

## Seasonal changes in spider diversity in subtropical riparian forests: what drives the seasonality of the araneofauna?

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**Abstract.** Spiders are usually found through all seasons in the subtropics, but little is known about their seasonality patterns and how they respond to abiotic factors, especially in species-rich regions such as Brazil. We investigated the seasonal variation in spider communities and the possible influence of abiotic factors (e.g., temperature, rainfall) on spider abundance, species richness and composition in subtropical riparian forest in four river basins. Changes in spider abundance among seasons differed between ontogenetic stages: there were more spiderlings in the autumn, and similar numbers of adults year round. Species richness, on the other hand, was highest in spring and summer. Species composition differed between seasons and river basins. Several factors may be behind diversity changes in the araneofauna among seasons, however, none of the abiotic factors evaluated showed a strong direct influence. Seasonal patterns varied, with different species having peaks in all three seasons but autumn. Seasonality is clear in these spider communities but not all patterns follow predictions from simple temperature changes.

**Keywords:** Araneae abundance, richness, tree-shrub strata, composition, seasonal variation

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Spiders play important ecological roles in a variety of terrestrial ecosystems, for example acting as predators, assuming the important function of maintaining population balance for a series of prey invertebrates (New 1999). Spiders in subtropical regions are recorded at all seasons and present high abundance throughout the year (Indrusiak & Kotzian 1998; Rodrigues 2005; Podgaiski et al. 2007; Rinaldi & Trinca 2008; Campuzano et al. 2019; Pitilin et al. 2019; Baldissera et al. 2020). However, they are thought to be more abundant during warmer periods of the year, when they would hunt most actively, avoiding adverse conditions of the colder periods (Arango et al. 2000; Avalos et al. 2007). For most species, little is known about their phenology, especially in regions with high diversity such as Brazil, and even less about spider community patterns.

Habitat structure has been considered a determinant for spider diversity and community composition (Hatley & Macmahon 1980; Baldissera et al. 2004, 2008; Avalos et al. 2007; Campuzano et al. 2019). However, we have already shown that forest structure may not always affect spider communities strongly (Rodrigues et al. 2014), with only canopy cover affecting spider abundance and richness. On the other hand, seasonal changes in abiotic conditions such as temperature and precipitation could have an indirect strong influence on environmental structure relevant to spiders, such as on vegetation, but also imposing direct limits to spider prey abundance (Wolda 1988). Seasonal variation can thus influence habitat selection by spiders (Uetz 1991), but few studies have actually evaluated spider seasonality in the Neotropical region. Temperature oscillations are minimal over the course of the year in tropical regions and marked in temperate ones; however, in the subtropics an intermediate situation is found. In southern Brazil, for example, there are distinct seasons in terms of temperature, but not in rainfall

(Maluf 2000), and spider populations are thus expected to be likewise seasonal, but not too strongly. In Brazil, sampling with a seasonal component was conducted in the south (Indrusiak & Kotzian 1998; Baldissera et al. 2004, 2020; Rodrigues 2005; Podgaiski et al. 2007; Pitilin et al. 2019; Baldissera et al. 2020), southeast (Rinaldi & Trinca 2008), midwest (Castilho et al. 2005) and northeast (Dias et al. 2006) regions, however, only a few ecosystems ended up being considered.

Despite their importance for the maintenance of water relations and regime and their high local biodiversity, riparian forests have not so far received the attention they deserve. Riparian forests are complex environments with mesoclimatic conditions differentiated by mild temperatures linked to increased atmospheric humidity recorded at these locations (Rodrigues & Leitão-Filho 2000). These environments have ideal conditions for the maintenance of diverse forms of wildlife and function as ecological corridors. Therefore, conservation and research involving these ecosystems are crucial for a better understanding of the associated fauna and its preservation. Spiders living in riparian forests are a potential indicator group, given the biological reasons above, but have been rarely studied directly. We have previously shown that distinct microhabitats (e.g., grassland-forest edge and river-forest edges) support different levels of spider diversity (higher abundance in forest interior, total richness higher in forest edge) (Rodrigues et al. 2014). Also, dividing spiders into guilds reveals again effects of microhabitats (more hunters on the edges, more weavers in the forest interior) but no responses to vegetation differences (Rodrigues & Mendonça 2012). Although we have explored spatial and microspatial patterns of spider communities in riparian forests, we have not yet studied their seasonal patterns.

Here, we evaluated spider community seasonality patterns and drivers in riparian forests over a period of two years. The aim of this study was to investigate the seasonal variation of the spider community in four riparian forests in southern Brazil, assessing changes in abundance (differentiating between juveniles and adults), species richness and composition throughout the annual seasons while also checking for the direct influence of abiotic factors. We expected spider communities to show seasonal patterns, with higher abundance and species richness during warmer seasons; we also expected juveniles to differ from adults in this clear preference for warmer months. We anticipated distinct spider assemblages for different seasons, and we expected all these differences to follow temperature changes, given this is an indication of spider activity and thus a higher probability of prey capture. The reverse was expected for the effect of rainfall, since it is known to reduce prey capture probability.

