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SEGREGAÇÃO ESPACIAL HORIZONTAL EM PEQUENA ESCALA ENTRE DUAS ESPÉCIES DA
FAMÍLIA THERIDIIDAE (ARANEAE)

João Custódio Fernandes Cardoso

2015

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Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais”.

Orientador

Prof. Dr. Marcelo de Oliveira Gonzaga

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FINE-SCALE HORIZONTAL SPATIAL SEGREGATION BETWEEN TWO RELATED THERIDIID SPIDERS

ABSTRACT

Niche theory predicts that coexistence between related species occurring sympatrically is unlikely. Due to the shared phylogenetically conserved ecological attributes, the stronger competitor may exclude competitively the related heterospecific. However, coexistence mechanisms may allow similar species to persist together. In this study, we investigated the coexistence between two related theridiid spider species: *Helviva longicauda* and *Chrysso intervalles*. Along riparian habitats of a tropical forest, *H. longicauda* occurs close to river margins, while *C. intervalles* occurs in higher abundance in further regions, after the zone occupied by *H. longicauda*, but always in shaded, humid regions. In this sense, this study aimed to investigate this fine-scale horizontal segregation pattern, exploring the relative contribution of different factors in generating the arrangement. Our results confirmed spatial segregation between spider species in both summer and winter, with *H. longicauda* populations being restricted to river margins and *C. intervalles* to contiguous regions. These species were positively related to the abundance of suitable sites used for web-building and negatively to the relative abundance of fern leaves, which seem to be unsuitable sites. Apparently, spiders also present niche differentiation in the height they build webs, with *C. intervalles* occurring at lower average heights. *Helviva longicauda* was the only one infested by fungi and the mortality rates were higher during winter. At this time, we found more *C. intervalles* individuals occupying areas close to the river than we did in summer. *Helviva longicauda* trophic niche breadth was wider than that of the heterospecific. However, we did not find differences in prey abundance across distinct distances from the river. Only the temperature was different, increasing away from the river. There were no differences in establishment rates between species in both environments. However, it is still possible that *H. longicauda* success far from the margins is lower during summer, once transplant experiments were performed during winter, in which temperature did

not differ between species zones. *Helvibis longicauda* was the most common species colonizing potential web-building sites at marginal regions, while *C. intervalles* colonizers were found mainly in areas further away. Agonistic interactions demonstrated that resident spiders present advantage in both intra and interspecific contests, once they remained alone in the web in most contests. Resident spiders effectively defended the web even against larger intruders. However, much larger intruders presented an increase in the probability of remaining in the alien web, sometimes taking it over. Although *C. intervalles* average body mass is higher than that of *H. longicauda*, this difference seems to represent no effect in *C. intervalles* reaching marginal regions. We hypothesized that capture rates of *H. longicauda* at further distances is compromised due to high temperature acting on the smaller viscid droplets, reducing adhesiveness. This abiotic factor restricts this species to cooler places. In the vertical axis, both species may potentially occupy the lower sites of the river margins. However, *H. longicauda* apparently displace *C. intervalles* through asymmetric exploitation competition. The fact that fungi reduced *H. longicauda* populations functioned as a natural removal experiment and resulted in a competitive release for *C. intervalles* individuals to reach margins, even with *H. longicauda* still being more abundant at this place.

Keywords: Ecological niche, coexistence, interspecific competition, agonistic interactions, Theridiidae.

INTRODUCTION

The modern concept of ecological niche is multidimensional. It refers to the ways in which environmental tolerances and requirements interact, defining conditions and resources required for an individual or species and enabling their lifestyle performance (Hutchinson, 1957). Accordingly, the definition of an animal's niche, for instance, emphasizes the role of resources, such as habitat and food availability, which propitiate to populations the maintenance of their reproductive rates over time (Hutchinson, 1957; Leibold & McPeck, 2006; Mayfield & Levine, 2010).

The ecological niche may be further divided into two: fundamental and realized niche (Hutchinson, 1957). The first, which is theoretical, is also known as potential niche and allude to the range of physical conditions in which a species can persist. Thus, the fundamental niche does not take into account ecological interactions between organisms, such as those with natural enemies. Alternatively, the realized niche definition considers biotic factors, and refers to the available niche region in which the species can persist in the presence of other organisms, antagonists or not, being the final product of the interaction between organism and environment (biotic and abiotic) (Hutchinson, 1957; Wharton & Kriticos, 2004; Pearman, 2007; Kearney et al., 2010). Thereby, in its realized niche, a species is subjected to interaction with predators, parasites, parasitoids and interspecific competitors.

Each species has a specific niche, so that absolute overlap does not occur in natural conditions. Classical explanation offered by ecological theory is the Gause principle, or principle of competitive exclusion, which establishes that stable coexistence of competing species requires the occupation of different realized niches (Gause, 1934).

The principle of competitive exclusion stemmed from laboratorial experiments performed by Gause (1934) with cultures of two protozoan species: *Paramecium aurelia* and *Paramecium caudatum* (Parameciidae). When the species were grown under identical conditions and separate locations, both thrived. However, *P. aurelia* was apparently a superior competitor, once individuals multiplied faster than *P. caudatum* ones, showing more efficient use of available resources. When populations of both species were cultivated together, *P. aurelia* multiplied faster, while *P. caudatum* was extinguished from the system. Under laboratorial conditions, post-Gause competitive exclusion cases have also been demonstrated for other systems such as in flour beetles (Park, 1948) and phytoplankton (Tilman, 1977).

Another classic example of competitive exclusion, in field conditions, was provided by Connell (1961). *Chthamalus stellatus* (Chthamalidae) and *Balanus balanoides* (Balanidae) are two species of barnacles that present fine-scale microhabitat segregation. In Scotland rocky shores, these species exhibit stratified spatial distribution (zonation). Traditionally, these barnacles do not occur together, since *B. balanoides* is concentrated on the lower vertical portion of the intertidal zone, whereas *C. stellatus* is abundant in the upper area of the shore. It is known that the free-swimming larvae of both species can settle in any region of the rocky shore. Initially, *C. stellatus* was experimentally removed from the upper portion, and *B. balanoides* did not colonize the place. The explanation is that this species cannot survive in areas where it is subjected to desiccation, due to the low tide. Thus, the realized niche of *B. balanoides* is apparently similar to its fundamental niche. Subsequently, *B. balanoides* was removed from the lower area, and *C. stellatus* was able to occupy it. In this way, it is possible to assert that *B. balanoides* is competitively superior in the lower portion of the shore. This indicates

that, in the case of *C. stellatus*, fundamental and realized niche are not similar, since the realized niche is compressed due to interspecific competition (Connell, 1961, 1983). Connell experiments demonstrated that competitive exclusion occurs in nature, and this may explain the distinction between fundamental and realized niches and also species spatial distribution. There are still some good recent examples in literature. Leathwick & Austin (2001), for instance, demonstrated that *Nothofagus* trees (Fagaceae) are highly efficient competitors, being able to displace other plant species. In the analyses, species that had large niche overlap with *Nothofagus* were the most affected.

In a given community, realized niche overlap and, therefore, competitive exclusion, will take place only if the species occur sympatrically in high densities and interact each other in direct or indirect ways for limiting resources. Nevertheless, empirically, competitive exclusion rarely occurs in natural settings (Stanley & Newman, 1980; Hubbell, 2005). Syntopic species displaying similar fundamental niches tend to present niche adjustments, by differentiating particular ecological features. Hence, the interspecific variation in the ecological characteristics of the species makes possible the partition of limited resources among competing species and niche differentiation in a community (Leibold & McPeck, 2006; Hunt et al., 2008). This reduces the conflict arising from competition for food, space and other limiting resources. Due to competition for the same niche occupation, different organisms tend to displace each other from their optimal initial niches. In this sense, the ecology of an organism depends on the presence of others with similar or overlapping niches. Responses of organisms to competitors and to resource distribution along the environment determine the niche to be occupied and influence the mechanisms by which different species solve disputes by resources (Bergmüller & Taborsky, 2010). The coexistence between species and the maintenance

of biodiversity is possible because, in ecological communities, ecological aspects differ between species (Chesson, 2000; Leibold & McPeck, 2006; Mayfield & Levine, 2010).

The niche concept has been used with the purpose of understanding differences of attributes between species according to resource utilization (Alatalo, 1987; Grant & Grant, 2003). In this sense, specialization in the exploitation of different resources in the environment is an important phenomenon concerning interspecific differentiation (Chesson, 2000; Hunt et al., 2008; Finke & Snyder, 2008; Devictor et al., 2010; Mayfield & Levine, 2010). If competition for a given resource is intense, there are two possible outcomes: one species induces the other to extinction via competitive exclusion; or, through natural selection, niche partitioning occurs through specialization in resource exploitation, reducing interspecific competition. Accordingly, each species evolves to use a different portion of the total resource available, partitioning the niches and avoiding direct interspecific competition (Chesson, 2000; Adler et al., 2007; Hunt et al., 2008; Devictor et al., 2010; Mayfield & Levine, 2010).

In the present study, the spatial relationship between two spiders of the Theridiid family was investigated. In the Intervales State Park, along the forest surrounding the Mirante river, two cobweb spiders are particularly abundant. *Helvibis longicauda* apparently occurs close to the river margins. On the other hand, preliminary observations suggest that *Chrysso intervalles* populations are restricted to regions a few meters away, after the zone occupied by *H. longicauda*. To date, such fine-scale horizontal segregation is not known yet. Interestingly, these species are phylogenetically related (Arnedo et al. 2004, 2007; Eberhard et al. 2008; but see Agnarsson, 2004) and, at a first sight, they present many niche similarities.

Several factors may underlie coexistence between *H. longicauda* and *C. intervalles*. For instance, environmental filtering may restrict species to distinct microhabitats due to abiotic factors acting differentially on species particular traits. In the niche partitioning possibility, on the other hand, each species is specialized on a particular microhabitat and/or diet. If this is the case, the microhabitats, near and far from the river, may differ in limiting resources availability, quality or type. Finally, through competitive exclusion, one species may be a superior competitor in the microhabitat it occupies.

The purpose of this study is to investigate the spatial segregation in *H. longicauda* – *C. intervalles* system, elucidating which factors are responsible for such pattern. With this scope, this study is divided in two chapters, one analytical and other experimental. In the first one, the spatial segregation per se is investigated. Also, data collection was performed aiming to found differences in environmental occupation attributes between species, and to associate then to microhabitat differences. The second chapter aimed to test the success of each species establishment in the microhabitats occupied preferentially by the other. In addition, were also investigated possible behavioural aspects which may contribute for species interactions and, consequently, spatial distribution.

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CHAPTER 1

Drift away: Fine-scale horizontal spatial segregation between two related cobweb spiders**Abstract**

Coexistence between closely related species is unlikely. Due to shared functional traits, niche theory predicts that the strong competitor tend to competitively exclude the others. In this study, we aimed to investigate the possible spatial segregation between two species of sympatric cobweb spiders, *Helvibis longicauda* and *Chrysso intervalles*, in an area of Atlantic Forest in southeastern Brazil. We surveyed spiders along different distances from the river, recording the plant species occupied, measuring occupied leaves, web height from the ground and identity and biomass of captured prey. We also collected data on biotic (availability of suitable web-building sites, unsuitable fern leaves, and potential prey items) and abiotic factors (temperature, moisture, canopy cover) across different environments. Concerning species relative utilization of distinct resources, we reanalyzed original datasets employing null models and calculated species niche breadth. Our results indicated that spatial segregation does occur between populations in both summer and winter. The abundance of spiders was positively related to the availability of web-building sites and negatively to the abundance of unsuitable fern leaves. Number of spiders occurring per plant species was also dependent on the respective number of available sites. *Helvibis longicauda* trophic niche is wider than the niche of *C. intervalles*. However, the number of prey available for the different populations did not differ, indicating that segregation does not occur due to prey availability differentiation (i.e. shadow competition). We suggest that environmental filtering restricts *H. longicauda* populations to the cooler river margins. Species present functional trait differentiation, with *C. intervalles* occurring at lower average heights. With this, potentially, both species may persist in lower regions

situated close to river margins. However, apparently, *H. longicauda* displaces the heterospecific to adjacent regions through indirect exploitation competition for sites. Evidences indicate that during winter, mortality per fungi reduced *H. longicauda* population, allowing more *C. intervalles* to occupy the river margins.

Keywords: Interspecific competition, coexistence, Theridiidae, Atlantic Forest

Introduction

“(...) the most closely-allied forms,—varieties of the same species, and species of the same genus or of related genera,—which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other. Consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them.” — Darwin, 1859.

The assertion of Mr. Darwin denotes that the notion of stronger competition between recently diverged species is a longstanding corollary in community ecology. Surprisingly, Darwin’s words not only encompass the modern phylogenetic limiting similarity hypothesis (Violle et al. 2011), but also the idea of competitive exclusion, reinforced only ¾ century later with the establishment of Gause’s principle (Gause 1934). Species coexistence is one of the oldest and most central issues in ecology. Niche theory predicts that few related species may coexist because they tend to exhibit similarity in functional traits and ecological niches occupied, increasing chances of competitive exclusion (phylogenetic limiting similarity hypothesis) (Chesson 2000; Webb et al. 2002; Chase and Leibold 2003; Dayan and Simberloff 2005; Jiang et al. 2010; Violle et al. 2011; Verdú et al. 2012, Allan et al. 2013; but see Mayfield and Levine 2010). Traditionally, the concept of ecological niche has been employed for understanding the ecology and evolution of species differences (Gause 1934; Hutchinson 1957). In this context of interspecific differences, an important phenomenon is the specialization in exploiting resources (Chesson 2000; Chase and Leibold 2003; Hunt et al. 2008; Finke and Snyder 2008; Devictor et al. 2010; Mayfield and Levine 2010). In this sense, within the

community, the stable coexistence between competing species requires the occupation of different realized niches (Gause 1934; Hutchinson 1957; Chesson 2000; Chase and Leibold 2003).

