

Substrate selection and spatial segregation by two congeneric species of *Eustala* (Araneae: Araneidae) in southeastern Brazil

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Abstract. Habitat and microhabitat selection by spiders are influenced by abiotic and biotic factors, including vegetation structure, natural enemies, and prey availability. Some species are highly dependent on particular conditions, such as the presence of substrates where they remain camouflaged, constantly humid sites or the occurrence of plants bearing glandular trichomes. Others are distributed in areas that include a wide range of physical conditions and interact with several types of prey, predators and competitors. In the present study, we evaluated spatial distribution and substrate selection of two sympatric congeneric species with distinct body shapes and colors, *Eustala taquara* (Keyserling 1892) and *E. sagana* (Keyserling 1893), in an area of Atlantic Forest in southeastern Brazil. We focused on the following factors regarding habitat selection: i) distance from the border (forest edge or interior); ii) altitudinal distribution, ranging from 740 to 1294 m; iii) web height above ground level; and iv) plant species used for web attachment. All individuals of both species were located at the forest edge, especially on dry branches. However, they occurred preferentially in different host plants and altitudes. *Eustala taquara* individuals were strongly associated with *Conyza bonariensis*, and *E. sagana* with *Hyptis suaveolens* and *C. sumatrensis*. Dry branch preferences might be important to reduce species conspicuousness to visually oriented predators, such as birds and wasps. Spatial segregation between closely related species possibly minimizes interference interactions, such as competition for particular sites or prey items.

Keywords: Orb weaver spider, coexistence, altitudinal gradient, habitat selection, web building

Microhabitat selection during web construction has important implications for web-building spiders, affecting the frequency of prey interception (Heiling 1999; Herberstein & Fleisch 2003; Heiling et al. 2006), prey species availability (Herberstein 1997), interspecific competition and/or frequency of agonistic interactions with other spiders or organisms (Herberstein 1998; Nahas et al. 2012; Purcell et al. 2012). Microhabitat selection could also expose spiders to inappropriate environmental conditions (Gillespie 1987; Gonzaga et al. 2006), to predators (Gonzaga & Vasconcellos-Neto 2005) and to other sources of mortality, such as infections by fungi (Gonzaga et al. 2006).

The first requirements for web establishment are associated with site structural conditions, such as spatial distribution of branches used in web attachment, and an open space large enough to facilitate construction of the web (Stevenson & Dindal 1982; Rao & Poyyamoli 2001). Spiders, however, often have more specific criteria, and can use several cues to assess site quality before initiating web settlement. For example, Schuck-Paim & Alonso (2001) showed that *Nephilengys cruentata* (Fabricius 1775) (Nephilidae) used signs of previous conspecific presence to evaluate habitat quality. Conspecific silk inside the enclosures employed in the experiments increased settlement likelihood by *N. cruentata* individuals.

Plant characteristics can also be integral in determining initial settlement, establishment success, and permanence of several spider species (Romero & Vasconcellos-Neto 2005). Selectivity for particular host plants has been previously described for many spider species (Romero & Vasconcellos-Neto 2005, 2011; Romero et al. 2008; Hesselberg & Triana 2010). Spiders select plants with specific attributes, e.g., presence of glandular trichomes, adequate branch and leaf

densities, pollination by potential prey, color pattern, and structural composition that can serve as suitable shelter, which consequently increases each species potential to improve prey capture success, and reduces the likelihood of capture by natural enemies.

The genus *Eustala* Simon 1895 (Araneidae), restricted to the Americas, is currently composed of 90 species (Platnick 2014). Individuals of several *Eustala* species are often distributed throughout shrub and tree vegetation (Poeta et al. 2010), and are the primary prey species of several hunting wasps (Gonzaga & Vasconcellos-Neto 2005; Buschini et al. 2008). In Serra do Japi, an area of Atlantic Forest situated in southeastern Brazil, three species have been previously collected (Indicatti et al. 2012): *Eustala perfida* Mello-Leitão 1947, which typically occurs in shaded areas of forest interior and constructs elongated orbs close to concavities on tree trunks (Messas et al. 2014); *E. sagana* (Keyserling 1893); and *E. taquara* (Keyserling 1892). Habitat selection and spatial distribution of *E. perfida* was previously studied by Messas et al. (2014), but there is no information available on the remaining species. We hypothesized that *E. sagana* and *E. taquara*, two species with distinct body shapes and colors, would exhibit differences in daytime resting substrates. In addition, we evaluated spatial segregation in these species by analyzing habitat selection based on vegetation height and altitude within the distribution area.