## METHODS

**Study areas.**—Samples of spiders were taken from four different river basins, along the main river of each basin in the state of Rio Grande do Sul, southern Brazil. All rivers were at low altitudes not far from the coast (less than 100 km). For more details on the rivers and forest vegetation see Rodrigues & Mendonça (2012).

Piratini river (PR): sampling was on the north bank of the lower Piratini, southern region of the Coastal Plain in the municipality of Arroio Grande (31°54'06.47"S, 52°39'08.29"W) in the Pampa biome (South American temperate grasslands). 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 driest (48 mm) (Oliveira & Ribeiro 1986). Climatic type is humid temperate (Maluf 2000).

Camaquã river (CR): study area was on the north bank of the lower Camaquã (31°01'01.7"S, 51°56'42.0"W), on the center-south portion of the Coastal Plain in the municipality of Cristal in the Pampa biome. It is at approximately 14 m a.s.l. and receives frequent seasonal flooding. Average annual temperatures are 18.9° C, with January/February warmer (24.3° C) and July colder (13.3° C). Average annual rainfall is 1,234 mm, with September the rainiest month (135 mm) and November the driest (65 mm) (IPAGRO 1989). Climate is humid subtemperate (Maluf 2000).

Sinos river (SR): study area in the municipality of Parobé, south bank of the river (29°41'06.94"S; 50°51'05.98"W), in the limits between the Pampa and Atlantic Forest biomes. 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), with monthly averages between 90 (driest) and 190 mm (rainiest), and rains more common in winter months (Oliveira & Ribeiro 1986), leading to higher river levels. Climate is subhumid subtropical (Maluf 2000).

Maquiné river (MR): this area was in a forest fragment on the east bank of the Maquiné river (29°40'47.99"S, 50°11'20.03"W), in the municipality of Maquiné, adjacent to the Coastal Plain. Average temperatures for the warmest month are 23–25° C and for the coldest month are 13–15° C; annual rainfall ranges from 1,400 to 1,800 mm, with elevated

frequency of rainy days throughout the year (Oliveira & Ribeiro 1986). The climate is perhumid subtropical (Maluf 2000).

**Sampling.**—Sampling occurred over two years (August 2007–June 2009), with two samples per season (spring: October to December, summer: January to March, autumn: April to June, and winter: July to September) on each of the four regions studied. In the subtropical region where 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: forest edge with the river, forest edge with the adjoining grassland/pasture, and forest interior. These three transects constituted a set; 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 70 × 70 cm 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). Spiders were transferred to 80% ethanol on the spot. For spider identification, they were examined under a stereo microscope Leica® MZ9.5 fitted with camera lucida, using data from the literature for identification (World Spider Catalog 2022). Identification was carried out by the first author. Spiders were deposited in the Museu de Ciências Naturais, Rio Grande do Sul, Porto Alegre, Brazil (curator: R. Ott).

**Abiotic data.**—We obtained minimum and maximum daily temperatures (°C) and daily rainfall (mm) of the five days prior to each sample for each basin, employing the mean to generate a single point. We thus aim to represent the environment in the period immediately before sampling, and not the general climate of the site. Abiotic data for Piratini, Camaquã, and Sinos rivers were supplied by the “8° Distrito de Meteorologia” (8° DISME) of “Instituto Nacional de Meteorologia” (INMET) and for Maquiné river the information was obtained from “Centro de Meteorologia Aplicada” of “Fundação Estadual de Pesquisa Agropecuária” (FEPA-GRO), both in Porto Alegre, Brazil.

**Data analysis.**—We investigated differences among seasons for three alpha diversity variables: (1) adult spider abundance, (2) young (juvenile) spider abundance and (3) species richness using a generalized linear model (GLMs). Continuous factors were the abiotic environmental conditions: (1) precipitation, (2) maximum temperature and (3) minimum temperature; categorical factors were: (1) year of sampling (2007–2008 and 2008–2009), (2) river basin (4 levels) and (3) seasons (also 4 levels: winter, spring, summer, and autumn). As we are focusing on seasonality effects, year and river basin are block variables and are interpreted only in interaction with the combined season–river basin variable. This is because the river basins are situated in slightly different climates, which may also indicate indirect abiotic effects. In cases of significance among seasons, separate ANOVA tests were employed to differentiate

Table 1.—Multivariate general linear model for different abiotic factors (precipitation, temperature, year, seasons, rivers) influencing spider diversity variables: abundance (N; adults, juveniles) and species richness (Species) (bold type indicates significant relationships).

