2016. Journal of Arachnology 44:36–45

The effects of habitat size and quality on the orb-weaving spider guild (Arachnida: Araneae) in an Atlantic Forest fragmented landscape

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Abstract. Fragmentation of natural habitats is considered one of the greatest threats to the maintenance of global biodiversity. In this study, we tested the importance of forest patch size and vegetation structure on the richness, diversity, abundance, and composition of the orb-weaving spider guild in an area of the Atlantic Forest (State of São Paulo, Brazil). We sampled 16 sites, grouped into the following categories composed of four sites each: continuous mature forest, continuous secondary forest, large (52–175 ha) secondary forest fragments, and small secondary forest fragments (14–28 ha). The richness ranged from 29 to 55 species per site, but was unrelated to forest size or vegetation structure. The communities from the continuous mature forests were more abundant and less diverse than those from the other categories, but this was due to a few dominant species. The changes in composition were related to the vegetation structure, suggesting that this variable is more important to the composition of orb-weaving communities than the size of the forest patch. Overall, the results indicate that the orb-weaving spider community in this region, even in the fragments, is still rich and diverse, which may be attributable to some characteristics of spiders, such as generalist behaviour and a good dispersal capacity. Nonetheless, our results also highlight the importance of continuous areas, especially those with mature vegetation that harbor a characteristic orb-weaving community that can serve as a source for the fragments.

Keywords: Araneidae, biodiversity, bioindicator, fragmentation, habitat loss, orb-weavers

The destruction of natural habitats is considered the main factor responsible for the biodiversity crisis (Dirzo & Raven 2003), and a common consequence of those human-induced changes are fragmented landscapes with forest remnant patches inserted into a deforested matrix. The biodiversity crisis is especially critical in the tropics due to the alarming rate of land clearing and the fact that tropical forests are the most species-rich terrestrial biome (Laurance 2007).

The two main impacts of fragmentation are habitat loss and alteration of the forest remnants (Fahrig 2003; Laurance et al. 2011), as the vegetation in forest fragments is usually more degraded than that of larger forested areas. Because of their larger edge to core habitat ratio, fragments are more exposed to edge effects (Murcia 1995) and are more vulnerable to other anthropogenic disturbances, such as logging, hunting, grazing, and fires (Laurance et al. 2011). Forest fragments may also consist of secondary vegetation simply because they can be formed through natural re-growth after the clearing and abandonment of the land.

Most of the knowledge on this subject was originally based on vertebrate groups (Turner 1996; Zuidema et al. 1996), but attention to invertebrate communities in fragments has been increasing, with a particular focus on insect taxa (Didham et al. 1996; Tscharntke et al. 2002; Nichols et al. 2007). Most recently, spiders have also been investigated. The majority of work has been aimed at assessing the effects of patch size on community richness (Abensperg-Traun et al. 1996; Miyashita et al. 1998; Bolger et al. 2000; Gibb & Hochuli 2002; Floren & Deeleman-Rheinold 2005; Major et al. 2006; Kapoor 2008), a common research subject, because it represents a direct measure of the impact of habitat loss on diversity (Debinski & Holt 2000).

The richness of spider communities is not usually related to patch size, but positive (Abensperg-Traun et al. 1996; Miyashita et al. 1998) or even negative (Bolger et al. 2000) relationships have been reported, suggesting a complex response. Vegetation quality is another factor that may have a significant influence on spider communities. The characteristics of the vegetation, especially its spatial structure, are among the most important factors for spider communities (Wise 1993; Malumbres-Olarte et al. 2013), and communities from diverse forest types may differ in richness (Pinkus-Rendón et al. 2006; Lo-Man-Hung et al. 2008) and, more frequently, in composition (Chen & Tso 2004; Floren & Deeleman-Rheinold 2005; Cabra-Garcia et al. 2010; Raub et al. 2014).

Some of the studies that investigated the effects of patch size on spider communities also verified the effects of the vegetation structure, but those factors have never been tested independently. For example, Kapoor (2008) reported differences in the composition of spider communities from larger and smaller fragments, but the former also had more preserved vegetation than the latter. A similar situation was found by Gibb & Hochuli (2002) in a study with large and small fragments under different disturbance regimes.

Our aim was to assess the importance of patch size and vegetation structure on the richness, diversity, abundance, and community composition of orb-weaving spiders by comparing the fauna of four different categories of habitats: continuous mature forest, continuous secondary forest, and large and small fragments of secondary forest. The use of spider communities in ecological studies is recommended due to their diversity and abundance, as well as for their unquestionable ecological importance as top predators among the invertebrates (Coddington et al. 1991; New 1999; Gerlach et al. 2013). Like all web-building spiders, orb-weaving spiders also seem to be particularly sensitive to vegetation structure, because the availability of attachment points for webs is considered one of the most important resources for these groups (Wise 1993).

This study was conducted in a fragmented Atlantic Forest landscape. This biome occupies a large area on the coast of eastern Brazil (5–30°S). It is considered a biodiversity hotspot (Myers 1988; perhaps even the "hottest" according to Laurance 2009) because it combines high levels of biological richness and endemism with equally high levels of deforestation and human threat. Currently, only about 12% of the forest remains, and more than 83% of the remnants are composed of small fragments (< 50 ha; Ribeiro et al. 2009) that are still under heavy anthropic pressure because the ecosystem is located on the Brazilian east coast, the most developed and densely populated region of the country. Thus, the Atlantic Forest unfortunately represents a very good example of a fragmented ecosystem, and the study of the impact of this process over its biological communities is urgent and of fundamental importance.

