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# What is better for sampling canopy spiders in the Amazon rainforest: a good tree or a good canopy?

O que é melhor para amostrar aranhas de dossel na floresta amazônica: uma boa árvore ou um bom dossel?

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**Abstract:** Despite being one of the largest Neotropical biomes, the Amazon rainforest presents a strong sampling bias. Most of its known spider fauna is reported from easily accessed environments, while canopy spider fauna is understudied. Sampling canopy spider fauna using fogging machines is based on two distinct approaches: (1) sampling the canopy of a target tree species ('single species'); or (2) sampling the fauna from a closed canopy, with overlapping branches of different tree species ('closed canopy'). These approaches have never been compared before. In the present manuscript, we provided evidence that fogging samples in both approaches yield a similar number of adult spiders and species. However, species composition differs between the two methods. The pros and cons of each approach are discussed and the choice between them should depend on project goals.

**Keywords:** Fogging. Araneae. Community ecology. Eltonian shortfall.

**Resumo:** Apesar de ser um dos maiores biomas neotropicais, a floresta amazônica apresenta um forte viés de amostragem. Grande parte da fauna de aranhas conhecida provém de ambientes de fácil acesso, enquanto a fauna de aranhas do dossel é pouco estudada. A amostragem da fauna de aranhas do dossel usando máquinas de nevoeiro baseia-se em duas abordagens distintas: (1) amostrar o dossel de uma espécie de árvore-alvo ('uma única espécie'); ou (2) amostrar a fauna de um dossel fechado, com galhos sobrepostos de diferentes espécies de árvores ('dossel fechado'). Essas abordagens nunca foram comparadas antes. No presente manuscrito, fornecemos evidências de que as amostras de nevoeiro em ambas as abordagens resultam em um número semelhante de aranhas adultas e espécies. No entanto, a composição das espécies difere entre os dois métodos. Os prós e contras de cada abordagem são discutidos e a escolha entre elas deve depender dos objetivos do projeto.

**Palavras-chave:** *Fogging*. Araneae. Ecologia de comunidades. Déficit eltoniano.

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## INTRODUCTION

The Amazon forest is well recognized as the most species rich tropical forest in the world, also serving as a primary source for Neotropical biodiversity (Antonelli et al., 2018). However, for spiders, this pattern is not fully recovered, in part owing to strong sampling biases (Oliveira et al., 2016, 2017). While the Amazon forest occupies an area ca. 3.8 times that of Atlantic forest, the Amazon forest presents ca. 62% of the spider species richness recorded for the Atlantic forest (1,036 vs 1,672 spp., respectively; Oliveira et al., 2017). These differences reflect sampling heterogeneity: only about 12% of the Amazon forest area presents at least one spider distribution record, while about 92% of the Atlantic forest area has records of spider species (Oliveira et al., 2017). Disregarding this sampling deficiency, both of these biomes share a particular bias with regard to the known taxa: they are mostly known from easily accessible environments, while the leaf litter and the forest canopy are poorly studied microhabitats (Basset, 2001; Oliveira et al., 2017).

A significant part of this biodiversity is found in the forest canopy, a critical habitat that harbors a unique and often underexplored array of species (Basset, 2001; Erwin, 1989). The canopy, functioning as a distinct ecosystem, plays a key role in photosynthesis, sexual reproduction, light absorption, shading, nutrient cycling, atmospheric-meteorological interaction, hydrologic interactions, and biological diversity (Shaw & Bible, 1996). Its complex vertical stratification supports different species assemblages compared to the forest floor (e.g., Lindo & Winchester, 2006; Oguri et al., 2014), making it essential for understanding overall forest biodiversity. However, sampling the canopy spider fauna is not an easy task, in terms of access and spatial heterogeneity (Mupepele et al., 2014; Ozanne, 2005). For example, at low canopy sites (e.g., under 20 m) the sampling can be carried out from the ground (e.g., fogging and branch clipping) (Adis et al., 1984; Ozanne, 2005). However, at sites with higher canopy (e.g., over 20 m), effective sampling can only be

attained from within the canopy (e.g., rope climbing, hoisting the fogging machine, or using drones, hoisted pitfall traps, canopy sweeping or arboreal traps) (Madden et al., 2022; Matevski et al., 2020; Ozanne, 2005; Sena et al., 2010; Viana-Junior et al., 2021). Among the methods used, fogging (i.e., chemical knockdown) is arguably the most effective and widely used sampling method for assessing the canopy fauna (Ozanne, 2005).

The knowledge regarding the Brazilian canopy spider fauna is scarce, highly concentrated in a few localities and mostly based on samplings with fogging. During the 80s and 90s, several papers investigated the ecology of canopy spiders at Amazonian forest sites near Manaus (Adis et al., 1984, 1997; Höfer et al., 1994). Later, samplings were carried out in the Pantanal of Poconé (Battirola et al., 2004, 2016; Marques et al., 2006, 2007; Yamazaki et al., 2017), in the urban Atlantic Forest remains at Salvador (Sena et al., 2010) and in the Cerrado of Brasília (Gurgel-Gonçalves et al., 2006). These studies could be divided into two different sampling approaches. Most of them focused on the spider canopy fauna from a single tree species (Adis et al., 1997; Adis et al., 1998b; Battirola et al., 2004, 2016; Höfer et al., 1994; Marques et al., 2006, 2007; Yamazaki et al., 2017), while only a few studies focused on the canopy fauna from general forested sites (Adis et al., 1984; Sena et al., 2010), presumably with a closed canopy.