Explanatory Variable	df	N (adults)			N (juveniles)			Species		
		Mean Square	F	P	Mean Square	F	P	Mean Square	F	P
Season	3	1,858.08	2.32	0.096	278,401.48	26.46	<0.001	526.78	11.04	<0.001
Rainfall	1	9.44	0.01	0.914	2,522.79	0.24	0.628	46.77	0.98	0.330
Temper_min	1	401.59	0.50	0.485	14,667.65	1.39	0.247	47.98	1.02	0.324
Temper_max	1	632.04	0.79	0.382	6,190.27	0.59	0.449	13.69	0.29	0.596
River (block)	3	22,623.83	28.21	<0.001	45,732.46	4.35	0.012	220.21	4.62	0.009
Year (block)	1	329.33	0.41	0.527	47,268.90	4.49	0.043	20.84	0.44	0.514
River * year	3	1,317.75	1.64	0.201	738.57	0.07	0.975	1.61	0.03	0.991
River * season	9	4,082.60	5.09	<0.001	24,824.39	2.36	0.039	27.54	0.58	0.804
Year * season	3	1,008.09	1.26	0.307	26,246.27	2.49	0.080	24.29	0.51	0.679
River * year * season	9	317.62	0.40	0.927	7,184.95	0.68	0.718	50.02	1.05	0.428

which ones differed; tests were developed using the statistical analysis software PASW18.0 (SPSS®).

To test for statistical differences in spider composition (beta diversity) among sampling years, we used a one-way analysis of similarity (ANOSIM; with Bonferroni correction for repeated tests) (Clarke & Warwick 1994). To test for statistical differences in spider composition among seasons, we used a permutational multivariate analysis of variance (PERMANOVA; 9999 permutations) using season as explanatory variable and river basin as blocking factor. To determine whether there is distinct overlap in spider species composition among seasons, we compared the variation in the dissimilarity of the composition of spider assemblages in each season with the PERMDISP approach (Anderson et al. 2006). In specific, we used the *betadisper* function to test the null hypothesis of absence of differences in multivariate dispersion among seasons by calculating a F-statistic to compare the average distance of each sample to the centroid of the corresponding group, i.e., season (9999 permutations) (Anderson et al. 2006). To illustrate patterns in species composition among seasons and river basins, we used ordination diagrams based on non-metric multidimensional scaling (NMDS). For the ANOSIM, NMDS, PERMANOVA and PERMDISP, we employed as response dataset a resemblance matrix of spider composition, based on the Bray-Curtis (quantitative) dissimilarity index. The ANOSIM analyses was carried out in the PAST software (Paleontological Statistics - 4.0.1, Hammer et al. 2001). The NMDS, PERMANOVA and PERMDISP analyses were carried out in the R software (R Core Team 2019).

## RESULTS

A total of 42,057 spiders were sampled over the two years, 8,851 of these adults (21%) and 33,206 juveniles (79%). Overall (juveniles and adults), the highest absolute abundance was recorded in autumn ( $n = 12,969$ ) and the lowest in spring (8,241) (See supplementary Table S1, online at <https://doi.org/10.1636/JoA-S-21-049.1>). Table 1 presents the results for the GLMs for each of the three alpha diversity variables. For adult spiders, there were no significant differences among seasons for abundance (Fig. 1a). The abundance of juvenile spiders, however, differed among seasons with significantly lower abundance in winter and spring compared to the two

other seasons (ANOVA significances found between winter and summer ( $F = 9.09$ ;  $P = 0.02$ ) and winter and autumn ( $F = 26.89$ ;  $P = 0.002$ ), between spring and summer ( $F = 11.52$ ;  $P = 0.01$ ) and spring and autumn ( $F = 26.55$ ;  $P = 0.002$ ), Fig. 1b).

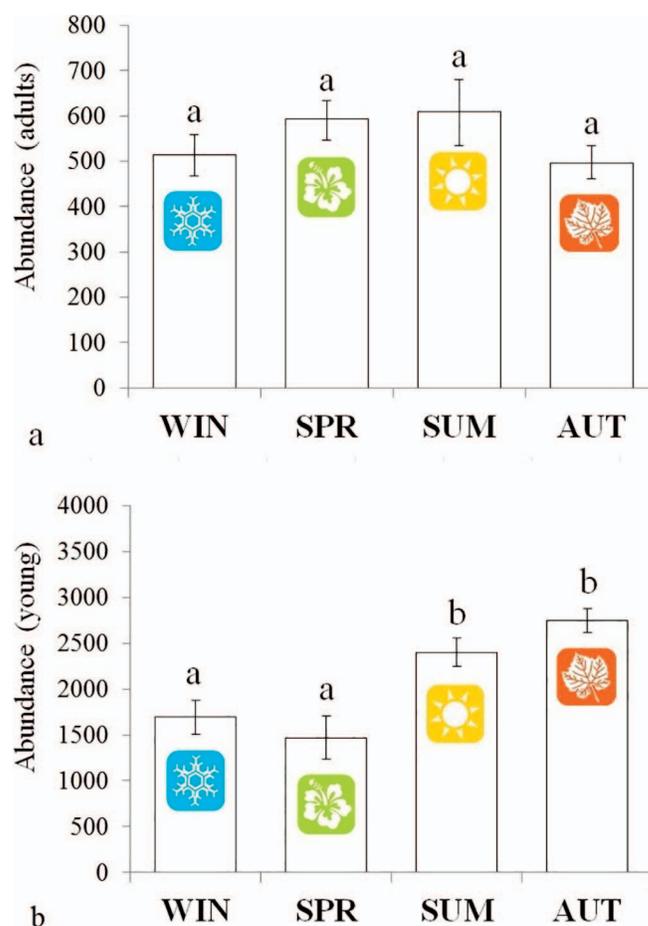


Figure 1.—Average abundance ( $\pm$ SE) of spiders during seasons for two years of sampling in riparian forests. a, Abundance of adult spiders. b, Young-juveniles (WIN, winter; SPR, spring; SUM, summer; AUT, autumn) (different letters above columns indicate significant differences).