METHODS

Study area.—Our sampling sites were located in the Reserva Florestal do Morro Grande (RFMG), a forest reserve, and in nearby forest fragments in the municipalities of Cotia and Ibiúna (State of São Paulo, Brazil; 23° 35′ S to 23° 50′ S; 46° 45′ W to 47° 15′ W). The RFMG covers 10,000 ha, but it is connected with other large forested areas at its southern edge, and together they are considered a continuous area. The altitude varies from 850 to 1,100 meters above sea level, and the natural vegetation is classified as 'montane ombrofilous forest' (Veloso et al. 1991). Its climate (Köppen climate classification: Cwa; Köppen 1948) is subtropical, characterized by a dry winter (mean temperature < 18° C) and a warm, rainy summer (mean temperature > 22° C).

We selected sixteen sampling sites, eight within the RFMG and eight forest fragments (Fig. 1). Four sites in the RFMG were composed of secondary vegetation at an intermediate to advanced stage of regeneration (Metzger et al. 2006), and four had mature vegetation. The fragments were also composed of secondary vegetation at an intermediate/advanced stage of regeneration (Uezu et al. 2005). The sites were divided into four categories (Table 1): continuous mature forest (hereafter called CM 1 to 4), continuous secondary forest (CS 1 to 4), large fragments (LF 1 to 4; 52–175 ha), and small fragments (SF 1 to 4; 14–28 ha). The average distance between one site and its nearest surveyed neighbor was 1561 m (SD = 474 m, range = 864–2395 m) and did not differ among the habitat categories (ANOVA, $F_{3,12} = 0.3$, $P = 0.842$). The entire landscape area, including all of the sampling sites, will be referred to as Caucaia, the popular name of that region.

Sampling.—We captured the spiders by manual nocturnal sampling and preserved them in 70% ethanol. We searched in logs, vegetation, and several other microhabitats in the soil and understory, from the leaf litter up to 2 m high. In all areas, we sampled for one hour along a 30 m long transect oriented perpendicularly to a main trail, always located at least 50 m from the forest edge, and 30 m from other transects. We sampled each of the 16 sites for two nights, one in December 2002, and one in March 2003. Sampling teams were composed of four collectors, each of whom investigated three transects per night for totals of 24 transects per site and 384 transects for all sites combined.

Voucher specimens were deposited in the Museu de Zoologia and the Laboratório de Artrópodes do Instituto Butantan. Immature individuals were discarded, while the adults were separated into morphospecies and identified to the lowest possible level. Thus, all of the results and analyses concern only adult individuals.

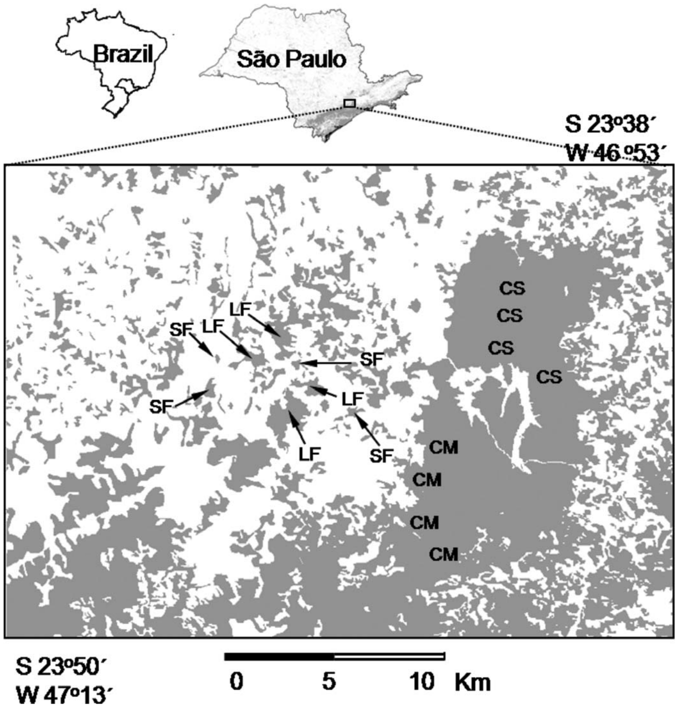

Figure 1.—Location and map of the study area. Forested areas are highlighted in grey, and the eight fragments sampled are indicated by arrows. CM, continuous mature sites; CS, continuous secondary forest sites; LF, large fragments; and SF, small fragments.

Forest characterization.—We described the forest structure by measuring the foliage density and stratification, which are good indicators of the tropical forest regeneration stage (DeWalt et al. 2003) and level of forest disturbance (Malcolm 1994). We used a modification of the method described in

Table 1.—The richness, abundance, diversity index exp(H′) and rarefied richness (Sraref) for the orb-weaving spider communities investigated in December 2002 and March 2003. The size (ha) of the fragments is in parentheses. CM, continuous mature sites; CS, continuous secondary forest sites, LF, large fragments; SF, small fragments; and exp(H′), exponential of the Shannon index (H′).