The effect of sampling with fogging using these two different approaches has never been tested. Samplings carried out in other regions worldwide share the same duality, either sampling single tree species (Floren et al., 2008, 2011; Mupepele et al., 2014; Otto & Floren, 2010; Pashkevich et al., 2022; Wildermuth et al., 2023) or, less commonly, closed canopies (Junggebauer et al., 2021; Ramos et al., 2022; Sørensen, 2004). Most of these studies were carried out in temperate forests, where targeting specific tree species is a viable alternative, owing to the particularly low tree diversity compared to tropical and subtropical moist forest biomes (Cazzolla-Gatti et al., 2022). However, in tropical forests, areas



where the crown canopy architecture and overlapping branches of different tree species hamper the process of carrying out fogging for single tree species, making it impossible to associate each animal species to specific tree species (Erwin, 1989). Owing to these structural characteristics of tropical forest trees, Erwin (1989) proposed that fogging should be carried out targeting single tree species, a proposal later followed as a rule of thumb (see Adis et al., 1998a).

In the present study, we aimed to compare the spider assemblages from an Amazon forest locality, collected using these two approaches for canopy fogging: sampling target tree species (hereafter only 'single species'), or sampling at sites with a closed canopy. Our study also provides an unique opportunity to discuss the vertical stratification of spider assemblage in the Amazon biome, as the spider fauna from the study site can be considered relatively well-known (Bonaldo & Dias, 2010; Carvalho et al., 2010; Dias & Bonaldo, 2012).

## MATERIAL AND METHODS

### SAMPLING SPIDERS

The study site is located at the Base de Operações Geólogo Pedro de Moura (4° 51' 7" S, 65° 16' 59" W), an oil and gas drilling area of the Petrobras S.A., at the Urucu River basin, Coari, Amazonas, northern Brazil. The area has approximately 520,000 hectares of continuous Amazon forest and it is located about 650 km west of the city of Manaus, Amazonas. The region is covered by dense, uniform-canopy *terra firme* rainforest, with few floodable areas, with *várzea* occurring only along the sandy banks of the Urucu River. Notable changes in vegetation structure occur where the soil is poorly drained or in clearings opened artificially for natural gas and oil exploration and production (see Bonaldo & Dias, 2010). The trees range between 23-32 meters in height and have low densities of epiphytes and lianas (Lima-Filho et al., 2001).

The sampling was carried out with canopy fogging in two occasions, at haphazard sampling sites. In the first expedition, nine areas (i.e., nine independent samples for statistical purposes) with closed canopies formed by a mixture of tree species with overlapping branches were sampled from October 28 to November 4, 2008. At each sampling, the spiders were intercepted by 13 fabric sheets of 1.5 x 4 m (total of 78 m<sup>2</sup> of interception area per sampling) placed directly under the sampled canopy (Figure 1A). In the second sampling, eight canopies (i.e., eight independent samples for statistical purposes) of *Eschweilera atropetidata* S.A. Mori (Lecythidaceae), commonly known as '*matá-matá branco*' or '*castanha-vermelha*', were sampled from August 30 to September 7, 2009. The sampled trees were selected according to the rule of thumb for single species fogging (see Adis et al., 1998a), by choosing a common species (for allowing replication), without flowers or fruits, and with few epiphytes. The genus *Eschweilera* is the most abundant angiosperm tree genus in the study site, although it is also one that most host epiphytes too (Irumé et al., 2013). At each sampling, the spiders were intercepted by 7-8 fabric sheets (same as for closed canopy samplings; total of 42-48 m<sup>2</sup> of interception area per sampling) placed directly under the sampled canopy. The number of fabric sheet used in each sampling differed owing to logistical reasons. These differences were considered in the analytical methods applied.

In both expeditions, the fogging was carried out in the morning to take advantage of the lower wind circulation, preventing the cloud of chemical droplets from dissipating away from the target canopy (Figures 1C-1D). A fogger model pulsFOG K-10 / 6 volt 0.5 A / 24 CV was used for 30 minutes per sample, with the smoke jet directed from the ground towards the tree canopies (Figure 1B). A non-residual synthetic pyrethroid (K-Othrine® insecticide) diluted in diesel oil at a concentration of 10% and permethrin (100 ml) was used as the active ingredient to increase the



Figure 1. Canopy fogging carried out at Urucu River basin: (A) fabric sheet disposed for intercepting the spiders before fogging application; (B) fogging application; (C-D) cloud of knockdown chemicals during fogging application. Photos: S. C. Dias (2008).

knockdown effect on organisms (see Adis et al., 1997). The collected individuals were fixed in 80% alcohol, stored in labeled vials, and later identified. Juveniles were not considered for the present study. Adults of both expeditions were grouped and identified to the species level or assigned to morphospecies when the identification to the species level was not possible. All specimens are deposited in the arachnological collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG; curator A.B. Bonaldo).

### STATISTICAL ANALYSES

The number of males and females was compared using chi-squared tests for equal proportions. A species richness estimative was calculated using the 'iNEXT' function of the

package 'iNEXT', for  $q = 0$  (Hsieh et al., 2016), which is based on the methods proposed in Chao (1984, 1987). The mean numbers of adult spiders and species per fabric sheet used in each sample was compared between treatments (i.e., 'closed canopy' vs. 'single species') using generalized linear models with gaussian distribution of errors. Dispersion issues were checked based on the raw dispersion parameters and using the 'rdiagnostic' function of the package 'RT4Bio' (Reis Jr. et al., 2015). To compare the spider species composition among treatments, we performed a permutational multivariate analysis of variance using distance matrices – PERMANOVA, using Bray-Curtis dissimilarity index (function 'adonis2', package 'vegan' Oksanen et al., 2024). To represent graphically the dissimilarity among spider assemblages

from each treatment, we also performed a nonmetric multidimensional scaling – NMDS, using Bray-Curtis dissimilarity index and calculated for two dimensions (function 'metaMDS', package 'vegan' Oksanen et al., 2024). Whittaker plots of the species abundance data were produced for each assemblage (function 'racurve', package 'goeveg'; von Lampe & Schellenberg, 2024). All analyses were carried out in R programming, through RStudio 2024.04.2 Build 764 (RStudioTeam, 2020).