If competition for a given resource is intense, there are two possible outcomes. In the first, as predicted by Darwin, one species leads other to extinction through competitive exclusion. However, empirically, competitive exclusion rarely occurs in the wild (Stanley and Newman 1980; Hubbell 2005). The other alternative states that, through natural selection, competition between species is reduced by means of specialization in resource exploitation (niche partitioning). Accordingly, each species evolves to use a different portion of the total resources available. In multispecies assemblages, the coexistence of syntopic species and biodiversity maintenance is possible because of interespecific functional trait differentiation, leading species to resource specialization and niche partitioning, minimizing competition effects (Chesson 2000; Chase and Leibold 2003; Leibold and McPeck 2006; Hunt et al. 2008; Mayfield and Levine 2010, Adler et al. 2013).

Even with such ecological attributes differentiation, during interactions occurring in ecological time, competition for similar niche occupation between different species tend to displace competitors from their optimal initial niches (fundamental niches). The responses of organisms to the distribution of resources and competitors are determinants of niche occupation and influence mechanisms by which individuals of different species solve conflicts over resources (Bergmüller and Taborsky 2010). The intensity of interspecific competition can influence the evolution, population dynamics and species coexistence (Schoener 1983; Leibold and McPeck 2006; Finke and Snyder 2008; Keddy 2001; Thompson 2014). Although interspecific competition is a central

mechanism structuring assemblages (Schoener 1983; Keddy 2001; Thompson 2014), it is poorly understood in some important species-rich groups. For instance, in spiders, the most diverse group of terrestrial predators with over 45.000 recorded species so far (WSC 2015), interspecific competition process is still elusive and understudied. Few studies have examined the impacts of interspecific competition in spatial distribution, behavioral interactions and population parameters in spiders.

Opinions remarkably contrast about the role of interspecific competition in structuring spider communities. Some authors treat competition among spider species as usually low or absent (Wise 1981; Riechert and Cady 1983; Horton and Wise 1983; Wise 1984; Hoffmaster 1985; Wise 1993). It was suggested that the high predation pressure exerted on these organisms precludes species to reach high densities in which interspecific competition takes place (Spiller 1984a; Wise 1984, 1993). The interspecific competitive impact between spider populations might be even more unlikely in environments in which the availability of prey is high (Wise 1993).

Apparently, when two or more spider species occur sympatrically, coexistence commonly takes place through niche partitioning, not necessarily occurring interspecific competition. In fact, taking orb-weaving spiders as an example, evidences suggest that communities are mainly niche partitioning structured (Shulov and Weissman 1959; Enders 1974; Olive 1980; Brown 1981; Horton and Wise 1983; McReynolds and Polis 1987; Ward and Lubin 1992; Herberstein 1998; Harwood and Obrycki 2005; Richardson and Hanks 2009; Novak et al. 2010; Butt and Tahir 2010; Tahir et al. 2012; Afzal et al. 2013; Michalko and Pekár 2014). Despite the absence of widespread strong interspecific competition evidences in spiders, other authors suggest that this interaction may be considered a determinant factor of spatial distribution patterns, population abundance

and species evolution (Spiller 1984 a, b; Nyffeler et al. 1986; Polis et al. 1989; Hann 1990; Bednarski et al. 2010; Jakob et al. 2011; Lewis 2013; Houser et al. 2014).

Concerning the trophic niche, although being considered generalist predators, the diet of many spiders has high dominance of a few prey types and sizes (Pekár et al. 2011). Pekár et al. (2011) also demonstrated that the diet breadth of tropical and subtropical spiders is generally narrower than that of temperate zone species. Accordingly, trophic niche similarity between syntopic species with similarities in body size and web traits can reinforce the possibility of interspecific competition, which could be minimized by spatial segregation (Ward and Lubin 1992). Moreover, web-building spiders are stationary predators. Thus, they may also experience interspecific competition as consequence of their spatial orientation in relation to the places occupied by other individuals. This influence of predators located in better places on others located at adjacent sites, considering the unidirectional source of a potential resource (e.g. prey), is known as "shadow competition" (Rao 2009). This mechanism is a possibility when there is a specific direction in prey movements throughout microhabitats, for instance, flying organisms emerging from a river moving toward the surrounding forest.

Preliminary field observations carried out in the watercourses surroundings of a dense tropical forest suggested that two Theridiidae spiders, *Helvibis longicauda* and *Chryso intervalles*, are arranged in a very peculiar spatial distribution. *Helvibis longicauda* build webs close to the river, while *C. intervalles* occupies adjacent areas. Apparently, the species are distributed in two well-defined zones, presenting accentuated fine-scale horizontal spatial segregation. These species are phylogenetically related (Arnedo et al. 2004; 2007; Eberhard et al. 2008; but see Agnarsson 2004) and

construct very similar webs, composed of several fully adhesive threads connected between laminar leaves (Gonzaga et al. 2006). At first glance, *H. longicauda* and *C. intervalles* exhibit high overlap in many niche axes. According to Gonzaga et al. (2006), diets of both species include a high proportion of insects with aquatic larvae, such as Diptera of the Tipulidae family. Considering this, individuals located close to the river margins can restrict the availability of resources to individuals located far from these sources through shadow competition. Furthermore, both species depend on humidity to maintain adhesive properties of the webs (Gonzaga et al. 2006). Thus, it is possible that *H. longicauda* is competitively more efficient in exploiting this resource, displacing *C. intervalles* to suboptimal microhabitats. As far as we know, this case may represent the first report of web-building spider fine scale horizontal segregation. Other potential novelty is the description of spider competitive exclusion in structurally complex environments (tropical forest), since empirical cases suggesting the principle are scarce in this taxa.

In this context, this study aimed to (1) describe qualitatively and quantitatively the spatial segregation between the two populations and (2) assess which potential factors are responsible for such pattern: (a) Environmental filtering, in which the abiotic environment operates as a selective force in determining species habitat occupation according to their traits, regardless of biotic interactions; (b) specialization in different resources or in the same resource available in different quantities in the two microhabitats, far and near river (e.g. prey, web-building sites); or (c) competitive interaction mediated by fundamental niche overlapping (trophic or spatial).

Materials and Methods

Study site

This study was conducted at Intervales State Park (24°16'S, 48°25'W), located at Ribeirão Grande, State of São Paulo, southeastern Brazil. The area comprises a large Atlantic Forest remnant (120,000 ha) in which the weather is subtropical with two defined seasons, a warm-wet from October to March and a cold-dry from April to September (Chelini et al. 2011). Fieldwork was carried out along the Mirante river margins. This locality corresponds to the “site 7” described in the study of Gonzaga et al. (2006) (see Gonzaga et al. 2006 for additional details).

Studied species

Helvibis longicauda and *Chryso intervalles* are restricted to riparian regions, occurring always in shaded, humid regions (Gonzaga et al. 2006). Webs of both species are composed entirely by viscid silk lines (i.e. adhesive droplets in all over the web extent), and positioned underneath laminar leaves, which are apparently used as retreat (Gonzaga et al. 2006). *Chryso intervalles* (mean \pm SD: 4.04 \pm 1.86 mg) is heavier than *H. longicauda* (mean \pm SD: 2.9 \pm 1.03 mg) (Cardoso & Gonzaga, in prep.). Only *H. longicauda* is attacked by fungi (the hyphomycete *Gibellula pulchra*), which causes the spider death (Gonzaga et al. 2006).

Procedures

Two sampling expeditions were performed, one during summer (2013 February) and other in winter (July). Each expedition lasted 15 days, and *in situ* procedures were performed between 08 – 17 h. Transects of 2 m width per 10 m length were demarked

parallel to the Mirante river margins, comprising three distances: 0 m (immediately after riverbank), 10 m, and 20 m far from the river (Fig. 1). Since surveys performed away from watercourses failed in finding this species (Gonzaga et al. 2006), the selected distances aimed to comprise studied spiders distribution. Moreover, after 20 meters, spider occurrence is scarce (Cardoso JCF, personal observation). Overall, we established five transects on each of the three categories, totalling 15 transects and 300 m² of surveyed area. Transects at distinct distances from the river were placed at parallel positions. Each triplet of transects at different distances from the river was positioned at least 25 m far from the others.

Spiders and web sites

In both surveys (summer and winter), female spiders of both species present in transects were counted between heights of 0 and 3 m from the ground. This height spectrum comprised spider occurrence, since spiders above 3 m were not found (JCF Cardoso, personal observation). We did not search for males, once their adult phase is not spent in webs, but roaming in search for mates (Gonzaga and Leiner 2013; Gonzaga et al. in prep). Spider condition was also recorded as solitary, taking care of egg sac or juveniles and attacked by fungi. All spiders found in transects during summer had their webs marked. In order to investigate web site abandonment frequencies, these webs were inspected daily during seven days. In summer survey, where spiders are more abundant and competition for sites more likely, plant species occupied were recorded to the nearest taxonomic group. We measured width of leaves supporting webs and the distance between these leaves and the ground (hereafter, height site). In addition, we counted the total availability of web-building sites between 0 – 3m height on each

transect, regarding plant species proportion. In this sense, we did not count the number of individuals of each plant, but the number of available leaves (or leaflets) appropriate to spider occupation. Accordingly, leaves were considered suitable when they presented more than 4 cm width and less than ¼ of area loss due to herbivory (estimated by sight). Narrower leaves and those with a higher proportion of consumed area are apparently avoided by the spiders. Excluding *Olfersia cervina*, a pteridophyte species with large and suitable leaflets, ferns are not used by *H. longicauda* and *C. intervalles*, despite being abundant. In order to investigate the occurrence of a negative relationship between spider and fern abundance, fern fronds (not individuals) were also counted. In these counts, we grouped the number of fern leaves found, mainly composed by *Didymochlaena truncatula* (Swartz) J. Smith and *Diplazium cristatum* (Desr.) Alston.

Prey items

To investigate prey composition consumed by both species, web inspection was performed during seven consecutive days in summer survey, in which each spider web was examined twice a day, at morning and afternoon. In order to reduce interference on resident spider, when located, prey items were carefully removed from the web using tweezers. In the lab, prey items found were classified to the Order-level, except for Acari. Prey body length was measured to the nearest 0.01 mm by using a digital calliper. We estimated prey availability on transects through vertically oriented sticky traps adhered to the vegetation. Each sticky trap was composed by a 15 x 10 cm plastic sheet, which was covered on one side with tanglefoot resin (The Tanglefoot Company®, Rapids, Michigan, USA). On each transect, we positioned six sticky traps, totalling 90. We adjusted trap position to the range of heights used by spiders, so on each transect two

traps were placed per height selected (30 cm, 1 m and 2 m). Sticky traps remained in the field for eight consecutive days. After this time, prey items captured were measured using the same procedures performed for spider captured preys.

For both prey, captured by spiders and surveyed in traps, we expressed data in number of individuals and biomass. The latter was estimated based on body length-weight equations. As the relationship between body length and biomass may differ across climatic regions (Schoener 1980), we used the methods proposed by Ganihar (1997), which measured arthropods collected in a tropical forest. Moreover, we choose these procedures because they included a wider range of taxa found in our study, and the estimates presented elevated r^2 values, indicating high accuracy. We used specific-taxa formulas when available. For Acari, we used Araneae equations and for Thysanoptera we used Dermaptera's. For categories Blattodea, Ephemeroptera, Psocoptera and unidentified prey items, the general equation for adult insects was employed. As suggested, we used power functions to convert body length into biomass, except for Thysanoptera (Dermaptera), in which we used the exponential function (see Ganihar 1997). Sticky traps are imperfect mimics of spider webs. For instance, they may cover a wider amplitude of prey biomass, including larger and smaller items than those naturally captured by spiders (Eberhard 1990). In order to minimize this bias, for descriptive and analytical procedures, we used only items within the capture range of estimate biomass recorded in the field, according to prey category.

Abiotic parameters

Data on temperature and moisture were collected in both surveys. In summer, we positioned thermo-hygrometers (IncoTerm® 7666) in the different distances from the river margin used to place the transects. These were positioned 30 cm above the ground, at shaded sites. Daily, data on maximum/minimum temperature and relative moisture were collected from a transect triplet. Devices were inspected at 9 AM and changed among triplets every day, during seven days. For five days of the winter survey, the same protocol used with thermo-hygrometers was performed, but in this time with data loggers (Instrutherm® HT-500). This electronic devices record temperature and moisture over time, and were programmed to collect data four times a day: 6 AM, 12 PM, 6 PM and 12 AM.

Direct light incidence was estimated through canopy photos. During five days, at noon, we took perpendicular pictures of each transect canopy with Canon EOS Rebel T3i digital camera and EF-S 18-55mm lens. On each transect, one picture was taken per day (totalling 75 pictures) and positions they were taken were 2m far apart. This procedure took into account the variation in canopy cover of the entire transect (10m). The average of canopy cover per transect was used for statistical analysis. Camera settings were the same during all days and pictures. For analysis, we followed Engelbrecht and Herz (2001) methodology. Using the software Photoshop CS4 v.11.0 (Adobe Systems Incorporated), images were initially transformed to greyscale and contrast regulated to +100 and brightness to -100. This procedure divided image in two tones: white is the proportion of canopy opening and black, canopy cover. In the software mode "histogram" we obtained the relative ratio of black and white pixels.