Sites	Richness	Abundance	exp(H′)	Sraref
CM 1	50	311	23.10	30.55
CM 2	44	256	21.13	27.90
CM 3	40	309	13.69	23.44
CM 4	35	266	13.23	22.12
CS 1	41	189	22.42	29.44
CS 2	49	216	31.34	34.55
CS 3	54	165	31.81	38.32
CS 4	46	205	33.11	36.16
LF 1 (52.2)	45	152	30.66	35.66
LF 2 (175.1)	48	153	32.56	37.23
LF 3 (53.1)	29	88	19.12	29
LF 4 (99.4)	31	128	18.19	27.51
SF 1 (14.1)	37	133	20.76	30.41
SF 2 (18.7)	49	249	21.84	29.47
SF 3 (28.8)	38	126	24.93	32.45
SF 4 (14.1)	38	202	16.74	25.81

Malcolm (1995). At each site, we established two parallel 165-m long lines separated by 20 m. Each line comprised 12 stations, one every 15 m. At each station, a 4-m pole was used to establish an imaginary 150-mm diameter vertical column. We used a telemeter to measure the height of the inferior and superior limits of all foliage that stretched along the imaginary column to calculate the length in meters occupied by the foliage in five strata (0–1, 1–5, 5–10, 10–15, >15 m). For each site, we calculated the mean foliage length in each stratum for the 24 sampling stations. For a more detailed description of this method, see Pardini et al. (2005).

Data analysis.—We calculated the richness and abundance at each of the 16 sampled sites. To minimize the differences in richness due to differences in the numbers of individuals, two diversity measures were also used, the rarefied richness (Sraref) and the exponential of the Shannon index [exp(H′); Jost 2006]. We also calculated the proportion of singletons (species represented by just one individual) for each site. A one-way ANOVA was used to test for differences in these parameters between the four habitat categories, and a Tukey test was employed when significant differences were detected. When there was no homogeneity of variances, we performed a Kruskal-Wallis test, with rank-transformed data.

Simple linear regression analysis was used to test the influence of the vegetation structure on the richness, diversity, proportion of singletons, abundance, the abundance of three dominant species, and the abundance of the community excluding those dominant species. To treat the vegetation structure as a continuous variable, we performed a Principal components analysis (PCA) (Fig. 2) using the foliage density measures for the five strata in the 16 sites in a correlation matrix (centered and standardized per species) using the package CANOCO for Windows 4.0 (ter Braak & Smilauer 1998). The first axis explained 54.8% of the variation and formed a gradient in which the lower values represented the sites with a taller canopy and more opened understory, characteristics of mature vegetation, while the higher values represented areas with the opposite characteristics. The scores from the first axis were used to perform the regressions.

We treated patch size as a categorical variable, with three levels: continuous area, large fragments, and small fragments. To measure the effect of patch size independently from that of the vegetation, we used the residuals of the regressions performed with the vegetation structure and the same community parameters cited above. To compare the categories, we performed two *t*-tests utilizing the orthogonal contrast procedure (Montgomery 2001). This procedure allows choosing a number of comparisons (k; contrasts) equal to the number of categories minus 1 (in this case, there are 3 categories, and k = 2). The total variance is partitioned among the contrasts, which are thus independent and do not increase the probability of a type-1 error. The first *t*-test compared the eight continuous areas (those located in the continuous forest) with the eight forest fragments, while the second compared the large and the small fragments. ANOVA, *t*-test, and regressions were performed with Statistica Software, version 6.0 (StatSoft 2003).

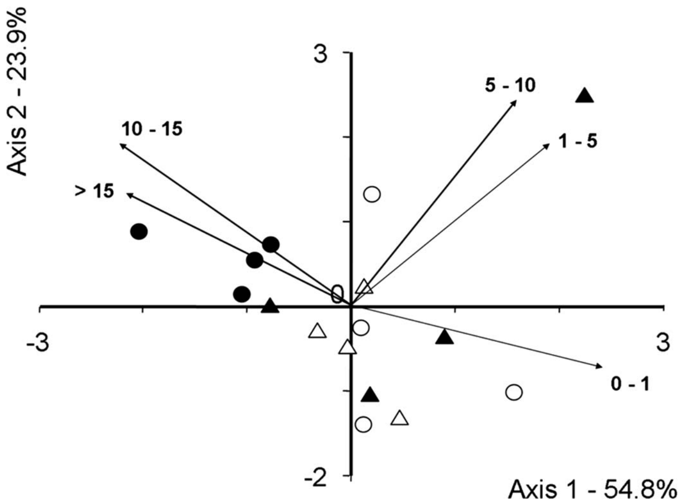

Figure 2.—Principal components analysis of the vegetation structure for the 16 sampled sites in the Reserva Florestal do Morro Grande and fragments in Cotia and Ibiúna, SP. The placement of the sites is based on the foliage density in five different strata of the forest. Numbers associated with the arrows represent the height (m) of the different strata of the vegetation. Black circles, continuous mature (CM) forest sites; black triangles, continuous secondary (CS) forest sites; white circles, large fragment (LF) sites; white triangles, small fragment (SF) sites.

The similarity of the sampled sites was studied using a detrended correspondence analysis (DCA). The DCA shows the sites in a two-dimensional plot based on the similarity of their fauna, as well as the species used in the analysis based on their distribution among the sites. Because species with low abundance that occur at only a few sites may not be very informative, only the 43 most abundant species (those represented by at least 20 individuals) were included in the analysis, which was performed with MVSP (Multivariate Statistical Package), version 3.1 (Kovach Computing Services 2000). A Mantel test was performed to test whether the changes in the spider community compositions at each site were related to the geographic distance between them. We calculated the similarity of the faunas with the Bray-Curtis index, and the resulting matrix was compared with a site-distance matrix. Three tests were performed, one for the sites in the RFMG, one for the fragments, and one for all sites combined. These tests were based on 5,000 permutations and were performed with the PAST (Paleontological Statistics) software (Hammer & Harper 2009).

Finally, we performed an indicator species analysis (ISA; Dufrêne & Legendre 1997) to see the association between the same 43 most abundant species and the sites sampled in more detail. ISA calculates an indicator value (IndVal) based on the frequency, relative abundance, and exclusivity with which a species occurs at the sites of a given category and then tests if it significantly differs from random based on a Monte Carlo permutation ($n = 1000$). The higher the frequency and exclusivity of a distribution within a given category, the higher will be the IndVal of a species, which range from 0 (the absence of a category) to 100 (exclusively present in one category and occurring at all sites). Those species whose distributions were evaluated as significant ($P < 0.05$) were considered indicator species.