## RESULTS AND DISCUSSION

We collected 723 adult spiders, including 338 males and 385 females (sex ratio males/females = 0.88;  $\chi^2 = 3.05$ ,  $df = 1$ ,  $p = 0.08$ ). Closed canopy fogging yielded 431 adults, including 192 males and 239 females (sex ratio = 0.80;  $\chi^2 = 5.125$ ,  $df = 1$ ,  $p = 0.02$ ); while single species fogging yielded 292 adults, including 146 males and 146 females (sex ratio = 1.0;  $\chi^2 = 0$ ,  $df = 1$ ,  $p = 1$ ). Spider abundance in both treatments was not significantly different (deviance = 0.212,  $df = 15$ ,  $p =$

0.777; Figure 2). The biased sampling towards females is similar to that observed for other spider inventories, not based on passive (i.e., pitfall traps) sampling methods (e.g., Bomfim et al., 2021; Mendes et al., 2018; Prado & Baptista, 2023; Rodrigues et al., 2009), including canopy fogging samplings (e.g., Battirolo et al., 2004). In fact, it is widely known that adult male spiders are relatively short lived and wander in search of mating pairs, which induces a higher mortality than in females (Coddington et al., 2009; Vollrath & Parker, 1992), but increases their capture by passive sampling methods (e.g., Engelbrecht, 2013).

A total of 272 spider species were recorded with fogging at the Urucu River basin, of which only 56 species (20.6%) were collected in both fogging treatments (Table 1). 197 species were collected in the closed canopy fogging, including 141 exclusive species (71.6%). 131 species were collected in the single species canopy fogging, including 75 exclusive species (57.3%). Spider species richness in both treatments was not significantly different (deviance = 0.592,  $df = 15$ ,  $p = 0.4345$ ; Figure 2).

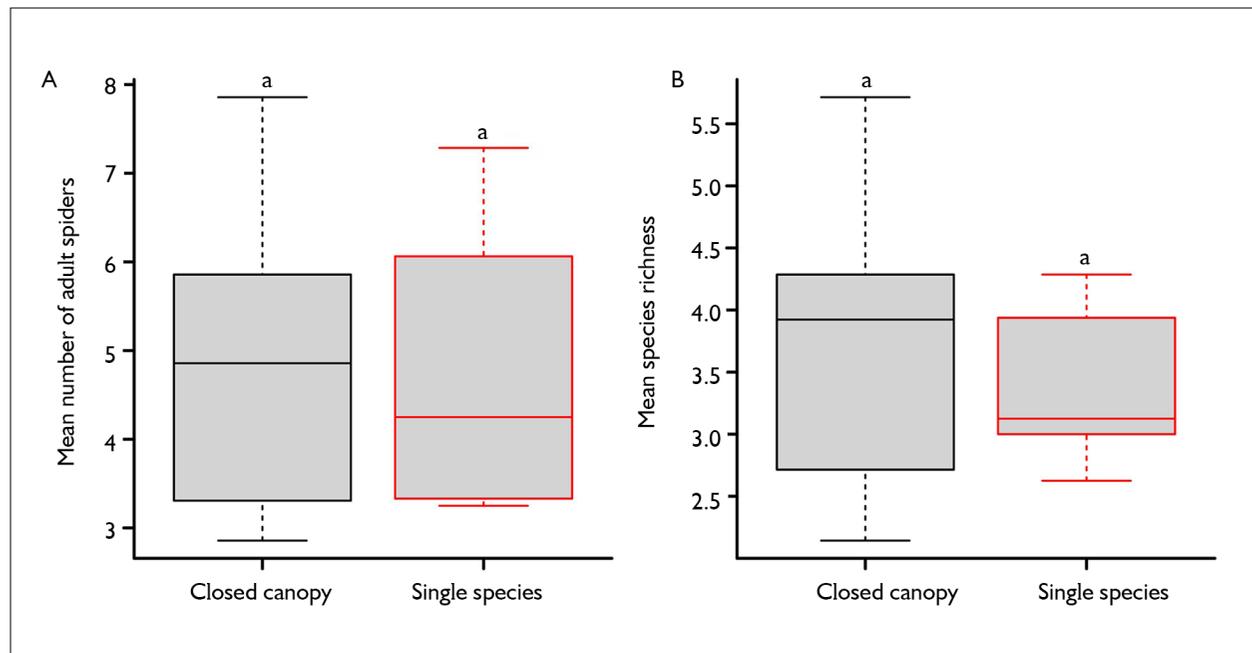


Figure 2. Comparison of the mean number of adult spiders (A) and mean species richness (B) collected per fabric sheet by fogging at closed canopy sites ('Closed canopy') and under the canopy of *Eschweilera atropetidata* ('Single species').