METHODS

Study site.—We conducted the present work in the Serra do Japi (23° 11' S, 46° 52' W), a forest reserve located near the city of Jundiá, São Paulo state, Brazil. The climate is seasonal, with average monthly temperatures from 13.5° C

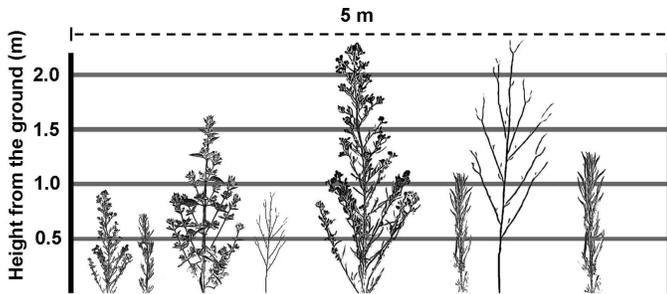


Figure 1.—Schematic drawing of the methodology employed to analyze the frequency of available sites (vegetation height) in the Serra do Japi, Jundiáí-SP. Four 5-m lines, separated vertically every 0.5 m, were arranged in the vegetation; all plants touched by the lines were included.

Table 1.—List of available plant species present on sample plots and frequency and number of individuals of *Eustala sagana* found occupying plants along the edge of the forest in Serra do Japi, Jundiáí – SP, Brazil. The data were collected at an altitude of 800 m during May and July 2011.

Family	Species	Plants		<i>E. sagana</i>	
		<i>n</i>	%	<i>n</i>	%
Anacardiaceae	<i>Lithraea molleoides</i>	1	0.15	0	0
Asclepiadaceae	<i>Asclepias curassavica</i> L.	1	0.15	0	0
Asteraceae	<i>Cyrtocymura scorpioides</i> (Lam.) H. Rob.	125	18.71	0	0
	<i>Eupatorium</i> sp.	32	4.79	0	0
	<i>Vernonanthura ferruginea</i> (Less.) H. Rob.	31	4.64	9	8.18
	<i>Vernonanthura phosphorica</i> (Vell.) H. Rob.	17	2.54	0	0
	<i>Trichogoniopsis adenantha</i> (DC.) R.M.King & H.Rob	12	1.8	2	1.82
	<i>Baccharis dracunculifolia</i> DC.	4	0.6	1	0.91
	<i>Bidens brasiliensis</i> Sherff	4	0.6	3	2.73
	<i>Calea pinnatifida</i> (R. Br.) Less.	8	1.2	0	0
	<i>Conyza bonariensis</i> (L.) Cronq.	5	0.75	0	0
	<i>Conyza sumatrensis</i> (Retz.) E. Walker	15	2.25	35	31.82
	<i>Erechtites valerianifolius</i> (Link ex Spreng.) DC.	0	0	3	2.73
	<i>Mikania</i> sp.	5	0.75	0	0
	sp.1	66	9.88	0	0
	sp.2	4	0.6	0	0
	<i>Acanthospermum hispidum</i>	0	0	1	0.91
	<i>Tagetes minuta</i> L.	0	0	1	0.91
Bignoniaceae	<i>Pirostegia venusta</i> (Ker-Gawl) Miers	2	0.3	0	0
Cecropiaceae	<i>Cecropia</i> sp.	2	0.3	0	0
Euphorbiaceae	<i>Croton floribundus</i> Spreng	1	0.15	0	0
Fabaceae	sp.1	6	0.9	0	0
Lamiaceae	<i>Hyptis suaveolens</i> L.	47	7.04	26	23.64
	<i>Hyptis</i> sp.1	13	1.95	3	2.73
Malvaceae	<i>Triunfetta semitriloba</i> Jacq.	36	5.39	1	0.91
	sp. 1	0	0	3	2.73
	sp. 2	1	0.15	0	0
Melastomataceae	sp. 1	9	1.35	0	0
Piperaceae	<i>Piper</i> sp.	2	0.3	0	0
Poaceae	<i>Brachiaria decumbens</i> Stapf.	168	25.15	0	0
	<i>Panicum maximum</i> Jacq.	21	3.14	0	0
	Grass	0	0	9	8.18
Pteridophytes		5	0.75	0	0
Rosaceae	<i>Rubus rosifolius</i> BP. MS.	4	0.6	0	0
Rubiaceae	sp.1	2	0.3	0	0
Solanaceae	<i>Solanum conccinum</i> Schott ex Sendtn.	10	1.5	0	0
	<i>Solanum variabile</i> Mart.	3	0.45	0	0
	<i>Sessea brasiliensis</i> Toledo	2	0.3	0	0
Verbenaceae	<i>Lantana camara</i> L.	4	0.6	0	0
Others	Rare species	0	0	10	9.09
	Dry branches	0	0	3	2.73
Total		0668	100	110	100