The ISA also allows partitioning of the sites into different typologies. For example, we could divide the sites according to the vegetation type [CM sites × (CS sites + Fragments)] or forest patch size [(CM + CS sites) × Fragments] and compare

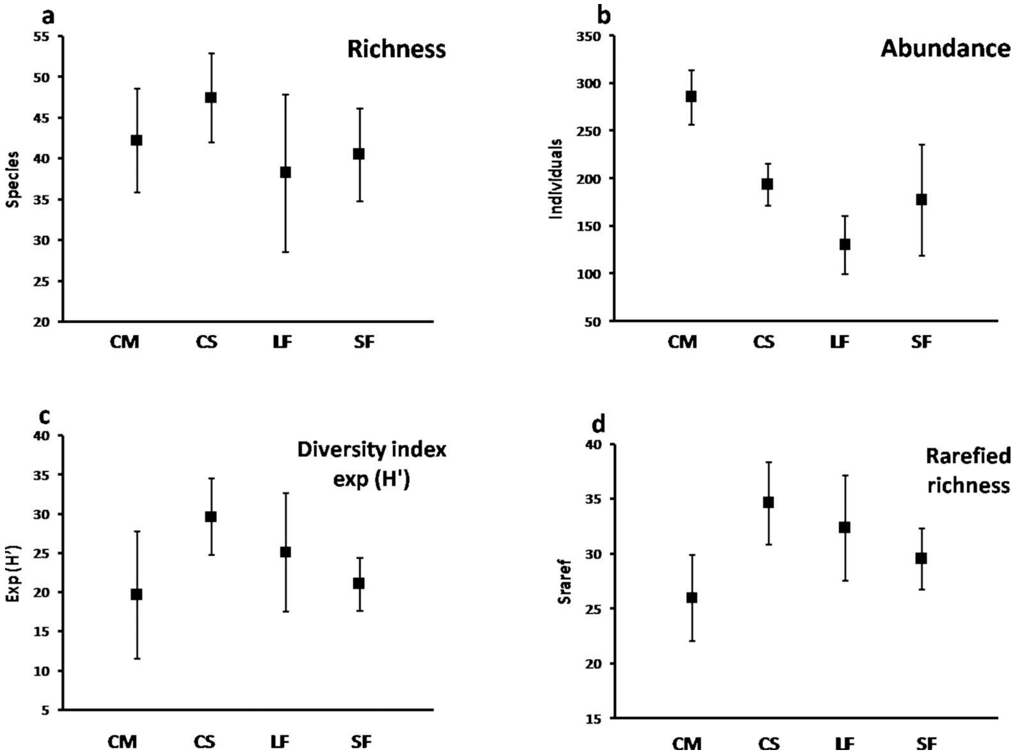

Figure 3.—Comparison of mean (standard deviation indicated by whiskers) of the orb-weaving spider communities in the four site categories for the following parameters: (**a**) richness; (**b**) abundance; (**c**) diversity index exp(H′); and (**d**) rarefied richness. CM, continuous mature forest sites; CS, continuous secondary forest sites; LF, large fragments; and SF, small fragments.

the results to determine which typology was more adequate to our data. Dufrêne & Legendre (1997) suggested that the sum of the IndVals for all species for each typology could be used as a criterion to reveal the best arrangement of the sites, as a higher total IndVal for a given typology means that more species were selected as indicator species, and/or that the IndVal of the indicator species was higher. Similarly, a species can also be assigned as an indicator for different typologies, and in this case, we consider the one in which it attains its maximum IndVal as the most appropriate to its distribution.

We analysed the species distribution among our sites under three different typologies. First, we separated the sites according to the type of vegetation, mature or secondary (including the CS sites and the fragments). Second, we opposed the sites in the RFMG (CM + CS sites), i.e., continuous forest sites, versus the fragments. For the third partition, we divided the sites into three categories, CM, CS, and fragments, to check whether a more detailed typology would be more appropriate for the distribution of the species. The ISA was performed with the "Ind Val" function of the "labdsv" 1.6-1 (Roberts 2013) package in the software R (R Core Team 2014).

For all the analyses, the result of the two sampling campaigns (December and March) were summed and considered together.

RESULTS

For all of the sites, we collected 12,683 orb-weaving spiders, 3,148 adults and 9,535 immatures. The adults belonged to 121 species and 8 families (a full species list is available as supplemental material online at http://dx.doi.org/10.1636/P15-19.s1, and for a community description, see Nogueira et al. 2006). All differences related to patch size presented below refer to comparisons between the continuous sites and the fragments, as none of the comparisons between the two classes of fragments was significant.

Richness.—The number of species in the sampled sites varied from 29 to 54 (Table 1, Fig. 3), but there were no significant differences between the four categories (ANOVA, F = 1.3, P = 0.33). The richness was unrelated to the patch size (Linear regression, $R^2 = 0.06$, $P = 0.36$) or vegetation structure (t-test, $t = -0.3$, $P = 0.78$).

Abundance.—The abundance per site ranged from 88 to 311 individuals (Table 1, Fig. 3), and significantly differed between the categories (ANOVA, F = 11.9, $P < 0.01$). A Tukey test revealed that the CM sites had significantly more adults than the other three site categories.