Table 1. List of adult spider species collected in both inventories carried out at Urucu River basin. 'Single species' refers to canopy fogging sampled carried out under *Eschweilera atropetidata* trees. 'Closed canopy' refers to canopy fogging samples under forests with closed canopies of different trees. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Anyphaenidae	13	9	19	17	58
<i>Isigonia limbata</i> Simon, 1897	0	0	0	1	1
<i>Macrophyes</i> sp.1	0	0	2	0	2
Anyphaenidae sp.1	0	2	0	5	7
Anyphaenidae sp.10	0	1	0	0	1
Anyphaenidae sp.11	0	0	3	1	4
Anyphaenidae sp.12	2	0	0	1	3
Anyphaenidae sp.13	0	0	1	1	2
Anyphaenidae sp.14	0	0	2	2	4
Anyphaenidae sp.2	1	1	0	1	3
Anyphaenidae sp.3	6	1	1	0	8
Anyphaenidae sp.4	1	0	5	1	7
Anyphaenidae sp.5	0	1	0	0	1
Anyphaenidae sp.6	0	1	1	1	3
Anyphaenidae sp.7	3	1	0	0	4
Anyphaenidae sp.8	0	1	0	1	2
Anyphaenidae sp.9	0	0	4	2	6
Araneidae	16	14	30	42	102
<i>Alpaida chickeringi</i> Levi, 1988	0	0	1	0	1
<i>Alpaida delicata</i> (Keyserling, 1892)	0	0	2	1	3
<i>Alpaida guto</i> Abraham & Bonaldo, 2008	0	0	0	1	1
<i>Alpaida truncata</i> (Keyserling, 1865)	0	0	0	1	1
<i>Alpaida</i> sp.1	2	0	2	1	5
<i>Alpaida</i> sp.2	1	0	0	0	1
<i>Alpaida</i> sp.3	1	0	0	1	2
<i>Alpaida</i> sp.4	0	0	2	0	2
<i>Alpaida</i> sp.6	1	0	0	0	1
<i>Amazonopeira</i> sp.1	0	1	1	2	4
<i>Bertrana elinguis</i> (Keyserling, 1883)	0	0	0	3	3
<i>Cyclosa fililineata</i> Hingston, 1932	0	1	0	0	1
<i>Enacrosoma</i> sp.1	0	0	0	1	1
<i>Encyosaccus</i> sp.1	2	0	0	0	2
<i>Eustala</i> sp.1	0	0	0	1	1
<i>Eustala</i> sp.2	0	0	0	1	1
<i>Eustala</i> sp.4	0	0	2	0	2
<i>Hypognatha belem</i> Levi, 1996	2	1	0	0	3
<i>Hypognatha</i> sp.1	0	1	0	2	3



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Hypognatha</i> sp.2	1	0	1	0	2
<i>Hypognatha</i> sp.3	0	0	1	0	1
<i>Mangora</i> sp.1	0	0	1	2	3
<i>Mangora</i> sp.2	0	0	1	0	1
<i>Mangora</i> sp.3	2	3	0	0	5
<i>Mangora</i> sp.4	0	0	0	1	1
<i>Metazygia</i> sp.1	1	0	0	1	2
<i>Micrathena acuta</i> (Walckenaer, 1841)	0	0	1	1	2
<i>Micrathena aff. agrilliformis</i> (Taczanowski, 1879)	0	0	1	0	1
<i>Micrathena aureola</i> (C. L. Koch, 1836)	0	1	0	0	1
<i>Micrathena clypeata</i> (Walckenaer, 1805)	0	0	0	2	2
<i>Micrathena miles</i> Simon, 1895	0	0	0	5	5
<i>Micrathena pungens</i> (Walckenaer, 1841)	0	0	0	1	1
<i>Micrathena sexspinosa</i> (Hahn, 1822)	0	1	0	0	1
<i>Micrathena triangularispinosa</i> (De Geer, 1778)	0	1	0	2	3
<i>Micrathena vigorsi</i> (Perty, 1833)	0	0	0	2	2
<i>Micrathena</i> sp.1	0	0	1	0	1
<i>Ocrepeira</i> sp.1	0	0	1	1	2
<i>Ocrepeira</i> sp.2	0	0	0	1	1
<i>Parawixia divisoria</i> Levi, 1992	0	0	1	0	1
<i>Parawixia kochi</i> (Taczanowski, 1873)	0	0	1	1	2
<i>Parawixia</i> sp.1	0	0	1	0	1
<i>Spintharidius rhomboidalis</i> Simon, 1893	0	0	1	0	1
<i>Testudinaria quadripunctata</i> Taczanowski, 1879	1	2	0	0	3
<i>Verrucosa</i> sp.1	0	1	5	3	9
<i>Verrucosa</i> sp.2	0	0	0	1	1
<i>Wagneriana jelskii</i> (Taczanowski, 1873)	0	0	1	0	1
<i>Wagneriana</i> sp.1	0	0	1	0	1
<i>Xylethrus</i> sp.1	0	0	1	0	1
Araneidae sp.1	1	0	0	0	1
Araneidae sp.2	1	1	0	0	2
Araneidae sp.4	0	0	0	1	1
Araneidae sp.5	0	0	0	2	2
Clubionidae	0	0	1	3	4
<i>Elaver sigillata</i> (Petrunkevitch, 1925)	0	0	1	3	4
Corinnidae	7	7	17	14	45
<i>Castianeira</i> sp.1	6	5	1	0	12
<i>Castianeira</i> sp.2	0	0	2	0	2



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Castianeira</i> sp.3	0	0	1	0	1
<i>Corinna ducke</i> Bonaldo, 2000	0	0	0	1	1
<i>Corinna</i> sp.1	0	0	3	1	4
<i>Corinna</i> sp.3	0	0	0	1	1
<i>Corinna</i> sp.4	0	0	2	2	4
<i>Creugas</i> sp.1	0	1	0	0	1
<i>Myrmecium</i> sp.1	0	0	1	2	3
<i>Myrmecotypus</i> sp.1	0	0	6	2	8
<i>Myrmecotypus</i> sp.2	1	0	0	1	2
<i>Parachemmis</i> sp.1	0	1	0	0	1
<i>Parachemmis</i> sp.2	0	0	0	1	1
<i>Sphecotypus niger</i> (Perty, 1833)	0	0	0	1	1
<i>Stethorrhagus lupulus</i> Simon, 1896	0	0	0	1	1
<i>Tupirinna</i> sp.1	0	0	0	1	1
<i>Tupirinna</i> sp.2	0	0	1	0	1
Ctenidae	0	0	1	1	2
<i>Ctenus crulsi</i> Mello-Leitão, 1930	0	0	0	1	1
<i>Ctenus</i> sp.2	0	0	1	0	1
Deinopidae	0	0	0	1	1
<i>Deinopis</i> sp.1	0	0	0	1	1
Dictynidae	4	2	0	0	6
<i>Thallumetus</i> sp.1	3	1	0	0	4
Dictynidae sp.1	1	1	0	0	2
Gnaphosidae	1	0	1	2	4
<i>Zimiromus</i> sp.1	0	0	1	2	3
Gnaphosidae sp.1	1	0	0	0	1
Hahniidae	0	5	0	0	5
<i>Hahnia</i> sp.n 1	0	5	0	0	5
Hersiliidae	0	0	1	0	1
<i>Ypyuera crucifera</i> (Vellard, 1924)	0	0	1	0	1
Linyphiidae	1	0	0	0	1
Linyphiidae sp.1	1	0	0	0	1
Mimetidae	1	0	0	1	2
<i>Ero</i> sp.1	1	0	0	1	2
Oonopidae	17	29	0	1	47
<i>Gradunguloonops mutum</i> Grismado et al., 2015	5	9	0	0	14