Statistical analysis

We tested the spatial segregation between spiders by using two-way ANOVAs designs (one for each season survey). Treating each transect as a replicate, we compared number of spiders found according to distance category and spiders identity. If spider species segregate along our proposed distances, there should be a significant interaction of distance category and spider species factors. Winter survey spider abundance were Log + 1 corrected for data homogenization. In order to avoid type I error, we used Bonferroni value and accepted $p < 0.025$ as significant. For this and all parametric analysis onwards, distance category was treated as a random factor. Intraspecific spider abundance between seasons were compared by Chi-square for overall spiders and according to condition (solitary, egg sac, juveniles or fungi infested). Bonferroni corrections were applied and we accepted $p < 0.01$ for *H. longicauda* results and $p < 0.0125$ for *C. intervalles* (absence of spiders attacked by fungi) as significant. Through a Chi-square test, abandonment frequencies were also compared between species. Due to the high *H. longicauda* mortality caused by fungi, we specifically tested if the number of *C. intervalles* differed between surveys in the first distance category (0 m) by using a paired t-test.

We tested if web site attributes differed between spider species through Student's t-tests. Leaf width were Log transformed and height from the ground square root transformed to fit test assumptions. Differences in canopy cover, relative humidity, and minimum/maximum temperature along the three distance categories during summer survey were investigated through one-way ANOVA. We accepted significance when Bonferroni corrected p value was < 0.0125 . For temperature and humidity collected by data loggers during winter, we performed two separated repeated measures ANOVAs, accepting $p < 0.025$ as significant.

Differences in the biomass of *H. longicauda* and *C. intervalles* prey were compared using Mann-Whitney U test. Taking each transect as a replicate, sampled prey differences in the three distance categories were investigated according to abundance and estimated biomass. Separated ANOVAs were performed for each arthropod group and also for total prey, comprising 11 repeated tests, with accepted Bonferroni p values < 0.0045 . Insect orders with insufficient sampling replicates were not included in statistical analysis. To suit test premises, when necessary, data were corrected (Log or Log + 1) or non-parametric analysed through Kruskal-Wallis test.

Web-building sites availability differences in the three distance categories were investigated for total sites and for specific ones. Analyses were performed only for plant species which occurred in five or more transects (out of 15). Seven ANOVAs were performed for species, one for total sites and another for fern leaves sampled, leading to a corrected Bonferroni p value < 0.0055 . Again, data were corrected (Log or Log + 1) when necessary or analysed through Kruskal-Wallis test.

Taking overall spider abundance as dependent variable, two separated linear regressions were performed with the total numbers of available sites and fern leaves found. Then, these two predictor variables were subjected to a Pearson correlation analysis. To investigate if the occupation rates are related to site availability also according to plant species, each plant identified was taken as a replicate. Another linear regression was performed taking the number of spiders found per plant species and the respective number of sites available.

Null modelling analysis

In order to detect non-random patterns in the studied system, we reanalysed original datasets using null models in the EcoSim Professional program (Entsminger 2014). This software runs Monte Carlo simulations in order to create "pseudo-communities" (randomized communities) (Gotelli and Graves 1996; Winemiller and Pianka 1990), then, patterns obtained are statistically compared to those of the real data matrix. Differences in utilization of distinct resources were investigated through niche overlap analyses. We calculated Pianka's (1973) and Czechanowski's (Feinsinger et al. 1981) indexes. Values obtained range from 0 (no resources utilization in common) to 1 (complete resource overlap). Null models random expectations are inferred under a given randomization algorithm. We used the two recommended randomization algorithms: RA2 and RA3 (Lawlor 1980; Winemiller and Pianka 1990). The first presents niche breadth relaxed and zero states retained, which respectively means a random equiprobable specialization and the prevention that a species that did not use a given resource in the real matrix would do it in the simulations. RA3, on the other hand, characterizes niche breadth retained and zero states reshuffled. In other words, this algorithm simulates specialization equivalent to the observed value and randomly varies used resources (Lawlor 1980; Winemiller and Pianka 1990). On each simulation, a standard of 50.000 interactions was performed.

We investigated niche overlap in different resources and circumstances of our system. First, we examined if *H. longicauda* and *C. intervalles* are distinctly distributed according to (1) distance category (0, 10 and 20m) in summer and winter surveys. (2) The abundances of prey items consumed according to the 12 preyed arthropod taxa were also analysed. We did not include the category "unidentified prey" in this procedure. However, this category was included in simulations concerning (3) prey

separated in five biomass classes, divided in every 5 mg along the mass continuum (the last class included prey items ≥ 25 mg). Possible differences in occupation of web-building sites were investigated concerning the (4) proportion of spiders found in each of the 22 vegetal species utilized. Specific site features overlap were examined in (5) leaf width (five size classes divided in every 5 cm) and (6) height from the ground (six size classes divided in every 50 cm). EcoSim default states that resource distribution is equiprobable (equally common) in the environment. We performed reshuffling using this mode for all datasets. However, in order to provide more accurate results, it is possible to correct resources to their respective availability through the user-defined option. This procedure was also employed in randomizations for our datasets that presented such estimatives of availability. We inferred non-random structure of *H. longicauda* – *C. intervalles* system whenever $p(\text{observed} \leq \text{expected}) \leq 0.05$ (Gotelli and Graves 1996).

Niche breadth

With the purpose of estimating species niche breadth, we used the Shannon–Wiener index (H) (Shannon and Weaver 1949) concerning the different resources used in null models. Specifically for prey items, we followed the values proposed by Pekár et al. (2010) to categorize food habits: $H = 0$ – 0.3 : stenophagy (narrow diet breadth), $H = 0.31$ – 1.1 : oligophagy (feeding mainly on particular prey groups but sporadically complementing diets with other prey types) and $H = 1.11$ – 3 : euryphagy (presenting a wide range of food items).

Results

Spider spatial and temporal distribution

We found a total of 515 spiders, 250 *H. longicauda* and 265 *C. intervalles* in summer survey and 299 in winter, respectively 159 and 140 (table 1). When using mixed model factorial designs for spider abundance investigation, we found significant interaction between distance category x species for both summer (Two-way ANOVA, $F_{2,1} = 33.39$, $p < .0001$) and winter (Log + 1 transformed: $F_{2,1} = 40.28$, $p < .0001$) surveys (Fig 2). This indicates that *H. longicauda* and *C. intervalles* present spatial segregation and this pattern exists in different periods of the year. However, when treated separately, there were no differences according to distance from the river (summer: $F_{2,1} = 0.17$, $p = 0.84$; winter: $F_{2,1} = 0.36$; $p = 0.73$) or spider species (summer: $F_{1,1} = 0.001$, $p = 0.97$; winter: $F_{1,1} = 0.42$; $p = 0.58$).

The abundance of both species was higher in summer than in winter (*H. longicauda*: $\chi^2 = 20.24$; $df = 1$, $p < .0001$; *C. intervalles*: $\chi^2 = 38.58$, $df = 1$, $p < .0001$) (Fig. 3, table 1). Solitary spiders were more abundant during summer (*H. Longicauda*: $\chi^2 = 16.06$, $df = 1$, $p < .0001$; *C. intervalles* $\chi^2 = 65.12$, $df = 1$, $p < .0001$), while *H. longicauda* infested by fungi were more numerous in winter ($\chi^2 = 58.29$, $df = 1$, $p < .0001$). Fungi occurrence was not recorded for *C. intervalles*. Other categories of conditions did not presented differences (Egg sac – *H. longicauda*: $\chi^2 = 5.71$, $df = 1$, $p = 0.016$; *C. intervalles*: $\chi^2 = 0.69$, $df = 1$, $p = 0.4$; Juveniles – *H. longicauda*: $\chi^2 = 0.47$, $df = 1$, $p = 0.49$; *C. intervalles*: $\chi^2 = 0.36$, $df = 1$, $p = 0.54$). Site abandonments were restricted to solitary spiders and higher for *H. longicauda* ($\chi^2 = 7.21$, $df = 1$, $p = 0.009$). Close to the river (0 m), more *C. intervalles* individuals were found in winter (5 ± 3.08) than in summer (1.6 ± 0.89) survey ($t = 2.36$, $df = 8$, $p = 0.045$). In fact, during winter survey, we found five *C. intervalles* individuals occupying sites that still had the presence of *H. longicauda* killed by fungi

(Fig. 4). *Chrysso intervalles* used wider leaves (10.25 ± 4.52 cm) than *H. longicauda* (9.51 ± 4.56) ($t = 2.37$, $df = 513$, $p = 0.018$; Fig 5A). On the other hand, height site was higher for *H. longicauda* (105.33 cm \pm 54.55 cm) than for *C. intervalles* (55.52 ± 34.87) ($t = 12.86$, $df = 513$, $p = 0.001$; Fig. 5B).

Spiders were distributed along 22 plant species belonging to 15 different families (Fig. 6; Table 2). Some plant species presented equivalent number of sites available for web establishment in all distance categories while others did not (Fig. 7; Table 2). Clearly, some plants species are riparian and others only occur far from the river. The availability of sites for web construction was higher close to river margins (Fig. 8A; Table 2). On the other hand, at this zone, the number of fern leaves was relatively low (Fig. 7; Fig. 8B).

The global number of spiders found was positively related to the number of suitable sites available in the transects ($r^2 = 0.58$, $df = 13$, $p = 0.0005$; Fig. 9A) and negatively related to the number of fern leaves ($r^2 = 0.34$, $df = 13$, $p = 0.012$; Fig. 9B). In fact, these two predictor variables are negatively correlated ($r = 0.56$, $p = 0.0007$; Fig. 9C). Finally, taking each plant species as a replicate, a positive relationship between the number of available sites per species (Log) and the respectively number of individuals occupying (Log) was observed ($r^2 = 0.75$, $df = 20$, $p < .0001$; Fig. 9D). Apparently, both spider species occupy sites according to their availability (see also Fig. 6, Fig. 7 and table 2 for comparison).

Prey

Helvibis longicauda captured 79 prey items while *C. intervalles* 28. Main prey items of both species were Diptera, followed by Hymenoptera. Overall, *H. longicauda*

captured 12 distinct arthropod groups, while *C. intervalles* only five (Fig. 10). Body mass of captured prey was similar between species (Mann-Whitney U test: $U = 1239.5$, $p = 0.34$; *H. longicauda*: mean \pm SD: 13.31 ± 22.58 mg; *C. intervalles*: 23.16 ± 38.33).

In sticky traps, we sampled 1986 items within the range of captured prey belonging to thirteen different groups (Table 3). Most common groups were those mainly captured by spiders: Diptera followed by Hymenoptera. No differences between distance categories were recorded. Biomass of the analysed groups was similar among distances, except for the order Hymenoptera and total prey (Fig. 11).

Abiotic variables

During summer survey, differences between transects in abiotic variables were not found for canopy cover ($F_{2,1} = 1.38$, $p = 0.28$; mean \pm SD **0 m**: 93.88 ± 1.22 %; **10 m**: 94.44 ± 1.16 ; **20 m**: 92.75 ± 2.28), relative humidity ($F_{2,1} = 0.2$, $p = 0.79$; **0 m**: 94.42 ± 1.13 %; **10 m**: 94.71 ± 0.75 ; **20 m**: 94.71 ± 0.75), and minimum temperature ($F_{2,1} = 0$, $p = 0.96$; **0 m**: 17.52 ± 0.86 °C; **10 m**: 17.64 ± 0.83 ; **20 m**: 17.62 ± 0.86). However, maximum temperature was different ($F_{2,1} = 7.65$, $p = 0.003$, mean \pm SD: **0m**: 21.38 ± 0.62 °C; **10m**: 22.11 ± 0.95 ; **20m**: 23.25 ± 1.06) between the distances 0 and 20 m (Tukey Post-hoc test: $p < 0.05$; Fig. 12).

During winter survey, there was not difference of relative humidity considering distance zones ($F_{2,3} = 0$, $p = 0.98$; mean \pm SD: **0 m**: 98.10 ± 0.76 %; **10 m**: 98.05 ± 0.88 ; **20 m**: 98.12 ± 0.9), period of the day ($F_{3,3} = 1.8$, $p = 0.15$; **6 AM**: 98.37 ± 0.64 °C; **12 PM**: 97.9 ± 1.08 ; **6 PM**: 95.95 ± 0.88 ; **12 AM**: 98.13 ± 0.66), or distance category \times period of the day ($F_{6,3} = 1.7$, $p = 0.15$). In temperature, there was an effect of the period of the day ($F_{3,3} = 8.29$; $p = 0.002$; mean \pm SD: **6 AM**: 12.35 ± 2.70 °C; **12 PM**: 14.58 ± 1.98 ; **6 PM**:

13.47 ± 1.8; **12 AM**: 12.21 ± 2.61). Noon is different from mid night and 6 AM (Tukey Post-hoc test at 0.05 level). However, distance category ($F_{2,3} = 1.95$, $p = 0.17$; **0 m**: 11.99 ± 3.22; **10 m**: 13.88 ± 1.66; **20 m**: 13.58 ± 1.81) and period of the day x distance category ($F_{6,3} = 0.16$, $p = 0.98$) were similar.

Resource partitioning

In summer survey, space partitioning was indicated by RA2 model (Table 4). During winter survey, RA2 and RA3 indicated non-random patterns in Czekanowski calculations. When corrected, prey abundance did not indicate dietary niche overlap between the species in RA2 (Pianka and Czekanowski) and RA3 (Czekanowski) models. All analysis for plant species, when corrected, demonstrated that the utilization between species is non-randomly structured along this niche axis. As predicted, when niche differentiations occurred, they were followed by low values of both indexes, especially when compared to the mean obtained on simulated matrices. All other analysis did not differ from random expectations. Our input matrices provided similar values for Pianka and Czekanowski and for RA2 and RA3 models.