The abundance was related to both patch size and vegetation structure. It was higher in sites with mature vegetation (Linear regression, $R^2 = 0.45$, $P < 0.01$), as well as in the continuous sites relative to the fragments (t-test, $t = 307.9$, $P < 0.01$). However, in both cases, the results were influenced by a few dominant species. *Micrathena sanctispiritus* Brignoli, 1983 (Araneidae) and *Chrysometa ludibunda* (Keyserling, 1893) (Tetragnathidae) were associated with continuous sites (t-test, $t = 2.6$, $P < 0.05$ and $t = 2.2$, $P < 0.05$, respectively), and *M. sanctispiritus* and *M. nigrichelis* Strand, 1908 were positively correlated with mature forests (Linear regression, $R^2 = 0.27$, $P < 0.05$ and $R^2 = 0.34$, $P < 0.05$, respectively). In both cases, when the species were removed from their respective analyses, the relationships became much weaker (continuous

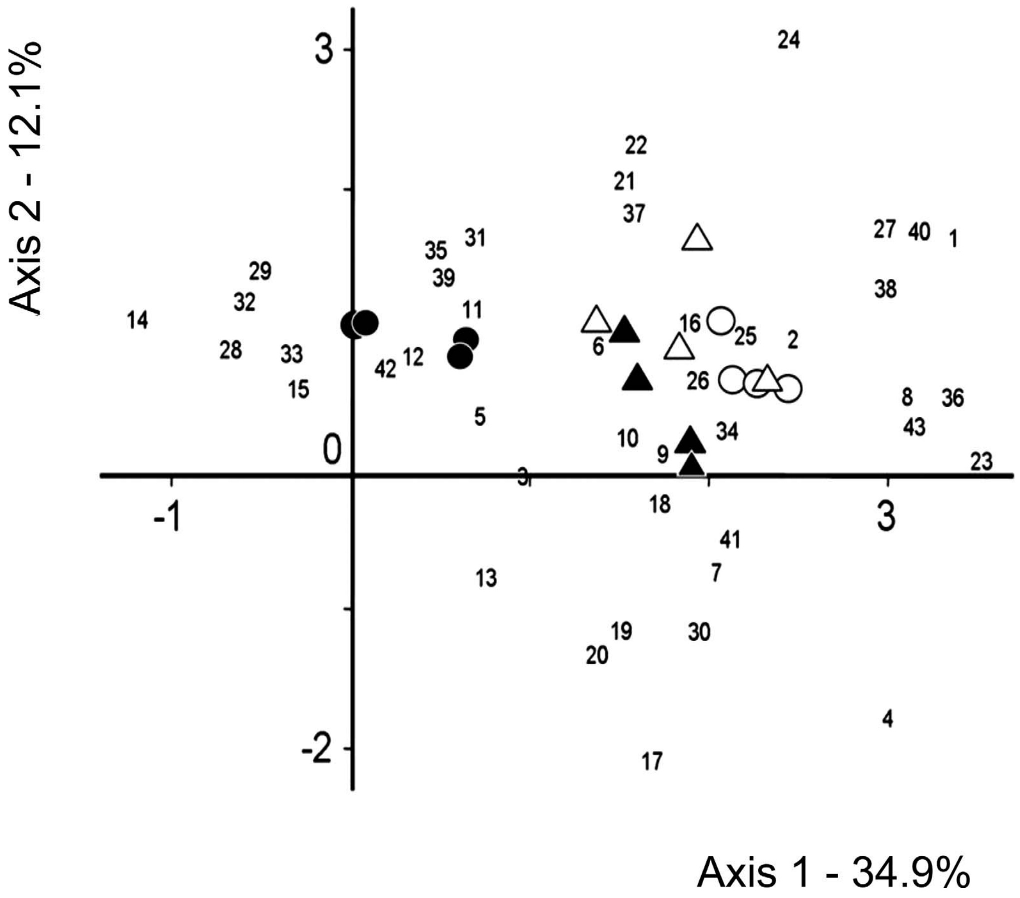

Figure 4.—Scatterplot from the detrended correspondence analysis performed for the 16 sites sampled in the Reserva Florestal do Morro Grande and fragments in Cotia and Ibiúna, SP (December 2002 and March 2003). The arrangement of the sites is based on the similarity of their fauna. The arrangement of the 43 species used in the analysis is based on the similarity of their distribution among the sites. Species are represented by numbers. Black circles, continuous mature (CM) forest sites; black triangles, continuous secondary (CS) forest sites; white circles, large fragment (LF) sites; and white triangles, small fragment (SF) sites.

sites × fragments: t-test, $t = 1.9$, $P = 0.07$ and Linear regression, $R^2 = 0.235$, $P = 0.0566$, respectively).

Diversity.—The diversity index exp(H′) and the rarefied richness varied significantly between the categories (exp(H′): ANOVA, $F = 3.6$, $P < 0.05$; Sraref: $F = 3.7$, $P < 0.05$; Table 1, Fig. 3). In both cases, the diversity of the CM sites was lower than that of the other categories and was significantly lower than that of the CS sites. However, the variation observed was unrelated to the patch size (exp(H′): t-test, $t = 0.3$, $P = 0.77$; Sraref: $t < 0.1$, $P = 0.95$) or vegetation structure (exp (H′): Linear regression, $R^2 = 0.01$, $P = 0.71$; Sraref: $R^2 = 0.03$, $P = 0.49$).