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Gradunguloonops urucu</i> Grismado et al., 2015	1	4	0	0	5
<i>Orchestina</i> sp.1	2	6	0	0	8
<i>Orchestina</i> sp.2	5	6	0	0	11
Oonopidae sp.1	4	1	0	1	6
Oonopidae sp.2	0	1	0	0	1
Oonopidae sp.3	0	1	0	0	1
Oonopidae sp.4	0	1	0	0	1
Oxyopidae	3	2	2	8	15
<i>Oxyopes argyrotrichus</i> Mello-Leitão, 1929	0	0	0	5	5
<i>Oxyopes hemorrhous</i> Mello-Leitão, 1929	1	1	0	0	2
<i>Oxyopes holmbergi</i> Soares & Camargo, 1948	2	0	0	0	2
<i>Oxyopes incertus</i> Mello-Leitão, 1929	0	0	0	1	1
<i>Oxyopes</i> sp.1	0	1	0	0	1
<i>Oxyopes</i> sp.2	0	0	0	1	1
<i>Schaenicoscelis</i> sp.1	0	0	1	1	2
<i>Schaenicoscelis</i> sp.2	0	0	1	0	1
Pholcidae	5	1	10	16	32
<i>Carapoia fowleri</i> Huber, 2000	0	0	1	0	1
<i>Mesabolivar aurantiacus</i> (Mello-Leitão, 1930)	1	0	4	4	9
<i>Metagonia beni</i> Huber, 2000	1	0	1	2	4
<i>Metagonia taruma</i> Huber, 2000	3	1	4	10	18
Pisauridae	0	2	0	1	3
<i>Architis cymatilis</i> Carico, 1981	0	1	0	0	1
<i>Architis tenuis</i> Simon, 1898	0	1	0	0	1
<i>Thaumasia</i> sp.1	0	0	0	1	1
Salticidae	19	18	27	59	123
<i>Aillutticus</i> sp.1	1	0	0	0	1
<i>Amycus</i> sp.1	0	0	0	7	7
<i>Amycus</i> sp.2	0	0	0	1	1
<i>Breda lubomirskii</i> (Taczanowski, 1878)	0	0	0	1	1
<i>Colonus aff. vaccula</i> (Simon, 1900)	0	0	0	1	1
<i>Coryphasia</i> sp.1	0	1	0	0	1
<i>Coryphasia</i> sp.2	0	3	0	0	3
<i>Cotinusa</i> sp.1	0	1	0	0	1
<i>Encolpius</i> sp.1	0	0	0	1	1
<i>Eustiromastix</i> sp.1	0	0	0	1	1



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Hasarius adansoni</i> (Audouin, 1826)	0	0	2	2	4
<i>Hypaeus</i> sp.1	1	0	0	0	1
<i>Hypaeus</i> sp.2	5	0	0	0	5
<i>Hypaeus</i> sp.3	0	0	0	3	3
<i>Hypaeus</i> sp.4	0	0	0	1	1
<i>Itata</i> sp.1	0	0	0	4	4
<i>Itata</i> sp.2	0	0	0	1	1
<i>Lyssomanes nigropictus</i> Peckham et al., 1889	1	1	2	1	5
<i>Lyssomanes</i> sp.1	0	1	0	0	1
<i>Lyssomanes</i> sp.2	1	0	1	0	2
<i>Lyssomanes</i> sp.4	1	1	0	0	2
<i>Lyssomanes</i> sp.5	0	0	2	0	2
<i>Lyssomanes</i> sp.6	0	0	1	0	1
<i>Lyssomanes</i> sp.7	0	0	1	0	1
<i>Lyssomanes</i> sp.8	0	0	0	1	1
<i>Matinta acutidens</i> (Simon, 1900)	0	0	1	0	1
<i>Myrmapana mocamboensis</i> (Galiano, 1974)	1	1	0	0	2
<i>Myrmarachne</i> sp.1	0	1	0	0	1
<i>Noegus niveomarginatus</i> Simon, 1900	0	0	2	1	3
<i>Nycerella</i> sp.1	0	0	1	0	1
<i>Pachomius</i> sp.1	0	0	2	0	2
<i>Psecas</i> sp.1	0	1	0	0	1
<i>Psecas</i> sp.2	0	0	0	1	1
<i>Scopocira tenella</i> Simon, 1900	1	0	1	5	7
<i>Sidusa</i> sp.1	0	0	1	0	1
Salticidae sp.1	2	0	0	10	12
Salticidae sp.10	0	0	0	1	1
Salticidae sp.11	0	0	0	2	2
Salticidae sp.12	0	0	0	1	1
Salticidae sp.13	0	0	1	2	3
Salticidae sp.15	0	0	1	0	1
Salticidae sp.16	0	0	1	0	1
Salticidae sp.17	0	0	1	0	1
Salticidae sp.18	0	0	1	0	1
Salticidae sp.19	0	0	0	1	1
Salticidae sp.2	1	2	0	1	4