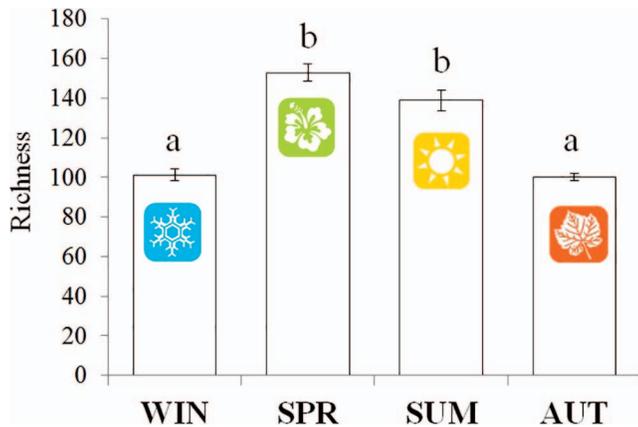


Figure 2.—Average richness ( $\pm$ SE) of spiders during seasons for two years of sampling in riparian forests (WIN, winter; SPR, spring; SUM, summer; AUT, autumn) (different letters above columns indicate significant differences).

The significance found for the interaction between seasons and river basins (Table 1), both for the abundance of adult spiders and for juveniles, points to differing seasonality patterns along the climatic gradient. Adult spiders were more abundant in summer in riparian forests of the Piratini, Camaquã and Sinos rivers basins, but in Maquiné (the northernmost basin) they occurred more in winter. Juvenile spiders were more abundant during the autumn for riparian forests of the Piratini, Camaquã and Maquiné rivers, with only the forest on the Sinos river (the driest basin) having more juveniles in the summer. There were no differences in seasonality between the two years of sampling, as indicated by the interaction between these two factors in the GLM (Table 1). Also, the three-way interactions among seasons, rivers and years were not significant for any diversity variable.

A total of 440 spider species were sampled, of which only 16 were recorded in all samples (See supplementary, Table S2, online at <https://doi.org/10.1636/JoA-S-21-049.1>). Over the two years, 46 species (10.5% of the sampled total) were recorded in all seasons. A total of 177 unique species from each season were found, most for spring (79) and fewest for autumn (20).

Spider species richness varied significantly with season and was higher in spring and summer but lower in autumn and winter (Table 1, Fig. 2), revealing a pattern similar in general shape with adult spider abundance (although the latter was not significant). There were significant differences for species richness between winter and summer (ANOVA,  $F = 37.04$ ;  $P = 0.0008$ ); winter and spring ( $F = 91.06$ ;  $P = 0.0007$ ); autumn and spring ( $F = 119$ ;  $P = 0.0003$ ); autumn and summer ( $F = 46.38$ ;  $P = 0.0004$ ). Species richness varied significantly among river basins but not between the two years of sampling. There was no significant interaction between seasons and river basins for species richness (Table 1), so seasonality patterns in this diversity variable appear similar across the climatic gradient. The species richness peaks (See supplementary Fig. S2, online at <https://doi.org/10.1636/JoA-S-21-049.1>) coincide with declines in the abundance curves of juvenile spiders (for all riparian forests, see See supplementary Fig. S1, online at

<https://doi.org/10.1636/JoA-S-21-049.1>), especially in spring, for both sampling years.

No relationship was found between abiotic factors and the araneofauna. Apparently, neither temperature (max or min) nor precipitation directly influence araneofauna abundance captures (or species richness) in these riparian forests (Table 1). It is important to remember that since we included season as a factor on the analysis as well, this test would only reveal effects of these abiotic factors isolated from the seasonality effects themselves. When season is dropped from the model, a positive relationship between spider abundance and minimum temperature is indeed found (Table 1).

Species composition did not differ between the first and second year of sampling (ANOSIM, Bray-Curtis:  $R = -0.081$ ;  $P = 0.818$ ). However, spider composition was significantly different among seasons (Seasons: PERMANOVA Pseudo- $F = 2.26$ ;  $R^2 = 0.176$ ;  $P = 0.005$ ) and river basins (River basins: PERMANOVA Pseudo- $F = 8.001$ ;  $R^2 = 0.603$ ;  $P = 0.001$ ). The first axis of the NMDS ordination diagram summarized the variation in spider composition over the seasons, segregating samples of colder seasons (autumn and winter) from warmer ones (summer and spring) (Fig. 3) and a segregation of spider composition among river basins (Fig. 3). The PERMDISP approach did not detect significant differences in the variation of spider composition among seasons ( $F = 0.156$ ;  $P = 0.92$ ; Fig. 4).