The lower diversity of the CM sites is a consequence of the high abundance of the two dominant species associated with *M. nigrichelis* and *M. sanctispiritus*, although the reasons for this association are not clear. Nonetheless, if we exclude the dominant species from the analyses, the differences in diversity are no longer significant (ANOVA. exp(H′): $F = 1.1$, $P = 0.38$; Sraref: $F = 1.3$, $P = 0.32$),

The proportion of singletons ranged from 15 % to 51 %, but the differences between the categories were negligible (ANOVA, $F = 0.9$, $P = 0.47$). The variation in this parameter was also unrelated to vegetation structure (Linear regression, $R^2 = 0.19$, $P = 0.09$) or patch size (t-test, $t = -1.5$, $P = 0.32$).

Composition and indicator species.—The DCA showed a site grouping pattern based on the vegetation type (Fig. 4). This division occurred in the first axis, which explained 34.9 % of the variation. The four continuous sites with mature vegetation (CM 1–4) were grouped together and separated from those with secondary vegetation. The placement of the secondary vegetation sites formed a gradient, where those in the continuous area (CS 1–4) and three of the four small fragments were closer to the CM sites than the four large fragments and the remaining fourth small fragment. The second axis explained only 12.1 % of the variation and did not seem to reveal any particular trends concerning the patch size or vegetation structure.

The Mantel test revealed a significant correlation between the similarity and distance matrices for all of the sites combined (Mantel test, $r = 0.40$; $P < 0.01$) and for the sites in the RFMG (Mantel test, $r = 0.81$; $P < 0.01$), but not for the fragments alone (Mantel test, $r = 0.29$; $P = 0.08$). However, we believe the positive results may be attributable to a characteristic of our study area.

In the RFMG, the CM sites are located in the southern part of the reserve, while the CS sites are in the northern part (Fig. 1), which means that sites with similar vegetation were closer to each other than to sites with different vegetation. Therefore, in the RFMG we had two factors, distance and

Table 2.—Species selected as significant indicators by an indicator species analysis for the three different typologies classifications. The indicator values (IndVal) of the species for each typology category are shown with the *p*-values in brackets. Bold font represents the maximum IndVal. M and CM, continuous mature forest sites; S, secondary forest sites; C, continuous forest sites; F and FR, fragments

	Vegetation type		Forest area size		3 categories		
Species	M	S	C	F	CM	CS	FR
Miagrammopes sp.1	**93.5 (<0.01)**		62.5 (<0.05)		82.8 (<0.01)		
Micrathena nigrichelis	**92.8 (<0.01)**		72.2 (<0.05)		89 (<0.01)		
Wagneriana iguape	**87.2 (<0.01)**		85.7 (<0.01)		74.7 (<0.01)		
Micrathena sanctispiritus	**78.5 (<0.05)**		78.1 (<0.05)		61.6 (<0.05)		
Chrysometa ludibunda	92.1 (<0.01)		**95.3 (<0.01)**		81.3 (<0.01)		
Chrysometa boraceia	79.9 (<0.05)		**82.1 (<0.01)**				
Chrysometa cambara	**100 (<0.01)**				**100 (<0.01)**		
Mangora blumenau	**94.1 (<0.01)**				88.1 (<0.01)		
Testudinaria gravatai	**81.2 (<0.05)**				69.6 (<0.05)		
Micrathena triangularis	**73.1 (<0.05)**				72.1 (<0.05)		
Azilia histrio	**77.4 (<0.05)**						
Cyclosa fililineata			**77.2 (<0.05)**			71.9 (<0.01)	
Araneus vincibilis						**62.5 (<0.05)**	
Acacesia graciosa		**83.3 (<0.05)**		73.1 (<0.05)			
Mangora ramirezi		75 (<0.05)		**95 (<0.01)**			90.5 (<0.01)
*Testudinaria lemnisca*ta		73.2 (<0.05)		**86.8 (<0.01)**			76.6 (<0.01)
Wagneriana dimastophora		**96.6 (<0.01)**					
Ogulnius sp.2		**83.3 (<0.05)**					

vegetation type, acting synergistically over the faunal similarity, which would explain the very high correlation coefficient obtained for the RFMG sites. This situation also influenced the results of the test performed for the sites combined, although the correlation became much weaker because the similarity in the samples from the fragments did not correspond as closely to distance, as shown by the Mantel test for the fragments alone. This last result is the most meaningful, because it shows that when only distances are considered, the correlation with faunal similarity is insignificant, providing evidence that the spiders are not spatially limited in the fragmented landscape we studied.

The ISA assigned 18 species as indicators for some categories in at least one of the typologies analysed (Table 2). The genus *Micrathena* Sundevall, 1833 was the most associated with mature forest, with three species designated as significant indicators and reaching a maximum IndVal in the vegetation-type partition. The genus *Chrysometa* Simon, 1984 also had three species designated as significant indicators of mature forest, but two of them, *C. ludibunda* and *C. boraceia* Levi, 1986, had a larger IndVal for the second typology, signalling that those species were more associated with continuous forest areas than with vegetation type. It is also noteworthy that some genera had species associated with different vegetation types, such as the araneid genera *Mangora* O. Pickard-Cambridge, 1889, *Testudinaria* Taczanowski, 1879, and *Wagneriana* F.O. Pickard-Cambridge, 1904.

Partitioning the sites according to vegetation type proved to be the most appropriate for our data, as it yielded the largest value for all of the parameters investigated: the number of indicator species, proportion of indicator species (in relation to the richness of the category), average IndVal, number of indicator species with their maximum IndVals, and the total sum of the IndVals (Table 3). In contrast, partitioning the sites according to the area size (continuous sites × fragments) produced the least number of indicator species and lowest total IndVal sum.