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Salticidae sp.20	0	0	0	1	1
Salticidae sp.21	0	0	0	1	1
Salticidae sp.3	3	2	0	0	5
Salticidae sp.4	1	0	0	1	2
Salticidae sp.5	0	1	0	1	2
Salticidae sp.6	0	1	1	0	2
Salticidae sp.7	0	1	1	0	2
Salticidae sp.8	0	0	1	4	5
Salticidae sp.9	0	0	2	1	3
Scytodidae	6	3	0	2	11
<i>Scytodes altamira</i> Rheims & Brescovit, 2000	1	0	0	2	3
<i>Scytodes romitii</i> Caporiacco, 1947	4	3	0	0	7
<i>Scytodes</i> sp.1	1	0	0	0	1
Selenopidae	1	0	2	1	4
<i>Selenops</i> sp.1	1	0	2	1	4
Senoculidae	0	1	1	3	5
<i>Senoculus</i> sp.1	0	1	1	2	4
<i>Senoculus</i> sp.2	0	0	0	1	1
Sparassidae	0	0	1	1	2
<i>Vindullus gracilipes</i> (Taczanowski, 1872)	0	0	1	1	2
Tetrablemmidae	0	1	0	0	1
Tetrablemmidae sp.1	0	1	0	0	1
Tetragnathidae	1	0	0	0	1
<i>Tetragnatha</i> sp.1	1	0	0	0	1
Theridiidae	40	41	42	42	165
<i>Achaearanea trapezoidalis</i> (Taczanowski, 1873)	0	0	1	0	1
<i>Achaearanea</i> sp.1	0	0	0	1	1
<i>Achaearanea</i> sp.2	0	0	0	1	1
<i>Achaearanea</i> sp.3	1	0	0	0	1
<i>Achaearanea</i> sp.4	0	1	0	0	1
<i>Anelosimus eximius</i> (Keyserling, 1884)	0	0	0	1	1
<i>Cerocida ducke</i> Marques & Buckup, 1989	0	0	1	2	3
<i>Chryso</i> sp.1	0	1	0	1	2
<i>Cryptachaea dalana</i> (Buckup & Marques, 1991)	0	0	2	1	3
<i>Cryptachaea pydanieli</i> (Buckup & Marques, 1991)	1	0	1	0	2
<i>Dipoena atlantica</i> Chickering, 1943	2	0	2	0	4



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Dipoena duodecimpunctata</i> Chickering, 1943	3	1	1	0	5
<i>Dipoena esra</i> Levi, 1963	1	2	0	1	4
<i>Dipoena militaris</i> Chickering, 1943	4	0	1	0	5
<i>Dipoena tingo</i> Levi, 1963	2	1	1	1	5
<i>Dipoena</i> sp.1	5	3	3	3	14
<i>Dipoena</i> sp.2	0	2	0	2	4
<i>Dipoena</i> sp.3	0	0	1	0	1
<i>Dipoena</i> sp.4	0	0	1	0	1
<i>Dipoena</i> sp.5	1	0	0	0	1
<i>Dipoena</i> sp.6	0	1	0	0	1
<i>Dipoena</i> sp.7	1	0	0	0	1
<i>Episinus immundus</i> (Keyserling, 1884)	1	0	2	2	5
<i>Episinus</i> sp.1	0	0	2	0	2
<i>Euryopis</i> sp.1	0	0	0	3	3
<i>Euryopis</i> sp.2	0	1	0	0	1
<i>Euryopis</i> sp.3	1	4	0	0	5
<i>Helvibis</i> sp.1	1	0	8	6	15
<i>Janula bicrucata</i> (Simon, 1895)	0	0	1	2	3
<i>Janula salobrensis</i> (Simon, 1895)	3	8	1	2	14
<i>Lasaeola donaldi</i> (Chickering, 1943)	1	0	0	0	1
<i>Phoroncidia studo</i> Levi, 1964	0	2	0	0	2
<i>Phoroncidia</i> sp.1	1	0	0	0	1
<i>Phycosoma altum</i> (Keyserling, 1886)	1	3	0	0	4
<i>Spintharus</i> sp.1	0	0	2	3	5
<i>Theridion</i> sp.1	0	0	0	1	1
<i>Theridion</i> sp.2	1	0	0	0	1
<i>Theridion</i> sp.3	0	1	0	0	1
<i>Thwaitesia affinis</i> O. Pickard-Cambridge, 1882	1	0	1	0	2
<i>Thwaitesia bracteata</i> (Exline, 1950)	0	0	6	3	9
<i>Thymoites piarco</i> (Levi, 1959)	1	0	2	2	5
Theridiidae sp.1	1	7	0	1	9
Theridiidae sp.10	1	0	0	0	1
Theridiidae sp.11	1	0	0	0	1
Theridiidae sp.13	1	0	0	0	1
Theridiidae sp.2	2	2	0	0	4
Theridiidae sp.3	0	0	2	0	2
Theridiidae sp.5	0	0	0	1	1
Theridiidae sp.7	0	0	0	1	1
Theridiidae sp.8	0	0	0	1	1



Table 1.

(Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Theridiidae sp.9	1	1	0	0	2
Theridiosomatidae	1	1	1	0	3
<i>Chthonos</i> sp.1	0	1	1	0	2
Theridiosomatidae sp.1	1	0	0	0	1
Thomisidae	4	3	17	8	32
<i>Aphantochilus rogersi</i> O. Pickard-Cambridge, 1871	0	0	0	1	1
<i>Epicadus</i> sp.1	0	1	4	0	5
<i>Epicadus</i> sp.2	0	0	3	0	3
<i>Epicadus</i> sp.3	0	0	0	1	1
<i>Tmarus</i> sp.1	1	0	0	2	3
<i>Tmarus</i> sp.2	0	0	2	0	2
<i>Tmarus</i> sp.3	0	0	4	1	5
<i>Tmarus</i> sp.4	0	1	0	0	1
<i>Tmarus</i> sp.5	0	1	0	0	1
<i>Tmarus</i> sp.6	1	0	0	0	1
<i>Tmarus</i> sp.7	1	0	0	0	1
<i>Tmarus</i> sp.8	0	0	0	1	1
<i>Tmarus</i> sp.9	0	0	0	1	1
Thomisidae sp.1	1	0	0	0	1
Thomisidae sp.2	0	0	0	1	1
Thomisidae sp.3	0	0	1	0	1
Thomisidae sp.4	0	0	1	0	1
Thomisidae sp.5	0	0	1	0	1
Thomisidae sp.6	0	0	1	0	1
Trachelidae	1	2	5	5	13
<i>Orthobula</i> sp.1	1	0	0	1	2
<i>Trachelas</i> sp.1	0	2	5	3	10
<i>Trachelas</i> sp.2	0	0	0	1	1
Trechaleidae	2	2	5	5	14
<i>Cupiennius bimaculatus</i> (Taczanowski, 1874)	0	0	1	0	1
<i>Rhoicinus urucu</i> Brescovit & Oliveira, 1994	0	0	0	1	1
<i>Syntrechalea adis</i> Carico, 2008	0	1	2	2	5
<i>Syntrechalea</i> sp.1	0	0	0	1	1
<i>Trechalea</i> sp.1	2	1	2	1	6
Uloboridae	3	3	9	6	21
<i>Miagrammopes</i> sp.1	3	2	6	3	14
<i>Miagrammopes</i> sp.2	0	0	0	2	2