Some species had particular seasonal patterns, being found mostly in one season of the year—for example, the theridiid *Theridion calcynatum* Holmberg, 1876, the araneid *Mangora strenua* (Keyserling, 1893) and the salticid *Cotinusa trifasciata* (Mello-Leitão, 1943) found mostly in summer, but the theridiid *Thymoites promatensis* Lise & Silva, 2009 primarily in winter and the theridiid *Phoroncidia reimoseri* Levi, 1964 primarily in spring. The most abundant species, *Sphecozone personata* (Simon, 1894) (Liniphiidae), was present throughout the year but peaked during fall and winter, as did *Hetschkia gracilis* Keyserling, 1886 (Theridiidae).

Of the adult spiders sampled 5,381 were female (61%) and 3,470 were male (39%). There was a predominance of females in both years of sampling. Males were collected more in spring ( $n = 920$ ; 26.5%) and less in autumn (806; 23.2%), while females predominated in summer ( $n = 1,575$ ; 29.3%) and were less sampled in winter (1,173; 21.8%).

## DISCUSSION

Environmental seasonality is a factor shaping spider diversity in this subtropical region. We corroborated our expectations that spiders would be seasonal, recording the greatest spider abundances in the autumn and the least in spring. However, these values did not corroborate our expectation that higher temperatures would lead to greater abundances. According to Dias et al. (2006) seasonality patterns of spider communities change according to the type and physiognomy of the forest. Rodrigues (2005) found that for a 'restinga' (sandy soil coastal) forest in southern Rio Grande do Sul, a greater abundance of spiders (both young and adult) existed in summer and a smaller abundance in spring. Indrusiak & Kotzian (1998) studied araneofauna in hillside forests in the central region of this same Brazilian State found more spiders in winter and fewer in spring. For different

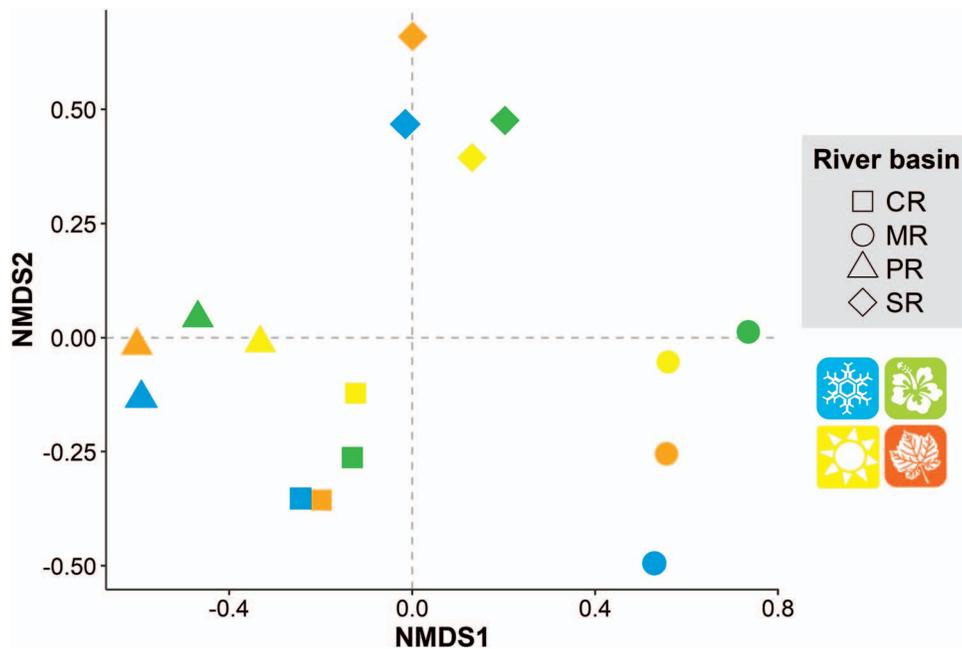


Figure 3.—Non-metric multidimensional scaling (NMDS) ordination diagrams showing the dissimilarity in species composition of the spider fauna among seasons (blue, winter; green, spring; yellow, summer; orange, autumn) and river basins (PR, Piratini River; CR, Camaquã River; SR, Sinos River; MR, Maquiné River).

regions in southern Brazil and in environments other than the ones evaluated here, seasonality patterns for spider assemblages seem to vary and no discernible universal pattern has been found except for the suggestion of lower spider numbers in spring, which our data seem to corroborate.

As hypothesized, a clear distinction in spider seasonality patterns occurs between ontogenetic levels. Adult spiders were

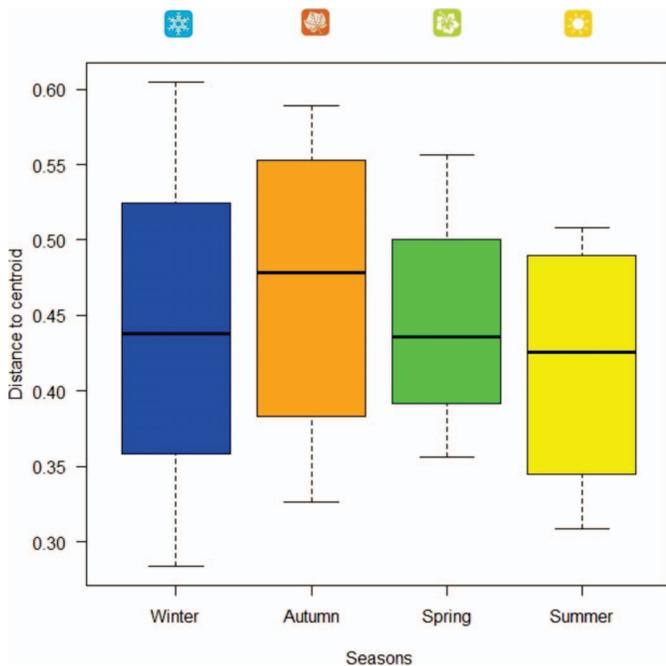


Figure 4.—Boxplots of the distance to centroids of spider species composition among seasons in subtropical riparian forests.

