Daniel, A. 1991. Estudo fitossociológico arbóreo/arbustivo da mata ripária da Bacia Hidrográfica do rio dos Sinos, RS. *Pesquisas, Botânica* 42:1–199.
- Dias, S.C., L.S. Carvalho, A.B. Bonaldo & A.D. Brescovit. 2010. Refining the establishment of guilds in Neotropical spiders (Arachnida: Araneae). *Journal of Natural History* 44:219–239.
- Diesel, S. 1991. Estudo fitossociológico herbáceo/arbustivo da mata ripária da Bacia Hidrográfica do rio dos Sinos, RS. *Pesquisas, Botânica* 42:201–257.
- Flórez, E.D. 1999. Estructura y composición de una comunidad de arañas (Araneae) en un bosque muy seco tropical de Colombia. *Boletín Entomología Venezolana* 14:37–51.
- Goetze, J.R., J. Tovar & A. Flores. 2001. Spider assemblages along the Rio Grande at Laredo, Texas. *Texas Journal of Science* 53:29–38.
- Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology* 59:743–752.
- Hammer, Ø. & D.A.T. Harper. 2008. PAST: PAleontological STatistics, Version 1.87b. Online at <http://folk.uio.no/ohammer/past>.
- Höfer, H. 1997. The spider communities. Pp. 373–383. In *The Central Amazonian Floodplain: Ecology of a Pulsing System*. (W. Junk, ed.). Springer, Berlin.
- Höfer, H. & A.D. Brescovit. 2001. Species and guild structure of a Neotropical spider assemblage (Araneae) (Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil). *Andrias* 15:99–120.
- Hore, U. & V.P. Uniyal. 2008. Diversity and composition of spider assemblages in five vegetation types of the Terai Conservation Area, India. *Journal of Arachnology* 36:251–258.
- IPAGRO. 1989. Atlas Agroclimático do Estado do Rio Grande do Sul. Secretaria da Agricultura e Abastecimento, Porto Alegre, Rio Grande do Sul, Brazil.
- Jennings, D.T. & D.J. Hilburn. 1988. Spiders (Araneae) captured in malaise traps in spruce-fir forests of west-central Maine. *Journal of Arachnology* 16:85–94.
- Kato, C., T. Iwata, S. Nakano & D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos* 103:113–120.
- Kilca, R.V. 2002. Alguns aspectos florísticos e estruturais de uma floresta de galeria no sul da Planície Costeira do Rio Grande do

- Sul, B.S. Biology Thesis, Universidade Federal de Pelotas, Pelotas, Rio Grande do Sul, Brazil.
- Laeser, S.R., C.V. Baxter & K.D. Fausch. 2005. Riparian vegetation loss, stream channelization, and web-weaving spiders in northern Japan. *Ecological Research* 20:646–651.
- Loeser, M.R., B.H. McRae, M.M. Howe & T.G. Whitham. 2006. Litter hovels as havens for riparian spiders in an unregulated river. *Wetlands* 26:13–19.
- Malavasi, U.C., M.M. Malavasi & M. Curti. 2004. III Simpósio Regional de Mata Ciliar. Ed. Unioeste, Cascavel, Paraná, Brazil.
- Marchi, T.C. 2005. Estudo do componente arbóreo de mata ribeirinha no rio Camaquã, Cristal, RS. M.Sc. Thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.
- Moulder, B.C. & D.E. Reichle. 1972. Significance of spider predation in the energy dynamics of forest-floor arthropod communities. *Ecological Monographs* 42:473–498.
- Nakano, S. & M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences USA* 98:166–170.
- Nentwig, W. 1986. Non-web building spiders: prey specialists or generalists? *Oecologia* 69:571–576.
- Oliveira, A.A.B. & A.G. Ribeiro. 1986. Climatologia. Pp. 757–776. In *Levantamento de Recursos Naturais, Volume 33*. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.
- Oliveira-Alves, A., M.C.L. Peres, M.A. Dias, G.S. Cazais-Ferreira & L.R.A. Souto. 2005. Estudos das comunidades de aranhas (Arachnida: Araneae) em ambiente de Mata Atlântica no Parque Metropolitano de Pituáçu – PMP, Salvador, Bahia, Brazil. *Biota Neotropica*. Special issue. Volume 5, Number 1A. Online at <http://www.biotaneotropica.org.br/v5n1a/pt/abstract?inventory+BN006051a2005>.
- Peres, M.C.L., J.M.C. Silva & A.D. Brescovit. 2007. The influence of treefall gaps on the distribution of web-building and ground hunter spiders in an Atlantic Forest remnant, northeastern Brazil. *Studies on Neotropical Fauna and Environment* 42:49–60.