Niche breadth

Values obtained for prey biomass and leaf width were quite similar for both species (Table 5). *Helvibis longicauda* niche breadth indexes were higher for prey type, plant species utilized and height site. Taking into account diet diversity, *H. longicauda* can be considered as euryphagous and *C. intervalles* as oligophagous. *Chryso intervalles*

niche breadth was wider only considering distribution on distinct distances zones from the river, in both surveys.

Discussion

Our results indicate that spatial distribution of the species investigated is not random in space and time. *Helvibis longicauda* abundance is positively associated with microhabitats located close to the river while *C. intervalles* occurs mainly at regions some meters away from it. This pattern was found in different seasonal surveys, far spaced from each other. Moreover, intraspecific clustering and interspecific segregation were pointed by both, statistical and null-modelling approaches. As our study is only a snapshot in time, one could argue that it is a middle of a process, and one of the species may completely displace the other over time. Moreover, is reasonable to infer that the natural process of spiders dispersion should mix then up. At least in ecological time, population mixing is unlikely, once we have been observing the pattern in different localities up and downstream the river and also in different years since 2004 (J.C.F. Cardoso & M.O. Gonzaga, personal observation). Although vertical segregation has been frequently reported (see spatial niche section), as far as we know, this is the first report of horizontal fine-scale spatial segregation in web-building spiders. In the following, we discuss our main findings according to resource utilization and niche axis occupied, highlighting possibilities that may explain coexistence between these related species. Many hypothetical assembly rules may underlie this system, so we suggest the most likely ones based on our data, pointing future directions.

Trophic niche

Considering the mass difference between species, it was expected that *C. intervalles* would capture larger prey than *H. longicauda*. Even with hymenoptera biomass and total prey differing between some distance categories, biomass of prey captured did not differ between species in null modelling and statistical designs, indicating overlapping in this axis. Comparing spider and prey biomass, both species are able to capture prey several times heavier than their own. *H. longicauda*, however, has a wider diet breadth. Despite null models corrected for prey availability indicated no overlapping, prey types were very similar. Moreover, in the corrected analysis, more weight is placed in *H. longicauda* capture of rare, low available prey. In fact, the diet of *C. intervalles* is apparently a sub set of *H. longicauda* trophic niche.

Diet differences may be explained by web features. Webs of both species are composed entirely by viscid silk lines (Gonzaga et al. 2006). These structures are composed by droplets, which are important to web viscoelasticity and adhesion (Opell and Hendricks 2010; Sahni et al. 2010). Recently, it was shown that high temperatures decrease droplet viscosity, decreasing extensibility due to the smaller volume and less hydration (Stellwagen et al. 2012). Viscid droplets are timing and energetically costly (Benjamin and Zschokke 2003). The capture of small flying prey items of both studied species depend on stickiness. As the abundance of potential prey, especially Diptera, do not differ according to microhabitats, the temperature increasing along the gradient from the river to adjacent regions may explain why *C. intervalles* captured less prey. Under these circumstances, the occupation of cooler microhabitats may be an advantage for *H. longicauda*. This temperature pattern was observed only in summer, but it is possible that the dispersion of spiders in winter, when overall spider abundance is lower, are not enough to cause population mixing between species.

Gonzaga et al. (2006) also demonstrated that viscid droplets diameter is larger in *C. intervalles* than in *H. longicauda*. Larger droplets may compensate *C. intervalles* hotter microhabitat occupation, allowing individuals of this species to still efficiently perform prey capture. This is in agreement with *C. intervalles* larger body size, because they may be able to invest more in glycoprotein, leading to larger droplets and compensating dehydration stress. In addition, *H. longicauda* spatial restriction at river margins may occur because prey capture of this species may be ineffective at higher temperatures (distances) due to its smaller viscid droplets. Transplant experiments should test this hypothesis.

However, even with the hypothesis that *C. intervalles* would capture more prey close to the river and *H. longicauda* would be less efficient in regions far from the coolest zone, due to the prey similarity attributes and the elevated number of individuals of both species found, it is probably that these populations are not food limited. The number of prey found in sticky traps corroborates this assumption. Although spiders are able to reduce the number of their prey in the environment (see Nyffeler and Sunderland 2003) and isolated evidence indicates that interspecific exploitative competition for food may limit orb weaving spider populations (Spiller 1984a), studies attempting to find trophic niche competitive basis did not find evidences of this process (e.g. Horton and Wise 1983; Riechert and Cady 1983, Houser et al. 2014). Moreover, although trophic niche partitioning between spider species may occur (Olive 1980; Brown 1981; McReynolds and Polis 1987; Richardson and Hanks 2009; Novak et al. 2010; Butt and Tahir 2010; Tahir et al. 2012; Afzal et al. 2013; Michalko and Pekár 2014), we did not find traits indicating it. Due to the overabundance and evenness of prey sampled in the distance categories, especially the most explored dipterans, we found no support to the

hypothesis of shadow competition or prey exploitation competition, even considering *C. intervalles* lower capture rates.

Spatial niche

When considered together, the total number of spiders was positively related to the number of available sites and negatively to fern abundance. In fact, these two predictors presented a negative correlation between them. These patterns indicate that the global abundance of the species studied may be related to local specific floristic composition and this gradient may occur in micro-scale. Since space is apparently also limited for plants, with a negative relation between plants that offer suitable sites and the unsuitable ferns, the proportion of these two groups in the environment determinates the abundance of these spiders. The relation of spiders and suitable sites indicate that both species are sensitive to these biotic factors. Despite presenting narrow leaflets, fern leaves are usually large, some of them surpassing one meter, with leaf agglomerations occupying high proportion of the understory, reducing space for plants with suitable leaf sites. Moreover, spider abundance presented a close relationship with site availability per plant species, corroborating that these theridiids are related to site availability, regardless of distance from the river and plant identities.

We found that both spiders share many plant species, indicating overlap of structural microhabitat selection. Shared species, however, were those occurring in both *H. longicauda* and *C. intervalles* zones. When corrected for availability, even with shared species, null modelling differed from non-random expectations. This pattern, however, is apparently not a specialization in specific sites, but rather a reflex of spider spatial segregation and specific microhabitat availability of plant species.

Our results indicated that larger leaves were occupied by *C. intervales*, and higher web-building sites by *H. longicauda*. These may be key results for spider distribution issue: they reveal possible spider preferences and limitations, suggesting niche differentiation in web-site selection traits along the vertical spatial axis. Besides the horizontal segregation pattern, this behavioural traits generate also a vertical stratification between the two spider populations where *H. longicauda* occur in all height extents (except in those much closer to the 3 m limit established), whereas *C. intervales* population is concentrated in lower web-building sites. This arrangement of interspecific vertical stratification in orb-weaving spiders is thought to represent spatial partitioning and have been frequently reported (Shulov and Weissman 1959; Olive 1980; Spiller 1984a; Ward and Lubin 1992; Herberstein 1998; Harwood and Obrycki 2005; Butt and Tahir 2010; Tahir et al. 2012; Richardson and Hanks 2009) including cases of larger spiders positioned underside (Enders 1974; Brown 1981; Horton and Wise 1983).

The interspecific differentiation in web height and occupied leaf width may further be related to other trait differences, investigated elsewhere. Gonzaga et al. (2006) demonstrated that *C. intervales* webs are placed in larger leaves, corroborating our findings. Moreover, these authors showed that the distance of vertical threads extending from upper leaves to the others directly below is higher for *C. intervales*. This is consistent with the vertical strata *C. intervales* occupies, composed mainly by larger herb leaves and with a higher distance from each other. We still do not know if these differences are preferences of the species or a consequence of spider's vertical arrangement. In any case, these web traits distinctions found herein and by Gonzaga et al. (2006) highlights that differentiation in web structure and web site traits occur. Through null models, however, we did not found such vertical differences. This random

resource utilization might be due to the lack of data for corrected function. For instance, data on potential prey abundance and plant species occupied were highly significant in corrected function, despite not in equiprobable. This input data should places weight in *H. longicauda* specialization at higher sites.

Temporal niche

By investigating species phenologies, we could infer temporal niche differentiation between the related species and temporal niche partitioning (e.g. Ward and Lubin 1992; Nieto-Castañeda and Jiménez-Jiménez 2009; Butt and Tahir 2010; Novak et al. 2010). Spider conditions indicated that there was no difference in spider egg sac and juvenile categories between seasons. The total number of individuals and solitary spiders were lower in winter, and this pattern was observed for both species.

Interestingly, just *H. longicauda* was infested by fungi, as already reported (Gonzaga et al. 2006). We do not know yet if *Gibellula pulchra* presents host specificity or attack only spiders close to the river. Fungi-infested spiders were only five in summer (2%), while in winter, they exceeded 30% of *H. longicauda* population. The high mortality caused by fungi acted as a natural removal experiment, and *C. intervalles* colonization in river margins suggests that competitive release has occurred. The observation of web sites previously occupied during winter by *H. longicauda* killed by fungi being occupied by *C. intervalles* corroborate this. Moreover, transplant experiments suggest that *C. intervalles* establishment rates do not differ between the distances of 0 and 20 m far from the river (Cardoso & Gonzaga, in prep.). Even so, *C. intervalles* individuals did not surpassed *H. longicauda* in the river margin transects, since the density of this was still elevated. We suggest that *H. longicauda* concentrated population hinder *C. intervalles*

to reach the lower sites of river margins regions, probably through asymmetric exploitation competition for space. Furthermore, the elevated motility of solitary *H. longicauda* spiders may contribute to buffering *C. intervalles* populations to reach and establish in river margins.

The horizontal spatial segregation

The spatial arrangement of these spiders rises two opposite, but complementary questions: Why do they occur together (in macro-scale)? Why do they occur separately (in micro-scale)? Environmental filtering abiotic selection on functional traits may explain species sympatry on riparian understory humid regions. The environmental filtering mechanism acts on phylogenetically conserved traits, which leads related species to cluster spatially (Cavender-Bares et al. 2009; Adler et al. 2013; Kraft et al. 2014), suggesting spider co-occurrence in this higher scale. Shared ancestry between these two theridiid spiders may be related to their ecological similarity in various niche axis such as trophic, spatial and temporal. The study of Gonzaga et al. (2006) treating web similarity properties and moisture dependency corroborate this. Despite being closely related and presenting similar and overlapping niches, these spider species exhibit interspecific trait variation as well. In the micro-scale, interspecific functional trait differentiation may be related to niche differentiation and cause coexistence through stratification instead of completely competitive exclusion by one of the species.

Apparently, the horizontal stratified pattern that prompted the current research arises from a mix of factors acting horizontally and vertically. We propose that the three mechanisms first suggested may interact and generate horizontal segregation: (1) environmental filtering, restricting *H. longicauda* to the regions close to the river margin.

As evidenced, *H. longicauda* exhibits a lower niche breadth in spatial horizontal axis, being limited to sites close to the river, apparently due to ineffective viscid adhesiveness at hotter environments. (2) Niche differentiation, acting in the vertical scale. The studied species present microhabitat specialization with *C. intervalles* occurring in lower heights whereas *H. longicauda* may also occur in higher heights, presenting a higher breadth in the vertical spatial axis. By taking this niche differentiations and ideal distributions, at lower sites of regions close to the river, both species may potentially persist. However, apparently (3) competitive exclusion takes place. *Helvibis longicauda* seems to be a dominant competitor at close river lower sites, dislodging *C. intervalles* through asymmetric exploitative competition for space and leading it to be restricted only to the adjacent horizontal microhabitats.

Spiders' spatial arrangement may be treated under the light of species fundamental and realized niches, taking into account respectively abiotic and biotic factors (Fig. 13). *Helvibis longicauda* fundamental spatial horizontal niche is restricted to the proximal river margins. In the vertical fundamental niche, this species occur along all our 3 m height surveyed, with a lower number of spiders occurring at higher sites. On the other hand, *C. intervalles* fundamental horizontal niche comprises all the three distance categories investigated, with fewer spiders occurring at 20 m and beyond. The vertical potential niche of this species is lower than that of the heterospecific, rarely occurring above 1 m height. When the two fundamental niches are superimposed, there is a spatial overlap area, at close river lower sites. Apparently, *C. intervalles* competitive abilities are not enough to cope with those of *H. longicauda*, which leads the first to be restricted to microhabitats further from the margins. In this sense, as a result of species interactions, the realized niche of *H. longicauda* is quite similar to the fundamental. On

the other hand, interspecific competition compresses *C. intervalles* realized niche. Treated together, these mechanisms of environmental filtering on *H. longicauda*, niche differentiation and competitive exclusion generate the horizontal pattern first observed in the field.

In this study, we focused efforts in investigating possible mechanisms that could explain interspecific segregation in this pairwise system. However, intraspecific competition may be an important phenomenon structuring this community. Interspecific segregation leads species to cluster spatially, increasing competition among conspecifics. For instance, intraspecific encounter probability may be high, as both species frequently abandon sites. Complementary studies may elucidate unclear mechanisms and corroborate processes suggested herein. For instance, our next step concerns the transplant of individuals between microhabitats and web-invasion experiments.