DISCUSSION

Our results indicate that the diversity in most sites is high and that vegetation structure is much more important to orb-weaving spider communities than the size of the habitat. While the fragments and continuous areas had similar diversity values, all of the important differences observed (diversity measures, abundance, and composition) were related to the vegetation type. Nevertheless, as most of those differences were heavily influenced by a few dominant species, we can also state that overall, the orb-weaving communities from different sampling sites were quite similar, especially in the sites with the same kinds of vegetation.

The influence of the vegetation on the results was expected, as there are several examples in the literature of its importance for spiders. The composition of the community seems to be particularly sensitive to changes in the vegetation structure. Differences in community composition are often found when comparing the fauna of secondary and mature forests or forests under different disturbance regimes (Chen & Tso 2004; Floren & Deeleman-Rheinold 2005; Rego et al. 2007; Kapoor 2008; Cabra-Garcia et al. 2010; Baldissera et al. 2012; Maya-Morales et al. 2012; Raub et al. 2014), which indicates some degree of habitat specificity. Not surprisingly, the ISA results revealed that the partition of the sites by vegetation type had the best fit to our data for all of the parameters available.

Although the biology of Neotropical orb-weaving species is still poorly known, some recent studies from the southern Atlantic Forest with spider species lists from fragments and other kinds of forests may offer the possibility of a comparison with our results. Baldissera et al. (2004) sampled web-spiders in forest interiors, forest edges, and pastures, and the species from the genera *Miagrammopes* O. Pickard-Cambridge, 1870 (Uloboridae) and *Micrathena* were more abundant in the forest interior. A species of *Miagrammopes* also preferred forest interiors over edges in a study on the diversity of spiders in riparian

Table 3.—Results of the indicator species analysis (ISA) for the three different typologies classifications. Categories: M and CM, continuous mature forest sites; S, secondary forest sites; C, continuous forest sites; F and FR, fragments. ISA parameters: S, richness; NIS, number of significant indicator species; %IS, proportion of indicator species/richness; Average IV, average indicator value (IndVal) of the species selected as significant indicators; Max IV; number of species reaching the maximum IndVal; and Total IV, sum of the IndVals for all species selected as significant indicators.

Typology	Category	S	N IS	% IS	Average IV	Max IV	Total IV
Vegetation type	M	38	11	28.9	86.35	9	9.50
	S	42	5	11.9	82.29	3	4.11
	Total	43	16	37.2	85.08	12	13.61
Forest area size	C	43	7	16.3	79.02	3	5.53
	F	40	3	7.5	84.95	2	2.55
	Total	43	10	23.3	80.8	5	8.08
3 categories	CM	38	9	23.7	79.93	1	7.19
	CS	41	2	4.9	67.19	1	1.34
	FR	40	2	5.0	83.55	0	1.67
	Total	43	13	30.2	78.53	2	10.21

forests (Rodrigues et al. 2014), which seems to be in accordance with our findings.

Raub et al. (2014) recently provided a list of spider genera identified as indicators of old-growth and secondary forest based on a study of the Atlantic Forest in southern Brazil, and the genera *Mangora* (Araneidae) and *Miagrammopes* were considered associated with old-growth forests. In our study, one species of each of these genera also showed a preference for mature forests. However, another species of *Mangora* was associated with the secondary forests and fragments, while the distribution of the remaining three species of the genus was more random. This represents further evidence that the response of orb-weaving spiders to the environment may be specific, and that an analysis at higher taxonomic levels may not be accurate enough to characterize habitat preferences.

Further studies are necessary to improve knowledge of the habitat preferences of orb-weaving spider species in the Atlantic Forest and to assess the consistency of the response of species to the environment, which may reveal potential biological indicators. The list presented in this study (Table 2) represents another contribution for this purpose, and the use of ISA or other analyses of habitat preference should be stimulated. The genus *Miagrammopes* could receive more attention, as it appears to be repeatedly associated with mature forest or forest interiors.

In contrast to what was observed for composition, our results suggest that richness is less variable in forested habitats. Indeed, most of the studies cited above reported a similar number of species for the different types of forests being compared (Blanco-Vargas et al. 2003; Chen & Tso 2004; Floren & Deeleman-Rheinold 2005; Baldissera et al. 2008; Cabra-Garcia et al. 2010; Prieto-Benítez & Méndez 2011; Raub et al. 2014; Rodrigues et al. 2014), although there may be some exceptions (Pinkus-Rendón et al. 2006; Maya-Morales et al. 2012). Significant differences in spider richness or diversity usually occur when communities from very different environments are compared (i.e., open field or agro-ecosystems versus forest), and a greater number of species is always found in the structurally more complex habitat (Fowler & Venticinque 1995; Baldissera et al. 2004; Banks et al. 2007). However, unlike most of these studies, we found significant differences in the diversity measures between the treatments, as the orb-weaving communities from the CM sites were less diverse than those in areas with secondary vegetation, especially the CS sites. Nevertheless, as already mentioned, this result is directly influenced by two dominant species associated with CM sites, and if they are excluded from the analysis the CM and CS sites does not present significant differences anymore, indicating that the structure of the remaining community is similar to that observed for the others categories.

The persistence of a rich and diverse spider community in the fragments signals that habitat reduction and the isolation of the remnants are not affecting the orb-weaving communities in a significant way. The resilience of spiders to these impacts, also recorded earlier in similar studies (Gibb & Hochuli 2002; Major et al. 2006; Kapoor 2008), may be attributable to some characteristics of these animals. Most spiders are generalist predators, and although predators may be more sensitive to environmental disturbance than other trophic groups (Didham et al. 1998; Davies et al. 2000; Ryall & Fahrig 2005), animals with generalist behaviours are usually less affected by fragmentation than species with more specialized requirements (Didham et al. 1996; Tscharntke et al. 2002; Fonseca et al. 2009). The small size of the animals may also be an advantage, as small species have smaller space requirements than large species and are thus less susceptible to fragmentation (Henle et al. 2004; Laurance et al. 2011).