not clearly seasonal, although with a marked peak, a little more abundant in summer and numbers dropping in autumn consistently for the two years of sampling. Podgaiski et al. (2007) reported more adult spiders in spring than autumn in another forest ecosystem, a Deciduous Seasonal Forest in southern Brazil. In contrast, Rinaldi & Trinca (2008) recorded higher abundance of adult spiders in summer and fewer individuals in spring for the Cerrado in southeastern Brazil. The works of these latter authors suggest that at lower temperatures, there is a reduction in the number of prey and consequent reduction in the abundance of spiders. Even with summer and winter in southern Brazil often being seasons with harsher temperatures (hot and cold), riparian forests (due to their vegetation structure and proximity to a water body) can probably provide more shelter and soften these rigors, thus contributing to a more-or-less constant abundance of spiders all year round. Although in warm seasons, there is a tendency for insect populations to increase (Wolda 1988) and spiders to tend to increase their numbers when higher insect abundances occur (Arango et al. 2000; Romero & Vasconcellos-Neto 2003), this evaluation is lacking presently for the subtropical riparian forests studied. This leaves open the question of how much prey abundance and diversity could affect spider seasonal patterns, perhaps a question to be pursued in more detail in the future.

In Rio Grande do Sul there are very characteristic climatic variations in each region of the state (IPAGRO 1989). Each of our study areas possesses a different climate type (Maluf 2000). These variations in climate types are likely to directly and/or indirectly influence the fauna associated with these locations, resulting in divergences in the communities sampled. Thus, seasonality was found to differ among riparian forest basins, which may be related to the divergent climatic types of each forest, such as seasons with differing rigors for

each location. In more severe environments, seasonality may more strongly influence the structuring of spider communities; in the Northern Hemisphere, for example, the pattern of temperature-dependent activity of spiders is widely known (Schaefer 1977, 1987). We already explored vegetation structure effects and they seemed to be relatively unimportant for these spiders in these riparian forests (Rodrigues & Mendonça 2012; Rodrigues et al. 2014). More subtle questions may be at play, such as biogeographic effects—southern sites are in the Pampa biome, but more northern sites are progressively more inside the Atlantic Forest biome.

Species richness also showed variation over the seasons, with higher density for spring and lower for autumn. A larger species richness in spring may be linked to higher prey supply and mild temperatures this season, keeping in mind that spider identification depends on adult spider sampling, and thus species richness is linked more strongly to adult abundance, which is not seasonal as shown here. Podgajski et al. (2007) also recorded more spider species in spring, similar to our results, and Baldissera et al. (2004) found higher richness and abundance in spring and lower values in winter for a region of southern Brazil with very severe winters. Avalos et al. (2007) reported highest species richness in spring in forests studied in Argentina. However, in Atlantic Forest fragments in northeastern Brazil, Dias et al. (2006) found no differences in species richness between seasons, demonstrating that along different latitudes, there may be variations in seasonality patterns for spiders.

Spiders are considered very sensitive to variations in abiotic conditions (Pitilin et al. 2019; Baldissera et al. 2020). However, we failed to find a clear pattern between spider diversity and abiotic conditions such as extreme (max and min) temperatures and rainfall. We already mentioned that our statistical treatment has hidden the direct effect of an abiotic factors (min temperature) by including season as a categorical factor. Arango et al. (2000) found that with the increase of rainfall, there is an increase in the number of insects and successively higher numbers of spiders. Precipitation in our case did not seem to influence the abundance of spiders, but again, the relationship with spider prey has not been evaluated. In the Pantanal and the Amazon, seasonality leads to periodic flooding and can have significant effects on the structure of riparian forest spider communities (Castilho et al. 2005; Raizer et al. 2005). However, we did not record floods or any evidence of them during the two years of work in our sampling sites, and in this case, it would be the river flooding that would affect communities, leading to migrations between different strata (Castilho et al. 2005), not the rain itself.

Our hypothesis of distinct spider communities during different seasons was confirmed: species composition differed between colder (autumn and winter) and warmer seasons (spring and summer). The latter are typified as having lower temperatures, as well as increased winds, which can interfere especially with weaver spiders (Baldissera et al. 2004). In another study in Southern Brazil, species composition also differed between the warmest and coldest months (Pitilin et al. 2019). Several other factors along the seasons, as discussed above for abundance and species richness, may be leading to differences in the composition of the spider fauna. Avalos et al. (2007) in forests of Argentina, found that the composition

of spider species from contrasting sites is related to microclimate conditions, reflecting a specific araneofauna for each set of abiotic factors. In this context, in this study, the effect of river basins was stronger than seasons to structure spider composition, suggesting that specific factors associated with the identity of each riparian forest also play important role to structure spider composition in subtropical regions. Our results are similar to those of Baldissera et al. (2020), who found that spider richness, abundance, and functional richness were affected by the season and species composition also differed among the study areas depending on the season.