Acknowledgments

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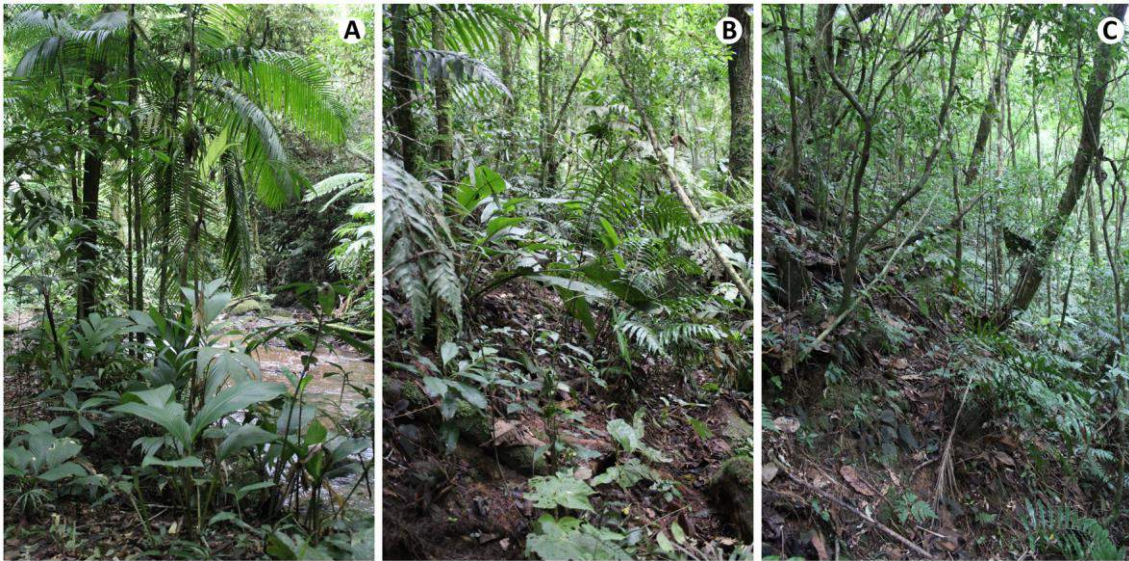
Figures and tables

Fig. 1 – Different distance categories surveyed include 0 (A), 10 (B) and 20m (C) far from the riverbank.

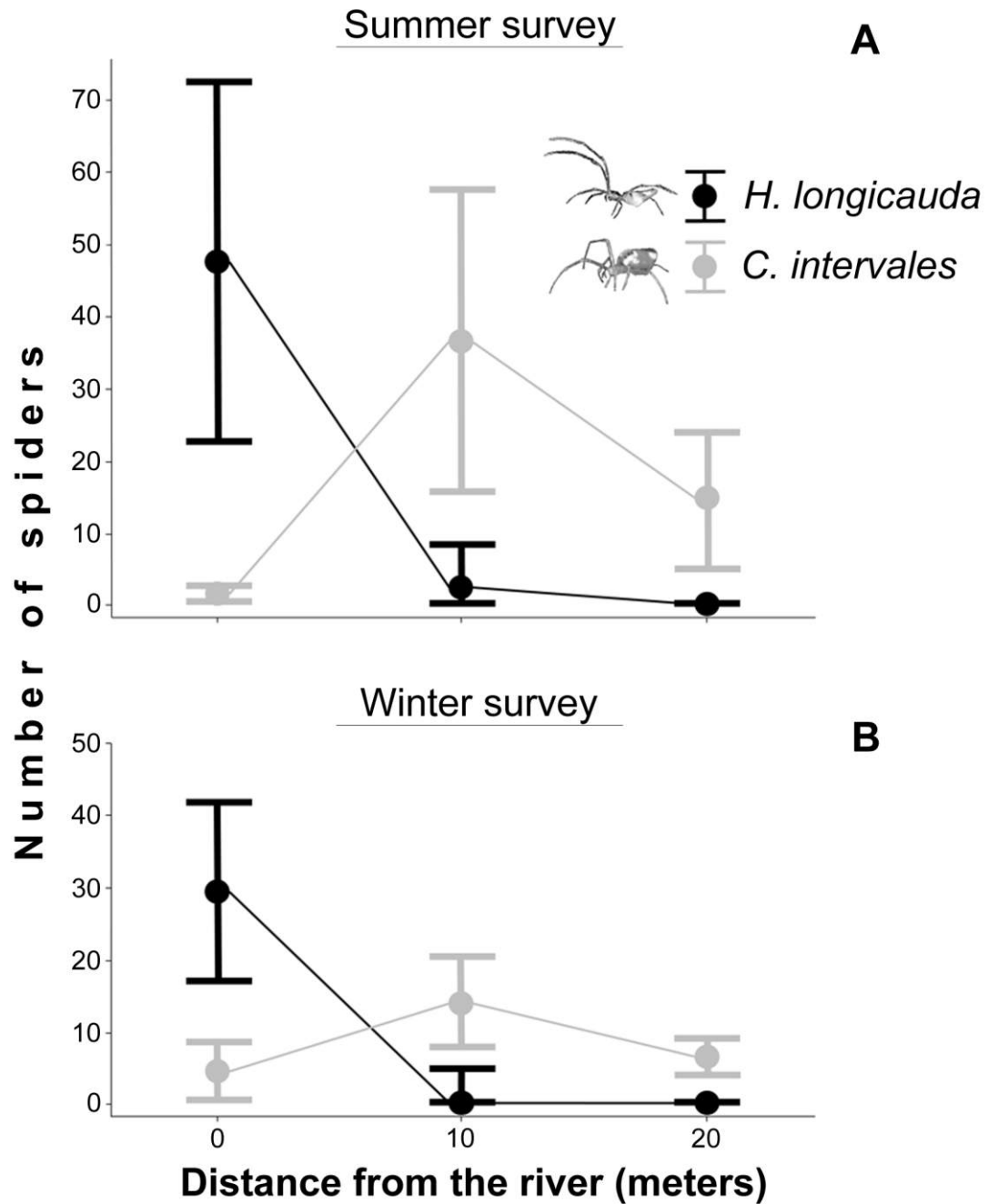


Fig. 2 – Spatial distribution of *H. longicauda* and *C. intervalles* in relation to the three distance categories in summer (A) and winter surveys (B). Despite winter survey data were Log + 1 transformed for analysis, raw data is exposed for comparison purposes. Data represented as mean \pm 0.95 confidence intervals.

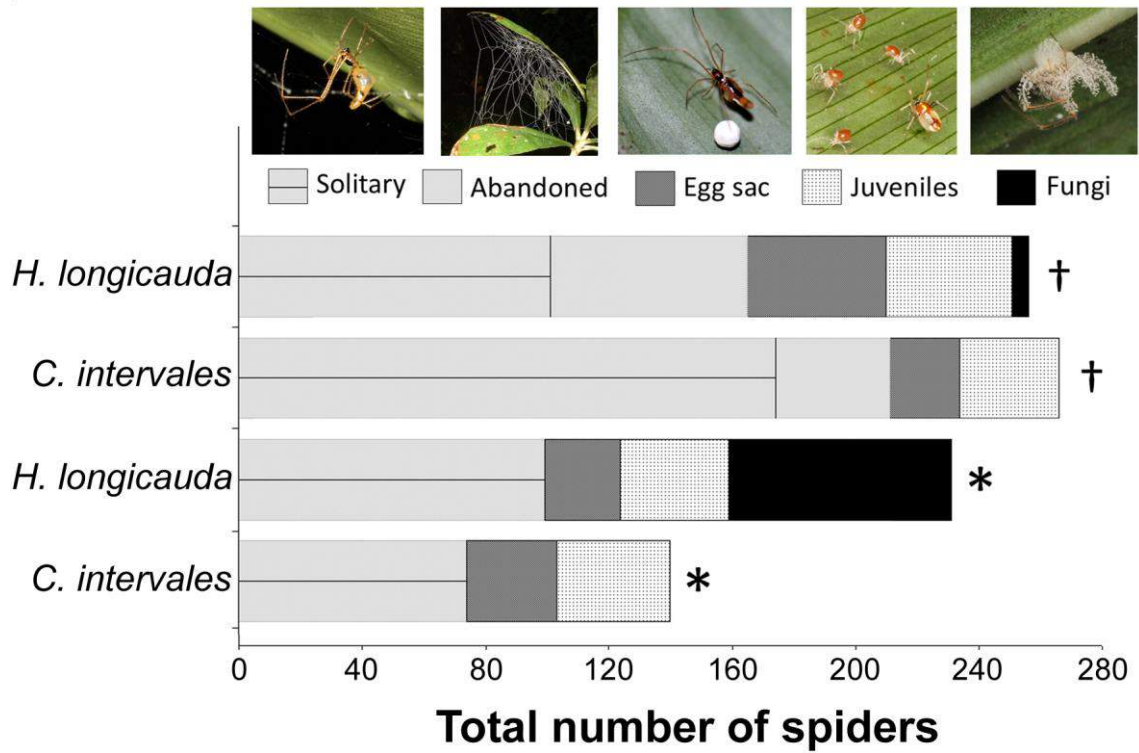


Fig. 3 – Total and relative number of spiders found according to condition in summer (†) and winter (*). Site abandonment rates (verified only in summer) were restricted to solitary spiders. Only *H. longicauda* was infested by fungi. All pictures are from *H. longicauda*, except juveniles.



Fig. 4 – *Chrysso intervales* female (left) in a site located at river margins previously occupied by a *Helvibis longicauda* individual (right) which was killed by *Gibellula pulchra* fungi. Scale bar: 5mm.

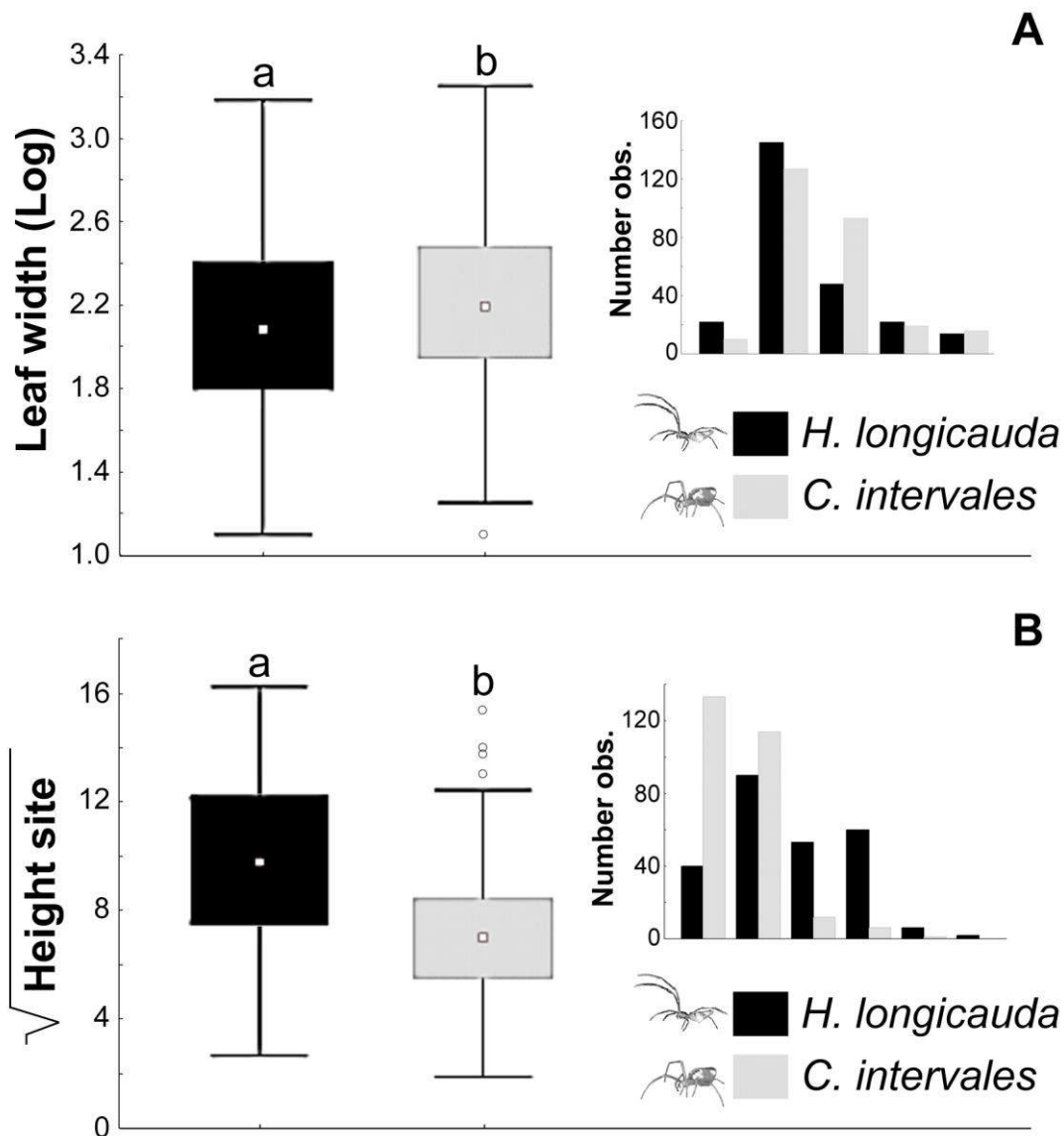


Fig. 5 – Web site attributes differences between *H. longicauda* and *C. intervalles* according to leaf width utilized (A) and height site (B). Box plots display median, quartiles and extreme values. Distinct letters represent significant statistical differences obtained by Tukey post-hoc test at 0.05 level. In the right top of each graph, a histogram displays respective data divided in the same intervals used for null models analysis.