Finally, dispersal capacity is considered a key feature for survival in fragments (Tscharntke et al. 2002; Moir et al. 2005). Spiders are usually very good dispersers, and several species can cross from hundreds of meters to several kilometres through an act known as ballooning (Bell et al. 2005). Although ballooning has traditionally been observed and studied in open habitats, recent work has demonstrated the ballooning propensity of several forest spider species in tempe rate forests, especially web-building spiders (Larrivée & Buddle 2011).

In a recent study conducted in fragments in southern Brazil, Baldissera et al. (2012) partitioned the compositional variation of the web-spider communities into environmental and spatial components and concluded that the web-spider meta-community was not limited by dispersal in the study landscape. An absence of spatial legacy was also reported for spiders in Spain due to the lack of a significant correlation between their composition and geographic distance (Jiménez-Valverde et al. 2010), as was observed in our results for the fragments. Finally, the capacity of orb-weaving spiders to colonize new habitats was highlighted in a study of the effects of fragmentation on canopy spiders in Borneo (Floren et al. 2011) because the relative importance of the orb-weaving guild increased in isolated fragments, suggesting they were more successful in the re-colonization process than other spider guilds.

Reviewing our results, we can conclude that the orb-weaving spider communities in Caucaia have not suffered a very large impact from the processes of habitat reduction and isolation occurring in the region. Despite some compositional changes due to the vegetation structure, their richness and diversity remain high, even in the fragments. However, those optimistic statements must be taken with care, and some caveats concerning the universality of our observations should be mentioned.

First, this region of Caucaia represents a best-case scenario with regard to forest conservation at the landscape level. The fragments studied are located within a region that still possesses a 37% forest cover (Uezu et al. 2005) in addition to the RFMG, a large forest patch (10,000 ha). This suggests that the whole landscape may still be functionally connected for a group with good dispersal capacities. Moreover, the fragments sampled are relatively large, ranging from 14 to 175.1 ha. Ribeiro et al. (2009) showed that the remaining Atlantic Forest is scattered in more than 245,000 fragments and that 83.4% of them are smaller than 50 ha, meaning that at least half of the fragments in Caucaia are larger than the vast majority of Atlantic Forest fragments.

Indeed, in the few studies reporting a negative relationship between forest patch size and spider species richness (Miyashita et al. 1998; Floren & Deeleman-Rheinold 2005; Floren et al. 2011), the fragments sampled were considerably smaller than the fragments in Caucaia (< 6.5 ha). Those studies also demonstrated that the presence of large forested areas in the landscape could prevent (or help to recover) the decrease in richness/diversity of spider communities by acting as a source for the fragments' fauna, which highlights the importance of the RFMG in our study area.

The second point is that, as discussed above, orb-weaving spiders seems to be less sensitive to the disturbances related to fragmentation than other groups. For instance, a study conducted at the same sites on harvestmen (Arachnida-Opiliones) depicted a much more negative situation, with a sharp decrease in richness from the continuous sites to the fragments, as well as from the sites with mature vegetation to those with secondary vegetation (Bragagnolo et al. 2007). This vulnerability was attributed to the narrow microclimatic requirements and the poor dispersal ability of these animals. Therefore, the same fragments that provide shelter to a diverse spider community may not be adequate for other components of the biota, even for other invertebrate groups.

Finally, one last question must be addressed. The communities from all of the sites sampled were characterized by a large number of rare species (average proportion of singletons and standard deviation was 37.9 ± 9.6 %). Although the proportion of singletons in the fragments was similar to that observed in the continuous areas, rare species are considered one of the most sensitive groups to fragmentation and other disturbances, mainly due to their low population numbers (Tscharntke et al. 2002; Henle et al. 2004). This suggests that, in the longer term, the persistence of these rare species in the fragments may be threatened.

Nevertheless, as a final conclusion, our study showed that fragments, even as small as 14 ha, still support a rich and diverse orb-weaving spider community and are therefore valuable for the conservation of local biodiversity. The large-sized reserves in the Atlantic Forest, such as RFMG, are very important, for its role as a source, and especially for usually harbouring sites composed of mature vegetation. As observed for many groups (Gibson et al. 2011), our mature forest sites presented a distinct fauna, and in this sense, may be considered irreplaceable for the maintenance of orb-weaving spider diversity in the Atlantic Forest.

ACKNOWLEDGMENTS

We would like to acknowledge Jean Paul Metzger for helping us with the sampling design and for his valuable comments; Renata Pardini for the statistical analysis; Adalberto Santos, Jimmy Cabra-Garcia, Cibele Bragagnolo, Stano Pekar and two anonymous reviewers for reviewing the manuscript; Cristina Rheims for reviewing the English; Antonio Brescovit for helping with the identification of the spiders, and all of the colleagues who helped us in the field. We also thank Renata Pardini, Ricardo Braga-Neto, and Sergio Marques for most of the vegetation measurements. This study was a part of two projects financed by the Biota-Fapesp program: 'Biodiversidade de Arachnida e Myriapoda do estado de São Paulo' (processo 99/05546) and 'Conservação da Biodiversidade em Paisagens Fragmentadas no Planalto Atlântico de São Paulo' (processo 99/05123-4). The first author also thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for a master degree fellowship, Fundação de Amparo à Pesquisa do Estado de São Paulo for a post-doctoral fellowship (2013/23736-2), and the Zoology Department of Instituto de Biociências of the University of São Paulo.

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Manuscript received 18 March 2015, revised 11 August 2015.