in July to 20.3° C in January. The driest period is from June to September, and the rainy season is from December to February (Pinto 1992). The local vegetation is characterized by a semi-deciduous rainforest with canopy height varying between 10–15 m. The higher mountain regions support a semideciduous forest composed of thinner trees (Leitão-Filho 1992). The altitude in the Serra do Japi ranges from 740–1294 m.

Spatial distribution.—All sampling was conducted in March 2011. We examined the distance from the border (forest edge or interior) and the altitudinal distribution of both species. *Eustala taquara* and *E. sagana* altitudinal distribution and edge effects were investigated by sampling forest edge and interior in four altitudinal ranges: 750–800 m, 1000 m, 1250 m, and 1294 m. In this study, we considered the forest edge as a

Table 2.—List of available plant species present on sample plots, and frequency and number of individuals of *Eustala taquara* found occupying plants along the edge of the forest in Serra do Japi, Jundiá – SP, Brazil. The data were collected at an altitude of 1000 m in March 2011.

Family	Species	Plants		<i>E. taquara</i>	
		<i>n</i>	%	<i>n</i>	%
Asteraceae	<i>Ageratum conyzoides</i> L.	1	0.54	0	0.00
	<i>Ambrosia artemisiifolia</i> L.	11	5.95	4	2.65
	<i>Bidens brasiliensis</i> Sherff	2	1.08	3	1.99
	<i>Calea pinnatifida</i> (R. Br.) Less.	2	1.08	0	0.00
	<i>Conyza bonariensis</i> (L.) Cronq.	14	7.57	103	68.21
	<i>Cyrtocymura scorpioides</i> (Lam.) H. Rob.	4	2.16	0	0.00
	<i>Erechtites valerianifolius</i> (Link ex Spreng.) DC.	1	0.54	2	1.32
	<i>Eupatorium</i> sp.	2	1.08	0	0.00
	<i>Trichogoniopsis adenantha</i> (DC.) R.M.King & H.Rob	0	0.00	2	1.32
Euphorbiaceae	<i>Croton floribundus</i> Spreng	8	4.32	0	0.00
	<i>Croton urucurana</i> Baill	5	2.70	0	0.00
Fabaceae	<i>Acacia plumosa</i> Lowe	1	0.54	0	0
	<i>Desmodium discolor</i> Vogel	0	0.00	3	1.99
Lamiaceae	<i>Hyptis suaveolens</i> L.	49	26.49	10	6.62
Malvaceae	sp.1	24	12.97	0	0.00
Melastomataceae	<i>Miconia</i> sp.	2	1.08	0	0.00
	sp.1	2	1.08	0	0.00
Myrtaceae	sp.1	0	0.00	2	1.32
Piperaceae	sp.1	8	4.32	0	0.00
Poaceae	Grass – sp.1	2	1.08	0	0.00
	Unidentified	5	2.70	0	0.00
Rosaceae	<i>Rubus rosifolius</i> BP. MS.	2	1.08	0	0.00
Rubiaceae	sp.1	3	1.62	5	3.31
Solanaceae	<i>Solanum concinnum</i> Schott ex Sendtn	2	1.08	0	0.00
	<i>Solanum variabile</i> Mart	2	1.08	0	0.00
	<i>Sesseia brasiliensis</i> Toledo	2	1.08	0	0.00
Verbenaceae	<i>Lantana camara</i> L.	2	1.08	0	0.00
Others	Pteridophytes	13	7.03	0	0.00
	Eudicotyledons	1	0.54	2	1.32
	Dry branches	15	8.11	13	8.61
Total		185	100	151	100