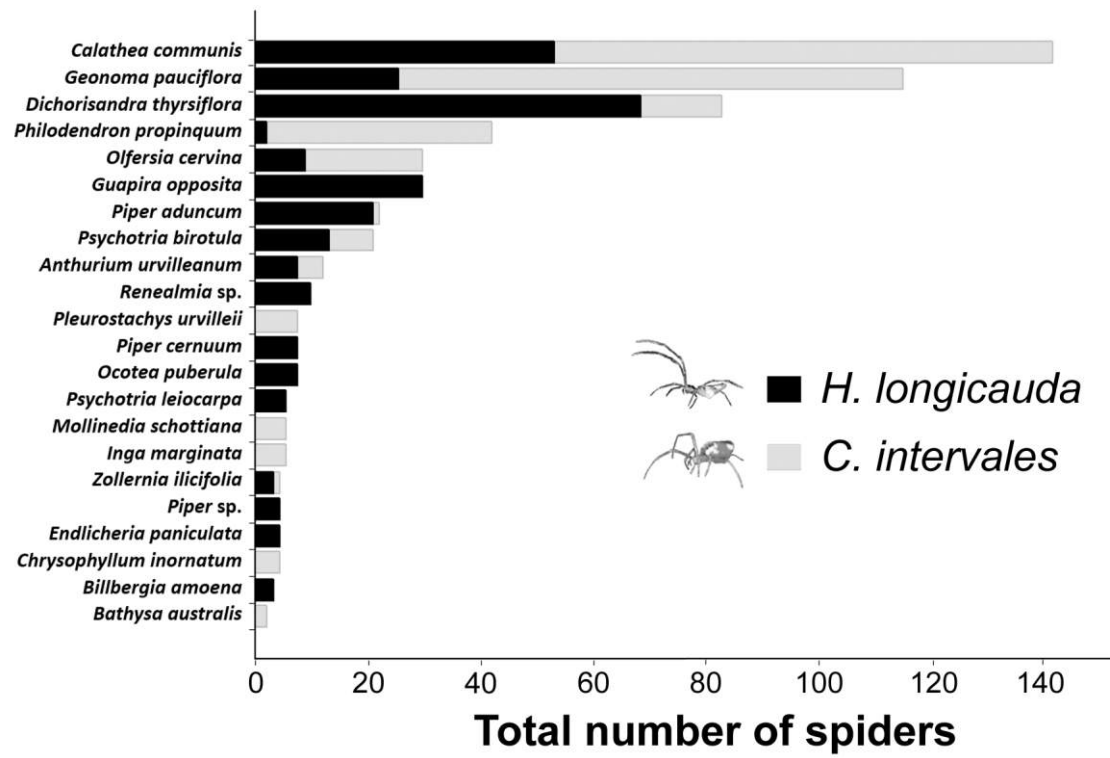


Fig. 6 – Relative proportion of plant species used by *H. longicauda* and *C. intervalles*.

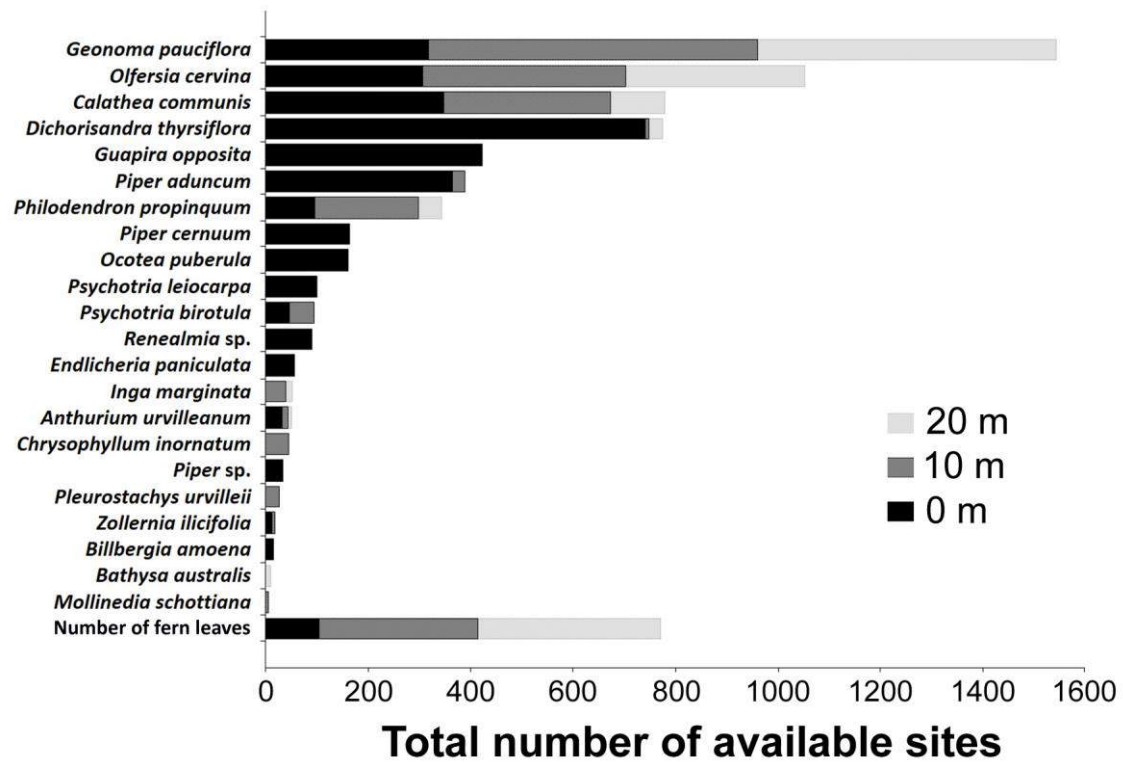


Fig. 7 – Relative proportion of suitable sites availability of plant species occupied according to the three distance categories investigated. Fern leaves abundance is also shown.

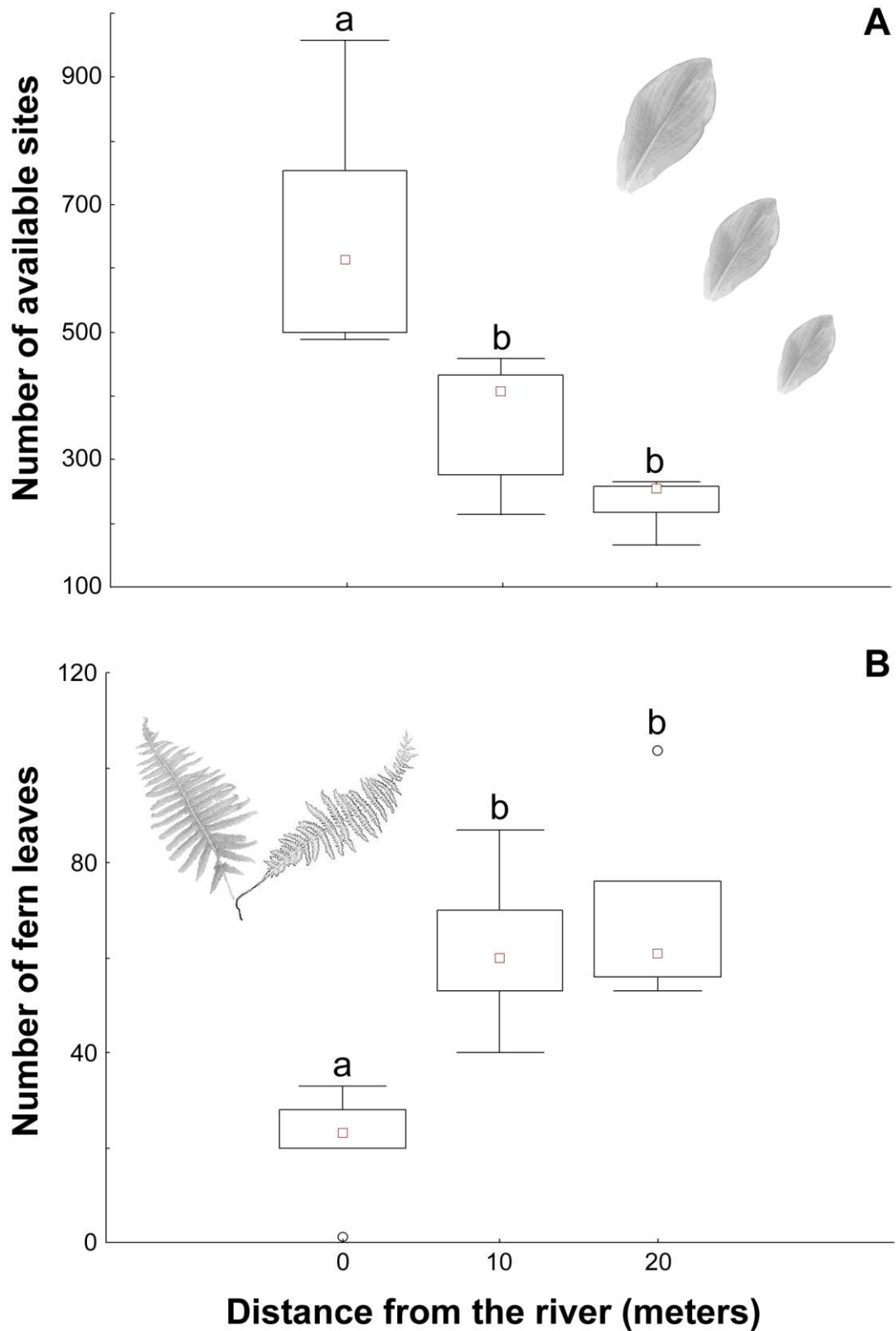


Fig. 8 – Differences in the number of available sites (A) and number of fern leaves (B) in relation to the three distance categories. Box plots display median, quartiles and extreme values. Distinct letters represent significant statistical differences obtained by Tukey post-hoc test at 0.05 level.

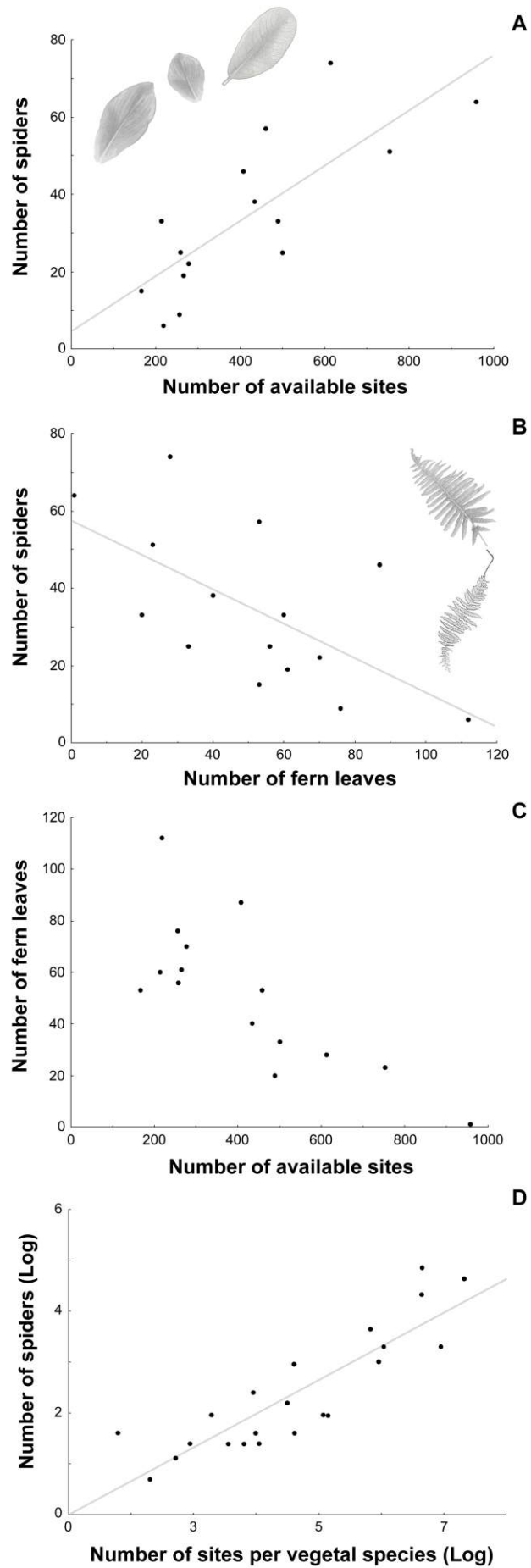


Fig. 9 – Number of available sites according to the total number of spiders (A); number of fern leaves in relation to the total number of spiders (B); negative correlation between available sites and fern leaves (C); and number of available sites per vegetal species (Log) according to the number of spiders found occupying the respective plant (Log) (D).