- Raizer, J. 2004. Comunidade de aranhas em capões de mata das sub-regiões Miranda e Abobral no Pantanal Sul-Mato-Grossense. PhD Thesis, Universidade de Campinas, Campinas, São Paulo, Brazil.
- Raizer, J., H.F. Japyassú, R.P. Indicatti & A.D. Brescovit. 2005. Comunidade de aranhas (Arachnida, Araneae) do pantanal norte (Mato Grosso, Brasil) e sua similaridade com a araneofauna amazônica. *Biota Neotropica*. Special issue. Volume 5, Number 1A. Online at <http://www.biotaneotropica.org.br/v5n1a/pt/abstract?inventory+BN951a2005>.
- Raizer, J., A.D. Brescovit, R.Y. Lemos & N.F. Carvalho. 2006. Inventário das aranhas no Complexo Aporé-Sucuriú. Pp. 69–78. In *Biodiversidade do Complexo Aporé-Sucuriú: Subsídios à Conservação e ao Manejo do Cerrado: área prioritária 316-Jauru*. (T.C.S. Pagotto & P.R. de Souza, eds.). Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil.
- Rodrigues, E.N.L., M.S. Mendonça, Jr. & R. Ott. 2009. Spider diversity in a rice agroecosystem and adjacent areas in southern Brazil. *Revista Colombiana de Entomologia* 35:78–86.
- Rubio, G.D., J.A. Corronca & M.P. Damborsky. 2008. Do spider diversity and assemblages change in different contiguous habitats? A case study in the protected habitats of the Humid Chaco ecoregion, Northeast Argentina. *Environmental Entomology* 37:419–430.
- Rypstra, A.L. 1986. Web spiders in temperate and tropical forest: relative abundance and environmental correlates. *American Midland Naturalist* 115:42–51.
- Sackett, T.E., C.M. Buddle & C. Vincent. 2008. Relevance of collected juveniles to the analysis of spider communities. *Journal of Arachnology* 36:187–190.
- Sevegnani, L. & L.R.M. Baptista. 1995. Composição florística de uma floresta secundária, no âmbito da Floresta Atlântica, Maquiné, RS. *Sellowia* 45–48:47–71.
- Silva, D. 1996. Species composition and community structure of Peruvian rainforest spiders: a case study from a seasonally inundated forest along the Samiria river. *Revue Suisse de Zoologie*. Volume hors série: 597–610.
- Silva, D. & J.A. Coddington. 1996. Spiders of Pakitza (Madre de Dios) Peru: species richness and notes on community structure. Pp. 241–299. In *The Biodiversity of Pakitza and its Environs*. (D.E. Wilson & A. Sandoval, eds.). Smithsonian Institution, Washington, DC.
- Simberloff, D. & T. Dayan. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22:115–143.
- Simó, M., F. Pérez-Miles, A.F.E. Ponde de León & M. Meneghel. 1994. Relevamiento de fauna de la quebrada de los cuervos; area natural protegida. *Boletín de la Sociedad Zoológica del Uruguay* 2:1–20.
- Sørensen, L.L. 2004. Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. *Biodiversity and Conservation* 13:437–452.
- Sørensen, L.L., J.A. Coddington & N. Scharff. 2002. Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afrotropical Forest. *Environmental Entomology* 31:319–330.
- Souza-Alves, J.P., A.D. Brescovit, M.S. Tinocô & M.C.L. Peres. 2007. Number of individuals of the hunting and web-building spider guilds of the dry grassland and gallery forest of Chapada Diamantina, Bahia. *Biologia Geral e Experimental* 7:5–8.
- Teixeira, M.B., A.B. Coura-Neto, U. Pastore & A.L.R. Rangel. 1986. Vegetação; as regiões fitoecológicas, sua natureza, seus recursos econômicos; estudo fitogeográfico. Pp. 541–632. In *Levantamento de Recursos Naturais, Volume 33*. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.
- Ter Brak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.
- Toti, D.S., A.C. Frederick & J.A. Miller. 2000. A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. *Journal of Arachnology* 28:329–345.
- Uetz, G.W. 1991. Habitat structure and spider foraging. Pp. 325–348. In *Habitat Structure. The Physical Arrangement of Objects in Space*. (S.S. Bell, E.D. McCoy & H.R. Mushinsky, eds.). Chapman and Hall, London.
- Uetz, G.W., J. Halaj & A.B. Cady. 1999. Guild structure of spiders in major groups. *Journal of Arachnology* 27:270–280.
- Whitmore, C., R. Slotow, T.E. Crouch & A.S. Dippenaar-Schoeman. 2002. Diversity of spiders (Araneae) in a Savanna Reserve, Northern Province, South Africa. *Journal of Arachnology* 30:344–356.



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