zone of 2 m from the road margin towards the inner forest. This area is covered by herbaceous plants and shrubs located between the road and arboreal vegetation. For each site, individuals from 20 × 2 m plots ($n = 15$) were sampled at the forest edge, and individuals from 10 × 10 m plots ($n = 12$) were sampled within the forest. Shape and size of the plots in the forest edge were restricted by the area available under the influence of the wide open trails and roads. We sprayed water in vegetation to locate webs during the searching procedure.

We compared the number of *E. taquara* and *E. sagana* individuals at distinct altitudes using a non-parametric Kruskal-Wallis test, as initial analyses showed the data distribution lacked homogeneity of variances. Only plots located at the edge of trails were considered as replicates because both species were absent from plots located in the forest interior. Post-hoc Dunn's multiple comparison tests (Dunn 1964) were applied to compare the abundances between altitudes.

Substrate selection.—We searched for spiders along the forest edge in order to obtain the observed values of web height from ground level, green and dead substrate and plant species occupied. Samples were collected where each species was more abundant, at altitudes of 800 m for *E. sagana* during May and July 2011, and at 1000 m for *E. taquara* in March 2011.

We evaluated whether *E. sagana* and *E. taquara* exhibited specific height preferences (above ground level) by establishing 5 m transects ($n = 8$) in the two altitudes with higher occurrence of each species. We extended lines at four different heights (0.5 m; 1.0 m; 1.5 m; and 2.0 m), and counted the number of times each line intersected vegetation (Fig. 1). The total number of intersections was used to establish the availability of sites at different sample heights. We used the number of intersections at each height as the expected frequency for spider occupation. These frequencies were compared with the frequencies of observed web heights used by *E. taquara* and *E. sagana* using a *G* test.

Substrate selection for web construction in *E. taquara* and *E. sagana* was investigated in 10 × 2 m plots ($n = 8$) also on the forest edge. Within these plots we calculated the number of sites available with green and dry branches (open spaces wide enough to allow web construction) and the proportion of each plant species (Table 1 and 2). We compared the available number of green and dead branches with the number of these kinds of branches occupied by *Eustala* spiders. We also compared the relative abundance of plant species in plots (expected frequencies), at the altitude with highest abundance of each spider species, with the relative abundance of plants used as web-building sites along the forest edge (observed frequencies) applying *G* test.



Figure 2.—*Eustala taquara* specimens resting on dead (dry) vegetation, with coloration pattern details. Scale bar: 0.5 cm.



Figure 3.—*Eustala sagana* specimens resting on dry vegetation. Detail of a free sector of the web which is lacking capture spirals. The arrow indicates the signal thread that connects the spider to the web center. Scale bar: 1.0 cm.

RESULTS

Results showed both *Eustala* species did not build shelters, but were instead found in shrub branches, which provided attachment points for web construction. Spiders remained in contact with branches, holding a web thread connected to the hub of the orb web. The spider color patterns were very similar to the substrate patterns used as resting positions (based on the human visual system) (Figs. 2, 3).