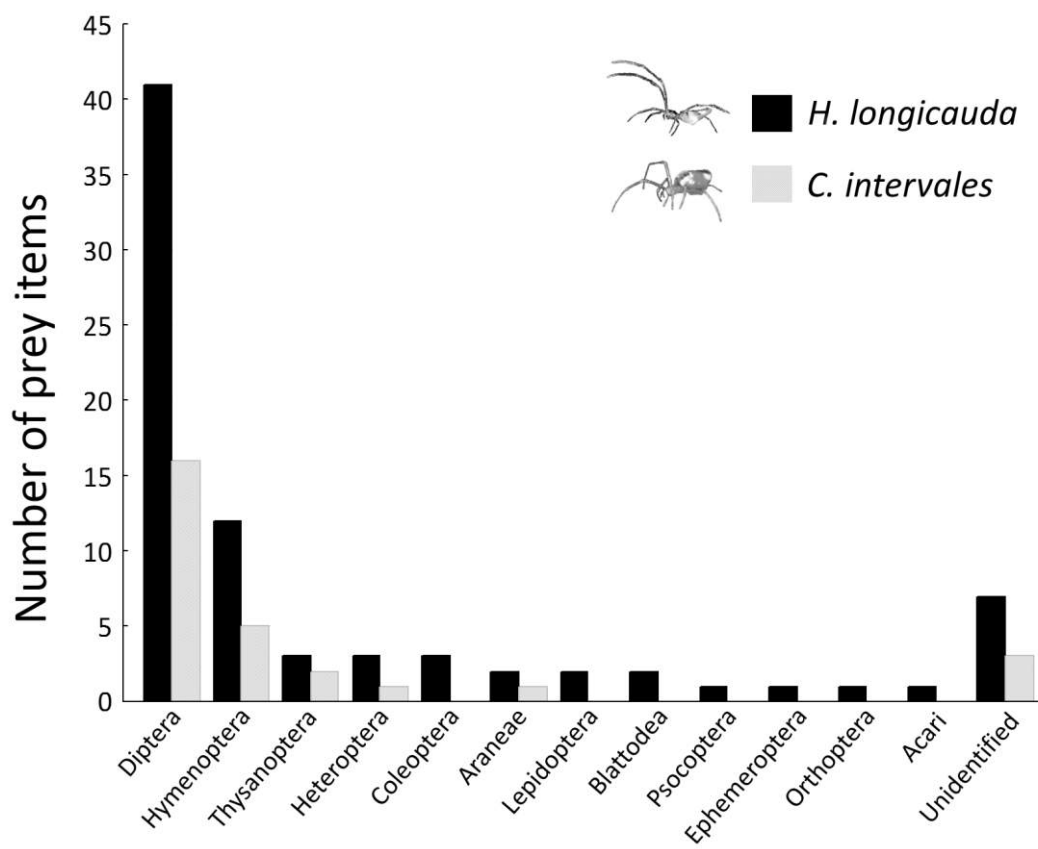


Fig. 10 – Identity and proportion of insects in *H. longicauda* and *C. intervalles* diets.

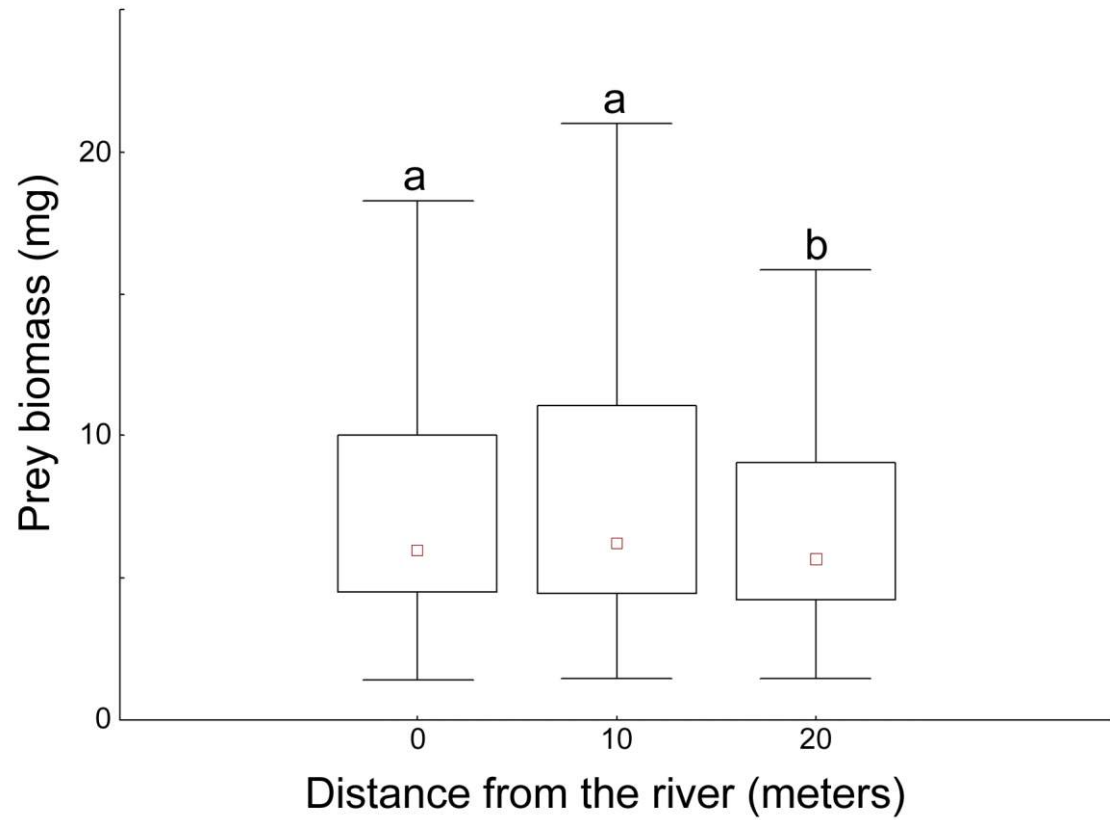


Fig. 11 – Total prey items estimate biomass according to the three distance categories. Box plots display median, quartiles and extreme values. Distinct letters represent significant statistical differences according to Dunn post-hoc test at 0.05 level. Outliers are not shown.

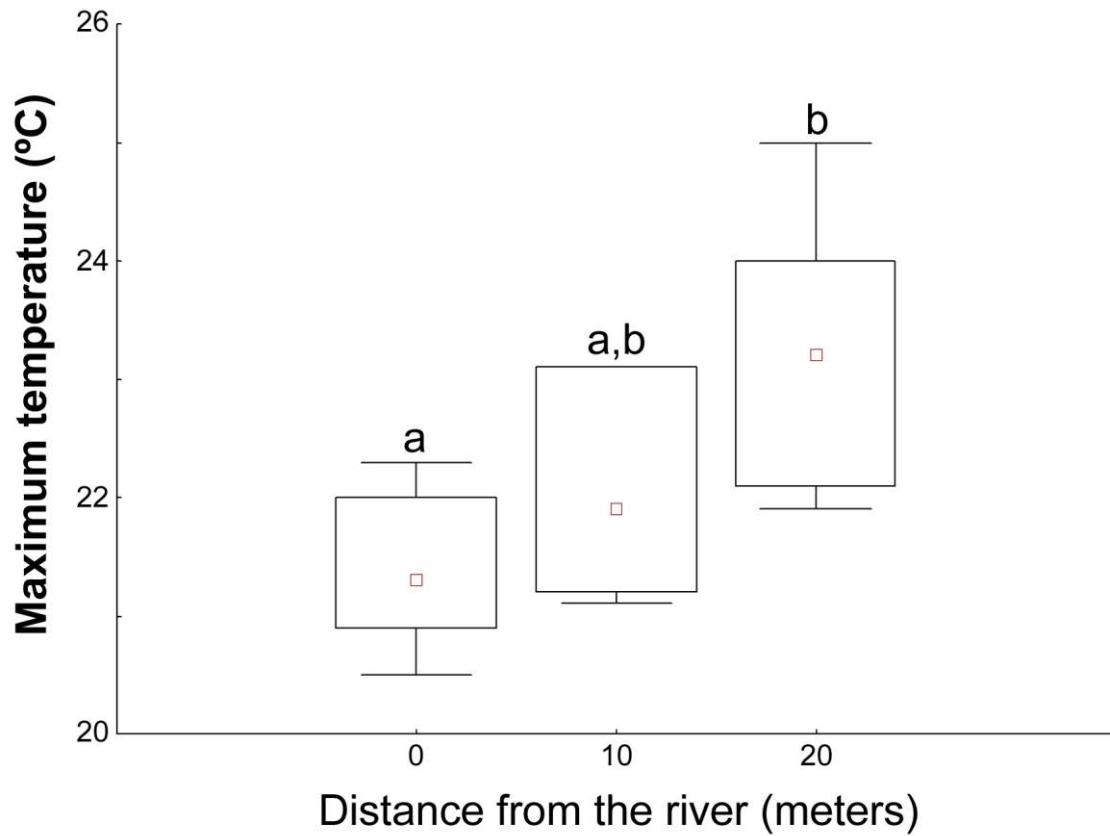


Fig. 12 – Maximum temperature differences according to the three distance categories. Box plots display median, quartiles and extreme values. Distinct letters represent significant statistical differences obtained by Tukey post-hoc test at 0.05 level.

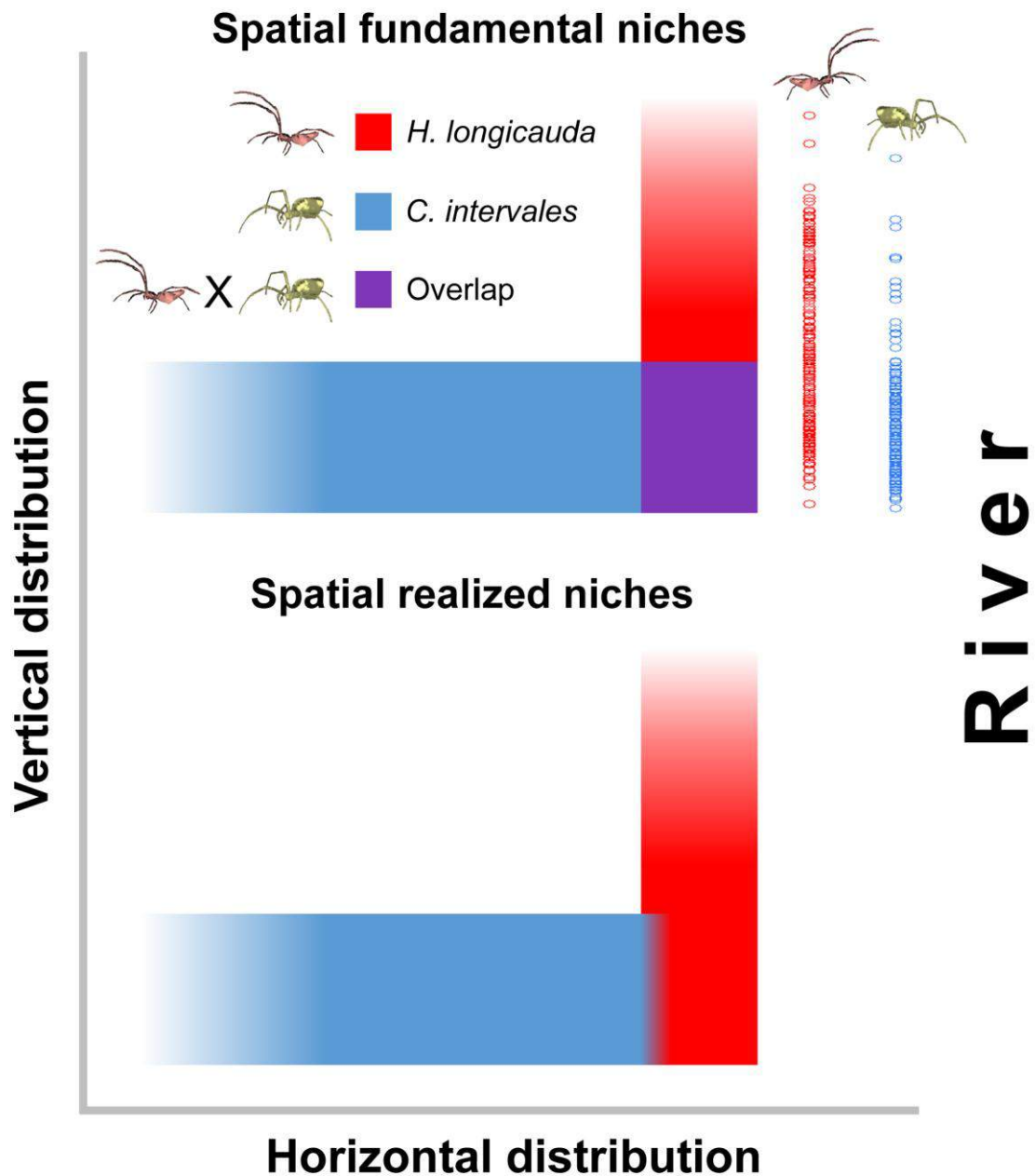


Fig. 13 – Scheme representing *H. longicauda* and *C. intervalles* fundamental and realized niches. *Helvibis longicauda* fundamental niche comprises regions close to the river in horizontal scale while *C. intervalles* may potentially occur in a wider range. In the vertical scale, however, *H. longicauda* fundamental niche is broader, once it may also occur at higher sites. Dots positioned in the upper right portion represent the vertical positioning of all spiders sampled during summer survey. Apparently, *H. longicauda* displaces *C. intervalles* from regions close to the river. In this sense, *H. longicauda* realized niche is quite similar to the fundamental. On the other hand, *C. intervalles* realized niche is compressed due to the heterospecific presence.

Table 1 – Mean (SD) of the number of female spiders found in the different distances according to condition (solitary, taking care of egg sacs or juveniles and infested by fungi). Total number of spiders found takes into account only living spiders, so fungi spiders are not included in these counts. In the first visit, we followed spiders in the field for six days and the abandonment frequencies of web sites after this time are also presented.