*Sphecozone personata* was the most abundant species, with high prevalence in winter and autumn. The family Linyphiidae, to which *S. personata* belongs, is known for its diversity in the Northern Hemisphere and for maturing and reproducing during winter months (Schaefer 1977, 1987; Buddle & Draney 2004). Additionally, *S. personata* was sampled almost exclusively in the Maquiné River riparian forest, appearing to prefer the milder temperature in this region, also strongly influenced by the Atlantic Forest (Sevegnani & Baptista 1996). Importantly, for many spider species in the Neotropics and most species in riparian forests, no basic phenology information is known. On this matter, although most species show seasonal patterns of occurrence, their variable abundance peaks over the seasons could have explained the similar levels of dissimilarity in spider composition in each season. However, to complement phenological data presented here for the tree-shrub stratum, it would be interesting to apply other sampling methods, for example investigating whether a vertical migration by spiders could occur for seasons during which they are less recorded (Castilho et al. 2005). Campuzano et al. (2019) demonstrated that seasonal patterns of spider assemblages can vary between different strata in the forest for tropical rainforests in Mexico, but this question remains open for subtropical and temperate forests as sampled here.

We suggest future research for rapid fauna assessment in areas similar to the ones sampled here could focus on warmer months, given spring and summer sport the highest species richness, although adults, who allow identification to species level, are present year-round. A potentially efficient indicator group may be the Theridiidae family, which was well represented in this study and seems to be predominant in the tree-shrub strata throughout all seasons of the year. In the future, further studies may shed light on whether other abiotic factors, such as air humidity or evapotranspiration, and biotic factors, such as potential spider prey, exert a degree of influence on this araneofauna more specifically. This study represents only a first step in understanding the seasonal changes in spider diversity in subtropical riparian forests and provides a baseline for future work. Future studies that evaluate additional variables may be necessary to identify additional mechanisms that determine the seasonal changes of the spider communities in riparian forest.

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#### SUPPLEMENTAL MATERIALS

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Figure S1.— Average spider abundance variables in seasons for two years of sampling in riparian forests.

Figure S2.— Average spider richness variables in seasons for two years of sampling in riparian forests.

Table S1.— Spider abundance (N) and species richness (S) of spiders during seasons for two years of sampling in riparian forests.

Table S2.— Species/morphospecies list for spiders sampled in the 16 samples over four seasons of the year in riparian forests in southern Brazil.