Spatial distribution.—All *Eustala taquara* ($n = 97$) and *E. sagana* ($n = 46$) individuals were located at the forest edge. Both *Eustala* species were sampled at all altitudes of Serra do Japi, but with different density patterns. A significantly higher abundance of *E. sagana* was detected in the lower Serra do Japi area, between 750–850 m (91.3% of all sampled individuals) (Kruskal-Wallis: $H = 23.08$, $DF = 3$, $P < 0.0001$; $Dunn Z_{800m \times 1000m} = 3.73$, $P = 0.001$; $Z_{800m \times 1250m} = 3.99$, $P = 0.0004$; $Z_{800m \times 1294m} = 3.99$, $P = 0.0004$; $Z_{1000m \times 1250m} = 0.27$, $P = 1.0$; $Z_{1000m \times 1294m} = 0.27$, $P = 1.0$; $Z_{1250m \times 1294m} = 0.00$, $P = 1.0$; Fig. 4A). We found 20.6% of *Eustala taquara* individuals at 750 m; 52.6% at 1000 m; 16.5% at 1250 m; and 10.3% at 1294 m of altitude, with a significantly higher abundance at the intermediate zone (1000 m) (Kruskal-Wallis: $H = 19.24$; $DF = 3$; $P < 0.001$; $Dunn Z_{800m \times 1000m} = 3.27$, $P = 0.006$; $Z_{800m \times 1250m} = 0.005$, $P = 1.0$; $Z_{800m \times 1294m} = 0.66$, $P = 1.0$; $Z_{1000m \times 1250m} = 3.26$, $P = 0.007$; $Z_{1000m \times 1294m} = 3.93$, $P = 0.0005$; $Z_{1250m \times 1294m} = 0.66$, $P = 1.0$; Fig. 4B).

Substrate selection.—Lines intersected vegetation more frequently at the 0.5 m level above the ground, and decreased gradually as heights increased to 2.0 m. However, results

showed *E. sagana* occurrence was highest at 1.0 m (30.6%) and 1.5 m (46.4%) above ground level ($G = 115.29$; $P < 0.0001$; $n = 117$ sites; $n = 106$ spiders; Fig. 5A). *Eustala taquara* frequencies were significantly higher at 1.0 m (39.6%) and 1.5 m (44.3%) compared to the expected frequencies considering the available sites ($G = 97.80$; $P < 0.0001$; N sites = 188; N spiders = 108; Fig. 5B).

Almost all *E. sagana* individuals (96.9%) were observed using dead vegetation branches (Fig. 6A), indicating a preferential use for these sites ($G = 197.16$; $P < 0.0001$; N sites = 596; N spiders = 96). *Eustala taquara* exhibited the same pattern, with most individuals (96.6%) also sampled on dead branches (Fig. 6B), indicating preferred use of these sites ($G = 167.27$; $P < 0.0001$; N sites = 315; N spiders = 146).

Host plants.—*Eustala sagana* occurred preferentially on *Hyptis suaveolens* (L.) Poit (Lamiaceae), *Conyza sumatrensis* (Retz.) E. Walker (Asteraceae), and *Vernonanthura ferruginea* (Less.) H. Rob. (Asteraceae) ($G = 278.5$; $P < 0.0001$; Fig. 7A; Table 1), while *E. taquara* occurred mainly on *C. bonariensis* (L.) Cronquist ($G = 107.70$; $P < 0.0001$, Fig. 7B; Table 2).

DISCUSSION

Both species exhibited similarities in habitat selection, and showed preferential use and restriction to forest borders, dead vegetation branches, and heights between 1.0 and 1.5 m above ground level. In contrast, results showed each species was distributed preferentially at a specific altitude, and on distinct plant species. These results are consistent with our hypothesis that the species are spatially segregated.