Table 1. (Conclusion)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
<i>Philoponella</i> sp.1	0	0	1	1	2
<i>Philoponella</i> sp.2	0	0	1	0	1
<i>Zosis</i> sp.1	0	1	0	0	1
Uloboridae sp.1	0	0	1	0	1
Total	146	146	192	239	723

The observed species richness represents about 43.7% of the maximum species richness ever reported for the same locality in previous studies (393 spp. in Bonaldo & Dias, 2010; 623 spp. in Dias & Bonaldo, 2012). As the specimens' identifications between the present and past studies were not standardized, it is not possible to evaluate the proportion of the spider fauna from the Urucu River basin that lives exclusively in the forest canopy. However, this provides a good estimate of the spider assemblage in these different vertical strata. Only one additional locality in the Amazon biome has similar data for comparison. For the Reserva Florestal Adolpho Ducke, a nearby locality in Manaus, 62 species were reported from tree canopies (Höfer et al., 1994), representing ca. 12% of the total spider fauna (Höfer & Brescovit, 2001). For tropical dry forest from the Colombian Caribbean (Quijano-Cuervo et al., 2019) and Tanzanian montane forest (Quijano-Cuervo et al., 2019; Sørensen, 2003), there are also evidence of higher spider species richness in lower strata. Similarly, for insects, up to 50% of the fauna is likely to be exclusive to the canopy (Ozanne, 2005). Nonetheless, in the present sampling, there is evidence that the observed canopy fauna is not necessarily exclusive to that environment. Several recorded species are known to live in the understory vegetation (e.g., *Metagonia taruma*, *Wagneriana jelskii* and *Micrathena vigorsi*), tree trunks (e.g., *Syntrechalea adis* and *Yppuera crucifera*) or are associated with the leaf litter layer (e.g., *Cupiennius bimaculatus* and *Ctenus cruksi*) (Bonaldo et al., 2009; Carico, 2008; Carvalho et al., 2010; Levi, 1991; Rego et al., 2007; Rheims & Brescovit, 2004). This

suggests that the composition of Amazon forest canopy spider assemblages is complex and requires further studies to evaluate its uniqueness compared to other strata.

The relatively low species richness recorded also reflects the low sampling intensity, not reaching three individuals per species, on both treatments (Table 2). This results in a high proportion of singletons (50.4%) and doubletons (17.2%), in the closed canopy and single species treatments (Table 2). Consequently, the estimated species richness for both treatments was about twice the observed, with 406 and 317 species, respectively for the closed canopy and single species treatments (Table 2). The number of singletons was much higher than the average frequently reported (32%) for tropical arthropods surveys (Coddington et al., 2009). As canopy spider diversity is positively correlated with sampling effort (Mupepele et al., 2014), intensified additional sampling effort should be carried out, if aiming to provide a realistic survey for the canopy spider fauna from the Urucu River basin.

As expected, owing to a similar spider abundance and species richness, both treatments yielded similar rank-abundance curves, thus suggesting an overall similarity in spider abundance patterns as well (Figure 3A). The species composition, however, was statistically significant between treatments ( $R^2 = 15.2\%$ ,  $F = 2.692$ ,  $p = 0.001$ ; Figure 3B). The results shown in the present study do not corroborate our previous expectations. Single species fogging is likely to sample a more homogeneous canopy structure, which was expected to provide a lower species richness. On the other hand, the closed canopy approach, samples a

canopy formed by overlapping branches of different tree species and/or individuals, yielding a more heterogeneous canopy and a higher expected spider species richness. In fact, previous studies have shown that spider abundance, biomass and species richness correlate positively with structural complexity of the vegetation (Wildermuth et al., 2023). As such, the association of spiders with their host trees can be significant (Mupepele et al., 2014), as spiders rely on

structural attributes during microhabitat selection, such as leaf shape, branch and leaf density and bark structure (Mupepele et al., 2014; Villanueva-Bonilla et al., 2021). Therefore, our results suggest that the canopy sampled at both approaches had a similar level of structural complexity and/or biomass (hence supporting a similar number of specimens and species), but different structures that form the canopies (hence supporting different spider assemblages).

Table 2. Summary of the spider assemblage parameters collected by fogging at closed canopy sites ('Closed canopy') and under the canopy of *Eschweilera atropetidata* ('Single species'). Abbreviations: "sd", standard deviation; "se", standard error.