#### LITERATURE CITED

- Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- Arango AM, Rico-Gray V, Parra-Tabla V. 2000. Population structure, seasonality, and habitat use by the green lynx spider *Peucetia viridians* (Oxyopidae) inhabiting *Cnidoscolus aconitifolius* (Euphorbiaceae). *Journal of Arachnology* 28:185–194.
- Avalos G, Rubio GD, Bar ME, González A. 2007. Arañas (Arachnida: Araneae) asociadas a dos bosques degradados Del Chaco húmedo en Corrientes, Argentina. *Revista de Biología Tropical* 55:899–909.
- Baldissera R, Ganade G, Brescovit AD, Hartz SM. 2008. Landscape mosaic of *Araucaria* forest and forest monoculture influencing understory spider assemblages in southern Brazil. *Austral Ecology* 33:45–54.
- Baldissera R, Ganade G, Fontoura SB. 2004. Web spider community response along an edge between pasture and *Araucaria* forest. *Biological Conservation* 118:403–409.
- Baldissera R, Quadros SO, Galetti G, Rodrigues ENL, Lazzarotto LMV, Oliveira AD. 2020. Spider assemblage structure and functional diversity patterns in clear-cut, logged, and undisturbed areas in a large Atlantic Forest remnant. *Canadian Journal of Forest Research* 50(7):1–7. [dx.doi.org/10.1139/cjfr-2019-0302](https://doi.org/10.1139/cjfr-2019-0302)
- Buddle CM, Draney ML. 2004. Phenology of linyphiids in an old-growth deciduous forest in central Alberta, Canada. *Journal of Arachnology* 32:221–230.
- Campuzano EF, Ibarra-Núñez G, Machkour-M'Rabet S, Moron-Rios A, Jimenez ML. 2019. Diversity and seasonal variation of ground and understory spiders from a tropical mountain cloud forest. *Insect Science* 27(4):1–19. DOI: 10.1111/1744-7917.12693
- Castilho ACC, Marques MI, Adis J, Brescovit AD. 2005. Distribuição sazonal e vertical de Araneae em área com predomínio de *Attalea phalerata* Mart. (Arecaceae), no Pantanal de Poconé, Mato Grosso, Brasil. *Amazoniana* 18:215–239.
- Clarke KR, Warwick RM. 1994. Change in Marine Communities. UK, National Research Council.
- Coddington JA, Young LH, Coyle FA. 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 SC, Brescovit AD, Couto ECG, Martins CF. 2006. Species richness and seasonality of spiders (Arachnida, Araneae) in an urban Atlantic Forest fragment in northeastern Brazil. *Urban Ecosystems* 9:323–335.
- Hammer Ø, Harper DA, Ryan PD. 2001. PAST. Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1):1–9.
- Hatley CL, Macmahon JA. 1980. Spider community organization: Seasonal variation and the role of vegetation architecture. *Environmental Entomology* 9:632–639.
- Indrusiak LF, Kotzian CB. 1998. Inventário das aranhas arborícolas de três regiões de Santa Maria, RS, Brasil. *Ciência Natura* 20:187–214.
- IPAGRO. 1989. Atlas agroclimático do estado do Rio Grande do Sul. Porto Alegre, Secretaria da Agricultura e Abastecimento, v.1. 102 p.
- Maluf JRT. 2000. Nova classificação climática do Estado do Rio Grande do Sul. *Revista Brasileira de Agrometeorologia* 8:141–150.
- New TR. 1999. Untangling the web: spiders and the challenges of invertebrates conservation. *Journal of Insect Conservation* 3:253–258.
- Oliveira AAB, Ribeiro AG. 1986. Climatologia. Pp.757–776. In Levantamento de Recursos Naturais, v.33. IBGE, Rio de Janeiro.
- Pitilin RB, Buschini MLT, Brescovit AD, Prado-Junior J. 2019. Climatic conditions drive the abundance and diversity of spiders community in an Atlantic Forest fragment. *Oecologia Australis* 23:39–55. DOI <https://doi.org/10.4257/oeco.2019.2301.04>
- Podgaiski LR, Ott R, Rodrigues ENL, Buckup EH, Marques MAL. 2007. Araneofauna (Arachnida; Araneae) do Parque Estadual do Turvo, Rio Grande do Sul, Brasil. *Biota Neotropica* 7(2): <https://doi.org/10.1590/S1676-06032007000200023>
- R Core Team. 2019. R: A Language and Environment for Statistical Computing.
- Raizer J, Japyassú HF, Indicatti RP, Brescovit AD. 2005. Comunidade de aranhas (Arachnida, Araneae) do pantanal norte (Mato Grosso, Brasil) e sua similaridade com a araneofauna amazônica. *Biota Neotropica* 5(1): <https://doi.org/10.1590/S1676-06032005000200011>
- Rinaldi IMP, Trinca LA. 2008. Spider assemblages in widely-separated patches of cerrado in São Paulo State, Brazil. *Acta Biológica Paranaense* 37:165–180.
- Rodrigues ENL. 2005. Fauna araneológica (Arachnida; Araneae) arborícola de duas áreas em uma mata de restinga no sul do Brasil. *Acta Biológica Leopoldensia* 27:73–92.
- Rodrigues ENL, Mendonça M de S, Jr. 2012. Spider guilds in the tree-shrub strata of riparian forests in southern Brazil. *Journal of Arachnology* 40:39–47. doi: 10.1636/P10-105.1
- Rodrigues ENL, Mendonça M de S, Jr., Costa-Schmidt LE. 2014. Spider diversity responds strongly to edge effects but weakly to vegetation structure in riparian forests of Southern Brazil. *Arthropod Plant Interactions* 8:123–133. doi: 10.1007/s11829-014-9294-3
- Rodrigues RR, Leitão-Filho HF. 2000. Matas Ciliares: Conservação e Recuperação. EDUSP/FAPESP. São Paulo.
- Romero GQ, Vasconcelos-Neto J. 2003. Natural history of *Misumenops argenteus* (Thomisidae): seasonality and diet on *Trichogoniopsis adenantha* (Asteraceae). *Journal of Arachnology* 31:297–304.

- Schaefer M. 1977. Winter ecology of spiders (Araneida). *Zeitschrift für angewandte Entomologie* 83:113–134.
- Schaefer M. 1987. Life cycles and diapause. Pp. 331–347. *In* Ecophysiology of Spiders. (Nentwig W, ed.) Springer-Verlag, Berlin.
- Sevegnani L, Baptista LRM. 1996. Composição florística de uma floresta secundária, no âmbito da Floresta Atlântica, Maquiné, RS. *Sellowia* 45–48:47–71.
- Sørensen LL, Coddington JA, Scharff N. 2002. Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afromontane Forest. *Environmental Entomology* 31:319–330.
- Uetz GW. 1991. Habitat structure and spider foraging. Pp. 325–348. *In* Habitat Structure: the Physical Arrangement of Objects in Space. (Bell SS, McCoy ED, Mushinsky HR eds.). Chapman and Hall Press, London. DOI:10.1007/978-94-011-3076-9
- Wolda H. 1988. Insect seasonality: Why? *Annual Review of Ecology, Evolution, and Systematics* 19:1–18.
- World Spider Catalog. 2022. World Spider Catalog. Version 23.0. Natural History Museum Bern. Online at <http://wsc.nmbe.ch> Accessed on 12 January 2022. doi: 10.24436/2
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