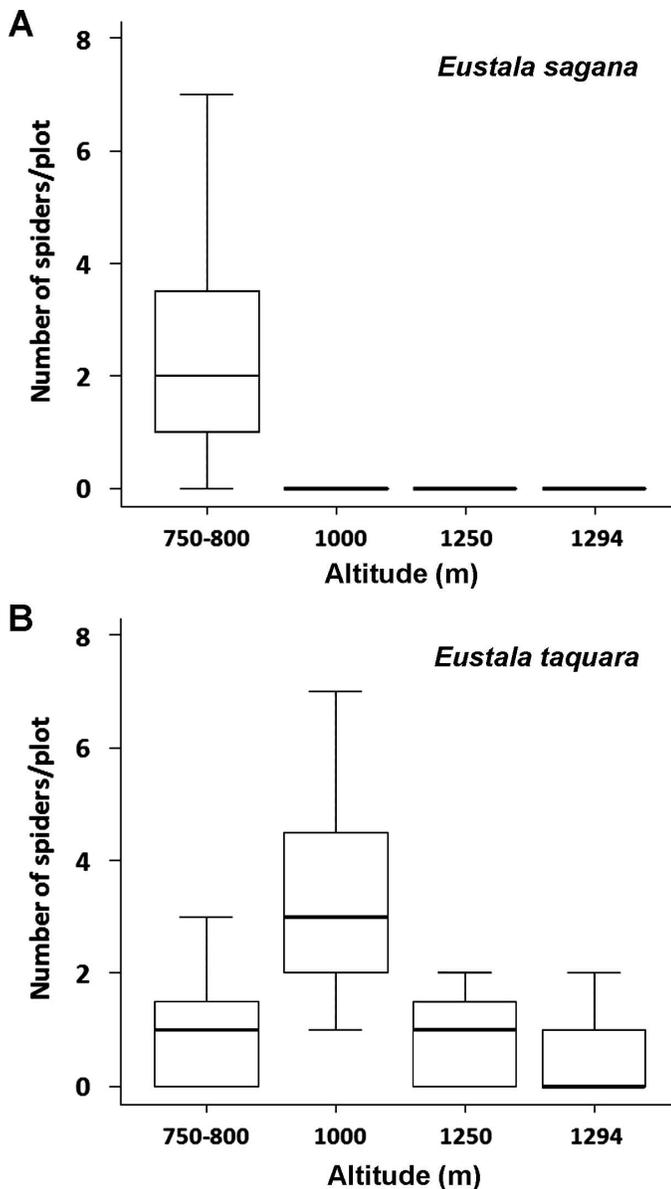


Figure 4.—*Eustala sagana* and *E. taquara* densities at different altitudes of the Serra do Japi, Jundiaí-SP. Box plots show median and interquartiles. Whiskers represent $1.5 \times$ interquartile ranges.

Eustala taquara occurred at a higher abundance at 1000 m, while *E. sagana* exhibited higher abundance at lower altitudes (750–850 m). Preferences regarding altitude might be a response to requirements for specific abiotic conditions (temperature, humidity, exposure to solar radiation), or to biotic criteria, including obtainable prey, exposure to predators, or availability of suitable web construction sites (Turnbull 1973; Brown 1981; Janetos 1986; Lubin et al. 1991; Marshall & Rypstra 1999). Similarly, Purcell & Avilés (2007) observed that altitude is an important factor affecting *Anelosimus* Simon 1891 (Theridiidae) species distribution and colony size (within social species of this genus) in Ecuador. The same authors suggested the influence of altitude occurred primarily in response to biotic factors, such as prey size and predator pressure; large insects were more common in