Parameters	Closed canopy	Single species	Total
Males	192	146	338
Females	239	146	385
Total specimens	431	292	723
Mean number of spiders per fabric sheet ( $\pm$ sd)	4.95 ( $\pm$ 1.62)	4.73 ( $\pm$ 1.56)	4.84 ( $\pm$ 1.54)
Sex ratio (males/females)	0.80	1.00	0.88
Observed species richness (exclusive)	197 (141)	131 (75)	272
Mean species richness per fabric sheet ( $\pm$ sd)	3.75 ( $\pm$ 1.18)	3.38 ( $\pm$ 0.61)	3.57 ( $\pm$ 0.94)
Sampling intensity	2.19	2.23	2.66
Singletons (% of total)	114 (57.9%)	82 (62.6%)	137 (50.4%)
Doubletons (% of total)	31 (15.7%)	18 (13.7%)	47 (17.2%)
Estimated species richness ( $\pm$ se)	406 ( $\pm$ 44)	317 ( $\pm$ 51)	471 ( $\pm$ 39)
Sampling completeness	48.52%	41.32%	57.75%

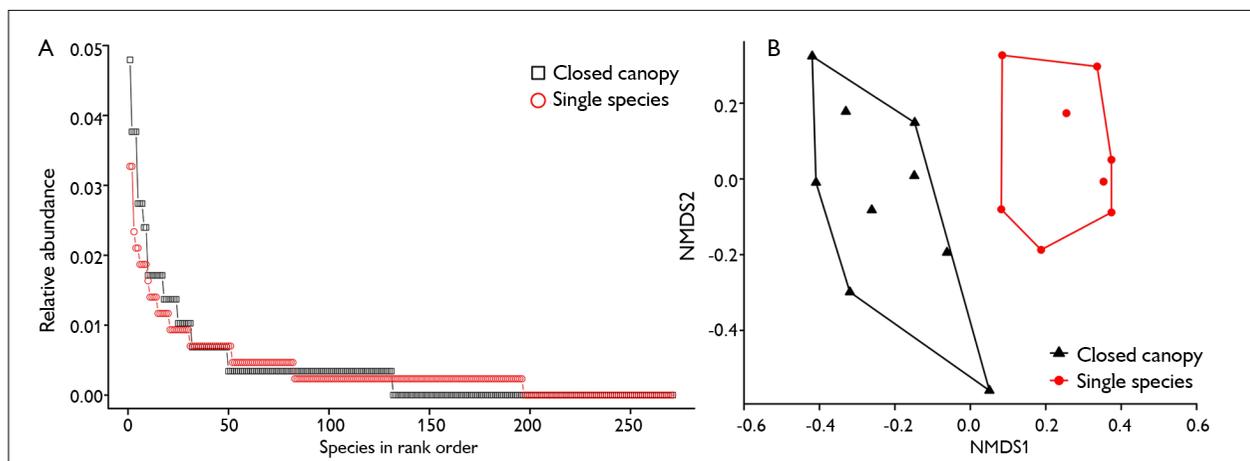


Figure 3. Rank-abundance plots (A) and nonmetric multidimensional scaling ordination using a Bray-Curtis similarity matrix of adult spider abundance (B; stress = 0.198), collected by fogging at closed canopy sites (in black; 'Closed canopy') and under the canopy of *Eschweilera atropetidata* (in red; 'Single species').



The rules of thumb followed for single species design should be reconsidered. The proposal for choosing tree specimens with fewer epiphytes and without flowers (taken from Adis et al., 1998a), might bias the samplings negatively. This proposal is based on the idea that epiphytic plants, phytotelmata and perched litter would hamper the penetration of knock down agents or prevent the dead specimens from falling from the trees (Erwin, 1989). However, in experimental studies, trees with epiphytes presented disproportionately more preys (such as insects) and predators (such as spiders), than those from which epiphytes were removed (Cruz-Angón et al., 2009; Díaz et al., 2012).

The present study revealed a canopy spider fauna from a central Amazonia locality much more diverse than previously reported for this region (see Höfer et al., 1994). We have shown that the choice between carrying out canopy spider inventories following the single species or the closed canopy approaches has its pros and cons. The closed canopy approach would be less time-consuming, as it does not require a previous survey for mapping isolated target trees that match the previously proposed rules of thumb. Conversely, this approach hampers getting information about the interactions among trees and spiders (i.e., the Eltonian shortfall; Hortal et al., 2015). The opposite would occur with the single species approach. A study aiming to collect as many species as possible (i.e., a taxonomy survey) for a given locality, should be treated as equally relevant as a study focusing on getting ecological information (e.g., species interactions). As such, a purely taxonomic study should include samples taken from both approaches to maximize the number of sampled species from a given locality, as they yield different assemblages. Therefore, to choose among both approaches, it is paramount to evaluate the goals of each study.

A purely taxonomic survey should focus on choosing the most structurally complex canopy site for sampling (i.e., based on a previous selection), which is likely to reveal a higher species richness; and include samples of single tree

species fogging. The absence of ecological information regarding tree-spider interactions should not be considered a significant negative result, considering the expedition goals. Conversely, a study aiming to evaluate the ecological interactions among trees and spiders (i.e., the Eltonian shortfall; Hortal et al., 2015), should focus on targeting specific tree individuals and focusing on sampling on them. However, contrarily to what is historically suggested (see Adis et al., 1998a; Erwin, 1989), maybe individuals trees with a high abundance of epiphytes, flowers or fruits should not be disregarded as preferable targets. Besides, studies focused on assessing the spider assemblage of a forested area, for conservation purposes, should not ignore its canopy fauna. Although this fauna is not easily accessible, it is highly diversified and exclusive, thus representing a significant portion of the spider fauna from the Amazon forest.

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### **AUTHORS' CONTRIBUTION**

L. S. Carvalho contributed to conceptualization, formal analysis, investigation, methodology, and writing (original draft, review, and editing), as well as data curation; E. L. S. Costa contributed to investigation, methodology, and writing (review and editing); N. F. Lo-Man-Hung contributed to investigation, methodology, and writing (review and editing); D. F. Candiani contributed to investigation, methodology, and writing (review and editing); B. V. B. Rodrigues contributed to investigation, methodology, and writing (review and editing); S. C. Dias contributed to investigation, methodology, and writing (review and editing); and A. B. Bonaldo contributed to project administration, funding acquisition, investigation, methodology, and writing (review and editing).