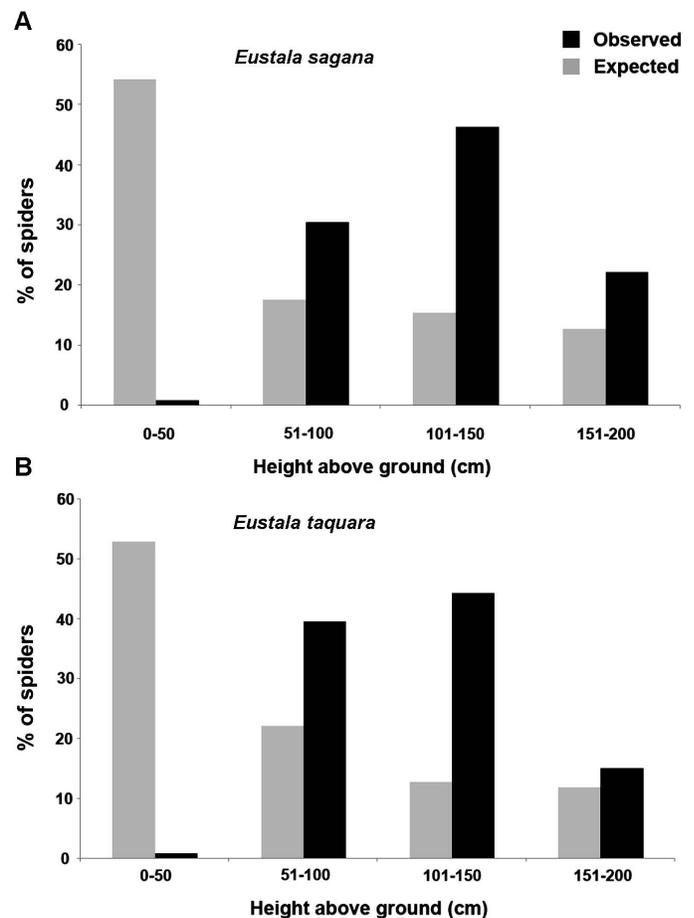


Figure 5.—Available (vegetation height) and observed sites used by *E. sagana* and *E. taquara* in Serra do Japi, Jundiaí-SP.

lowland rain forests, and predator pressures were reduced at higher altitudes. In addition, it is possible that spatial segregation between closely related species is a response to competition (but see Wise (1993) for evidence against competition in spiders). In a future investigations we intend to examine prey availability (types and sizes) for each species, web architecture variation, and possible variation in abiotic conditions along the altitudinal gradient to evaluate the causes of spatial segregation. It is also important to evaluate possible differences in the abundance of plant species along the gradient as a component of habitat selection.

Eustala taquara individuals were associated with herbaceous plants and shrubs that occurred on the forest edge, primarily *C. bonariensis*. This species apparently avoids constructing webs in *H. suaveolens*, which is preferentially used by *E. sagana*. Respective associations of *E. illicita* (O. Pickard-Cambridge 1889) and *E. oblonga* Chickering 1955 with *Acacia collinsii* Safford and *A. melanoceras* Beurl. have previously been characterized (Chickering 1955; Hesselberg & Triana 2010), suggesting habitat selection by some *Eustala* species. Despite the association of *E. illicita* with *A. collinsii*, Hesselberg & Triana (2010) also observed these spiders occupying dead vegetation along the study site, and concluded the relationships between *Eustala* and vegetation species are not obligatory.

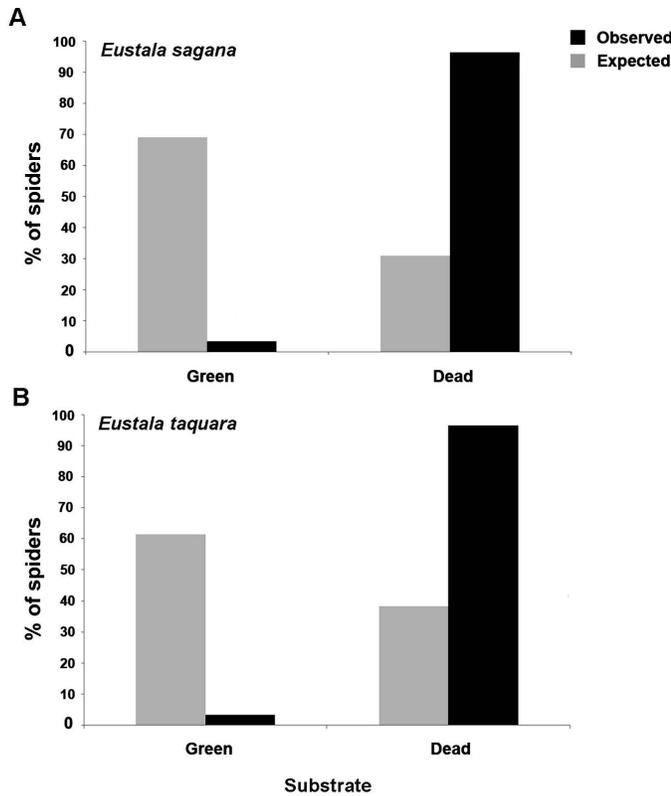


Figure 6.—Available green and dry (dead) vegetation sites and sites used by *Eustala sagana* and *E. taquara* in Serra do Japi, Jundiá-SP.

The selection of specific sites for web construction by *E. taquara* and *E. sagana* may be important to potentially reduce their conspicuousness and, consequently, exposure to visually oriented predators (such as birds and hunting wasps). We found that individuals of both species were apparently cryptic when resting in dry vegetation during the day. We have no information on their predators in Serra do Japi, but several empirical studies have demonstrated that *Eustala* species are hunted by *Trypoxylon* Latreille 1796 (Crabronidae) wasps (Rehnberg 1987; Gonzaga & Vasconcellos-Neto 2005; Buschini et al. 2008, 2010). *Eustala* is the most common prey found in nests of *Trypoxylon albonigrum* Richards 1934, for example, in another Atlantic forest area in São Paulo state (Gonzaga & Vasconcellos-Neto 2005; Araújo & Gonzaga 2007). It is important now to evaluate the ability of birds and wasps to perceive the chromatic and achromatic contrasts between the spiders and the substrates selected for web construction.

To conclude, this study showed that two congeneric sympatric species of *Eustala* present some similarities regarding habitat characteristics, such as preferential distribution close to the forest borders and occurrence on dead vegetation branches. However, there were also important differences in the two species' distributions. Their spatial segregation at distinct altitudes might reduce interference interactions between species. Future studies on prey preferences and experimental procedures manipulating the density of each species are essential to understanding the possible impact of each species on the abundance and habitat selection of the other.

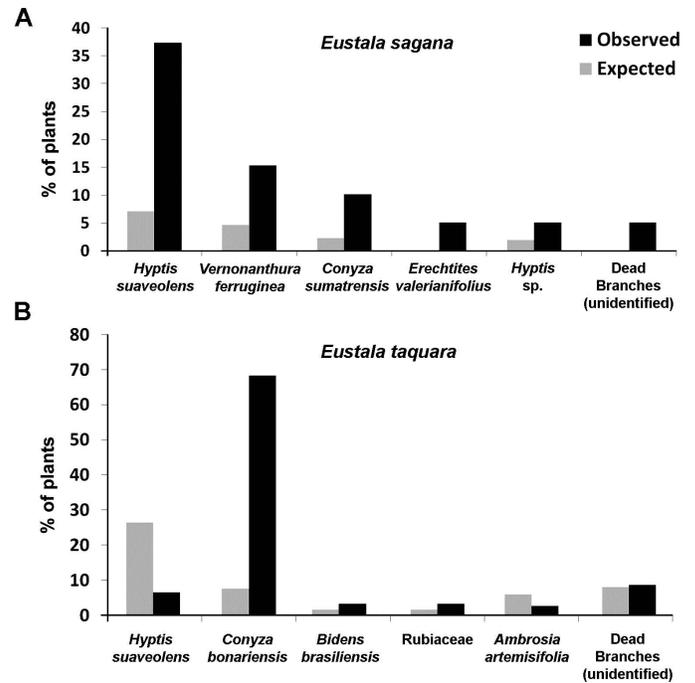


Figure 7.—Available plant species and plants occupied by *Eustala sagana* and *E. taquara* in Serra do Japi, Jundiá-SP.

ACKNOWLEDGMENTS

This project was supported by Instituto Nacional de Ciência e Tecnologia dos Hymenoptera Parasitoides da Região Sudeste (<http://www.hympar.ufscar.br>) and Fundação de Amparo à Pesquisa do Estado de São Paulo (processes: 2011/02535-3, 2011/15457-0, 2011/15456-4 and 2011/02537-6). We also thank Antonio Domingos Brescovit and Maria Rita M. Poeta for the identification of the spiders, and we appreciate the valuable suggestions of the reviewers.

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Manuscript received 18 April 2014, revised 24 September 2014.