Fieldwork	Condition	Total	Mean (SD) total	Distance from the river (meters)		
				0	10	20
Summer survey	<i>H. longicauda</i>					
	Solitary	164	10.93 (16.44)	31.2(12.85)	1.6(3.05)	0
	Egg sac	45	3(4.84)	8.6(4.72)	0.4(0.89)	0
	Juveniles	41	2.73(4.71)	7.8(5.35)	0.4(0.89)	0
	Abandoned	64	4.26(6.68)	12.4(5.59)	0.4(0.89)	0
	Fungi	5	0.33(0.72)	1(1)	0	0
	Total	250	16.66(25.29)	47.6(20.45)	2.4(4.82)	0
	<i>C. intervalles</i>					
	Solitary	210	14(14.82)	1.4(0.89)	29.8(14.67)	10.8(5.45)
	Egg sac	23	1.53(2.03)	0	3.4(2.07)	1.2(1.64)
	Juveniles	32	2.13(2.16)	0.2(0.44)	3.4(2.07)	2.8(2.16)
Abandoned	37	2.46(2.72)	0.4(0.54)	5.4(2.51)	1.6(1.51)	
Fungi	0	0	0	0	0	
Total	265	17.66(17.93)	1.6(0.89)	36.6(16.9)	14.8(7.62)	
Winter survey	<i>H. longicauda</i>					
	Solitary	99	6.6(9.59)	18.6(6.65)	1.2(2.68)	0
	Egg sac	25	1.66(2.74)	5(2.34)	0	0
	Juveniles	35	2.33(3.22)	6.6(1.14)	0.4(0.89)	0
	Fungi	72	4.8(7.56)	14.4(5.22)	0	0
	Total	159	10.6(15.36)	30.2(9.57)	1.6(3.57)	0
	<i>C. intervalles</i>					
	Solitary	74	4.93(2.46)	3.4(1.94)	7(2.91)	4.4(0.54)
	Egg sac	29	1.93(1.48)	1(1)	3.6(1.14)	1.2(0.44)
	Juveniles	37	2.46(1.95)	0.6(0.89)	4.6(1.14)	2.2(1.09)

Fungi	0	0	0	0	0
Total	140	9.33(5.49)	5(3.08)	15.2(4.81)	7.8(1.92)

Table 2 – Total and relative number of individuals found on each plant species according to spider species. In addition, total and divided by transect category mean (SD) availability of suitable and non-suitable sites (ferns). Tests searching for availability differences between distance categories were performed only for plant species that presented five or more occurrences (in 15 transects). Statistical values F/H (respectively ANOVA and Kruskal-Wallis) include non-corrected ANOVA tests, Log + 1 correction (†), Log correction (‡) and Non-parametric Kruskal-Wallis test (°). Bonferroni correction was used and included total sites and fern leaves, but not infrequent species. Only p values lower than 0.0055 were considered significant (expressed in bold). Different letters displayed in distances indicate significant differences obtained by Tukey post-hoc test.

Taxon	Spider species			Number of sites available – Mean (SD)				F/H	p
	<i>H. longicauda</i>	<i>C. intervalles</i>	Total spiders	Total	Distance from the river (meters)				
					0	10	20		
Araceae									
<i>Anthurium urvilleanum</i> Schott	7	4	11	3.46(6.24)	6.6(9.04)	2(4.47)	1.8(4.02)	—	—
<i>Philodendron propinquum</i> Schott	2	36	38	22.93(43.32)	19.2(21.53)	40.6(72.81)	9(12.36)	0.43†	0.66
Arecaceae									
<i>Geonoma pauciflora</i> Mart.	23	81	104	102.93(59.08)	63.4(25.41)	128.8(76)	116.6(52.64)	2.32‡	0.13
Bromeliaceae									
<i>Billbergia amoena</i> (Lodd.) Lindley	3	0	3	1(3.87)	3(6.7)	—	—	—	—
Commelinaceae									
<i>Dichorisandra thyrsoiflora</i> Mikan	62	13	75	51.66(86.67)	148.2(93.67) ^a	1.6(3.57) ^b	5.2(4.97) ^b	27.86†	<.0001
Cyperaceae									
<i>Pleurostachys urvillei</i> Brongn	0	7	7	1.8(6.97)	—	5.4(12.07)	—	—	—
Dryopteridaceae									
<i>Olfersia cervina</i> (L.) Kunze	8	19	27	71.46(54.68)	61.2(71.99)	79.6(43.43)	73.6(56.37)	0.12	0.88
Fabaceae									
<i>Inga marginata</i> Willd.	0	5	5	3.6(6.2)	—	7.8(8.89)	3(4.12)	2.51†	0.12
<i>Zollernia ilicifolia</i> (Brongn.) Vogel	3	1	4	1.26(2.68)	2.6(3.71)	1.2(2.68)	—	—	—
Lauraceae									
<i>Endlicheria paniculata</i> (Sprengel) MacBride	4	0	4	3.8(8.21)	11.4(11.3)	—	—	—	—
<i>Ocotea puberula</i> (Rich.) Nees	7	0	7	10.66(41.31)	32(71.55)	—	—	—	—
Marantaceae									
<i>Calathea communis</i> Wanderley & Vieira	48	80	128	51.93(34.84)	69.6(25.34)	65(36.38)	21.2(22.33)	4.34	0.038
Monimiaceae									
<i>Mollinedia schottiana</i> (Spreng) Perkins	0	5	5	1.33(3.83)	—	4(6.16)	—	—	—
Nyctaginaceae									
<i>Guapira opposita</i> (Vell.) Reitz	27	0	27	28.2(78.55)	84.6(125.02)	—	—	—	—
Piperaceae									

<i>Piper aduncum</i> L.	19	1	20	25.93(44.61)	73.2(51.54) ^a	4.6(10.28) ^b	— ^b	27.64 [†]	<.0001
<i>Piper cernuum</i> Vell.	7	0	7	11(24.37)	—	—	33(34.22)	—	—
<i>Piper</i> sp.	4	0	4	2.33(8.24)	7(14.03)	—	—	—	—
Rubiaceae									
<i>Bathysa australis</i> (A. St.-Hill.) Benth. & Hook f.	0	2	2	0.66(1.75)	—	—	2(2.73)	—	—
<i>Psychotria leiocarpa</i> Cham. & Schltr.	5	0	5	6.66(25.82)	9.6(21.46)	9.2(12.67)	—	—	—
<i>Psychotria birotula</i> L. B. Sm. & Downs	12	7	19	6.26(14.09)	20(44.72)	—	—	—	—
Sapotaceae									
<i>Chrysophyllum inornatum</i> Mart.	0	4	4	3(11.61)	—	9(20.12)	—	—	—
Zingiberaceae									
<i>Renealmia</i> sp.	9	0	9	6(20.29)	18(34.22)	—	—	—	—
Total of available sites	250	265	515	417.73(223)	662.6(196.51) ^a	358.2(106.85) ^b	232.4(41.36) ^b	14.18	0.0006
Fern leaves	—	—	—	51.46(28.7)	20.8(12.63) ^a	62(17.73) ^b	71.6(24.25) ^b	10.28	0.002

Table 3 – Total and relative abundance and biomass of captured prey items according to Order and distance category (mean (SD)). Raw number of individuals trapped is also expressed in total numbers of abundance. Tests searching for abundance/mass differences between distance categories were performed only for groups with enough replicate (in 15 transects). Statistical values F/H (respectively ANOVA and Kruskal-Wallis) include non-corrected ANOVA tests, Log + 1 correction (†), Log correction (‡) and Non-parametric Kruskal-Wallis test (°). Bonferroni correction was used and included Unidentified and Total prey, but not rare groups. Only p values lower than 0.0045 were considered significant (expressed in bold). Different letters displayed in distances indicate significant differences obtained by Dunn post-hoc test.

Taxon	Total number	Distance from the river (meters)			F/H	p
		0	10	20		
Diptera						
Abundance	1039[69.26(20.18)]	85.2(16.66)	65.6(21.55)	57(12.7)	3.46	0.064
Mass	10.72(11)	11.36(12.07)	10.84(11.17)	9.64(8.88)	2.3°	0.31
Hymenoptera						
Abundance	428[28.53(8.65)]	30.8(4.14)	24.8(11.43)	30(9.35)	0.67	0.52
Mass	6.6(3.91)	5.92(3.18) ^a	7.48(4.24) ^b	6.57(4.17) ^{a,b}	9.25°	0.009
Coleoptera						
Abundance	118[7.86(2.66)]	6.2(1.92)	9(3.39)	8.4(2.07)	1.67	0.22
Mass	11.73(18.27)	13.46(16.04)	8.54(7.85)	13.86(26.08)	0.46°	0.79
Araneae						
Abundance	116[7.73(3.19)]	7(2.34)	6.6(3.78)	9.6(3.05)	1.36	0.29
Mass	8.82(14.25)	8.2(9.83)	7.55(9.92)	10.13(18.9)	0.46°	0.79
Hemiptera						
Abundance	71[4.73(2.73)]	3.8(1.3)	4.6(4.03)	5.8(2.38)	0.64	0.54
Mass	18.76(16.56)	22.44(14.17)	22.18(22.7)	13.64(10.25)	3.70‡	0.029
Acari						
Abundance	49[3.26(2.71)]	2.2(2.16)	2.8(1.92)	4.8(3.56)	1.31	0.30
Mass	3.50(0.34)	3.38(0.16)	3.5(0.24)	3.56(0.44)	3°	0.22
Lepidoptera						
Abundance	29[1.93(2.05)]	1(0.7)	1.6(2.07)	3.2(2.58)	1.68	0.22
Mass	18.54(16.96)	26.2(21.81)	20.08(15.77)	15.37(16.20)	1.45‡	0.25
Isoptera						
Abundance	24[1.6(1.54)]	1.4(1.67)	1.6(1.14)	1.8(2.04)	0.072	0.93
Mass	49.81(44.26)	38.09(43.9)	50.45(56.93)	58.36(33.89)	1‡	0.38
Thysanoptera						
Abundance	21[1.4(1.12)]	1.4(0.54)	0.6(0.89)	2.2(1.3)	3.42	0.066
Mass	1.54(0.1)	1.6(0.14)	1.5(0.039)	1.59(0.12)	2.87‡	0.082
Efemeroptera						
Abundance	4[0.26(0.59)]	0.2(0.44)	0.4(0.89)	0.2(0.44)	—	—
Mass	17.04(10.15)	14.42	21.8(14.46)	10.11	—	—
Orthoptera						
Abundance	4[0.26(0.59)]	0.2(0.44)	0.4(0.89)	0.2(0.44)	—	—
Mass	44.60(45.21)	60.07	56.69(63.46)	4.94	—	—
Psocoptera						
Abundance	2[0.13(0.35)]	—	—	0.4(0.54)	—	—
Mass	7.10(3.87)	—	—	7.10(3.87)	—	—
Unidentified						
Abundance	81[5.4(6.05)]	3.2(2.95)	4.2(2.16)	8.8(9.62)	1.93‡	0.18
Mass	5.47(7.26)	3.87(0.58)	7.89(12.04)	4.89(5.15)	3.25°	0.19
Total prey						
Abundance	1986[132.33(30.53)]	142.2(25.83)	122.2(36.73)	132.6(31.54)	0.49	0.61
Mass	10.25(13.07)	10.49(12.39) ^a	11.75(13.76) ^a	9.53(13.13) ^b	11.85°	0.0027

Table 4 – Czekanowski and Pianka indexes and null modelling Niche Overlap results obtained using RA2 and RA3 algorithms applied to different resources. Mean (Variance) refer to simulated matrices. Significant values (≤ 0.05) of p (observed \leq expected) are expressed in bold. When existing data, in addition to equiprobable, analysis were also performed correcting for resource availability

Table 5: Shannon–Wiener index values (H) indicating niche breadth of *H. longicauda* and *C. intervalles* according to different resources.

Resource	<i>H.</i> <i>longicauda</i>	<i>C. intervalles</i>
Distance category		
Summer	0.2	0.73
Winter	0.2	1
Prey type	1.54	1.07
Prey mass	1.44	1.46
Plant species	2.44	1.89
Leaf width	1.22	1.21
Height site	1.46	0.94

CHAPTER 2

The role of agonistic interactions between two related syntopic cobweb spiders (Araneae: Theridiidae) in horizontal spatial segregation**Abstract**

Species may present different competitive performances and strategies. Due to similarities in functional traits, stronger competitors tend to competitively exclude related species. Even though, some close relatives may still coexist. Fine-scale horizontal segregation between web building spiders has been recently described for a pairwise species system. Along a riparian forest understory, *Helvibis longicauda* occurs in river margins, while the related *C. intervalles* is abundant a few meters away. Due to this arrangement, populations are divided in two well-defined zones. In such context, the present study aimed to investigate the relative role of species agonistic interactions in the process of spatial segregation and the success of establishment and colonization of both species in both microhabitats. We induced spiders to directly interact by experimentally simulating web invasion events, intra and interspecifically. In order to investigate the role of resident spiders in web defense, procedures were replicated without the presence of these. Contestants were weighted for investigating mass dependent outcomes. We also performed transplants between the two different microhabitats in order to examine the establishment success of both species in both microhabitats, near and far from the river. Finally, we investigated colonization of spiders in empty suitable sites. Intruder fleeing behavior was a common outcome. Moreover, intruders inserted in empty webs remained most of the times, suggesting that the mere presence and vibratory behavior of residents is important against intruders. Agonistic interactions demonstrated that resident spiders present advantage over intra and interspecific intruders, once they remained solely in the web in most contests. In fact, resident spiders effectively defended the web even against larger intruders. However, much

larger intruders have a higher probability of remaining in the new web, sometimes driving away the resident. *Chryso intervalles* females are usually larger, but this advantage is not enough to assure the occupation of suitable sites close to river margins. However, establishment rates did not differ between species in both zones and each spider was the most common colonizer on the zone where it is more abundant. We hypothesize that the observed high success of *H. longicauda* in zones away from the river margins was influenced by temperature evenness during experiments, which were performed in winter. In this sense, transplant experiments need to be replicated during summer, when temperature is higher away from the river.

Keywords: microhabitat selection, interference competition, *Helvibis longicauda*, *Chryso intervalles*, Araneae, Theridiidae

Introduction

Ecological interactions play an important role in communities structuration and species evolution (Thompson, 1988, 1999, 2014; Wisz et al., 2013). Among interspecific biotic interactions, competition is a key factor (Schoener, 1983; Keddy, 2001; Thompson, 2014), despite the difficulty to detect its occurrence in nature (Schoener, 1983). It is consensual that interspecific competition has an important role in shaping species ecological and evolutionary attributes, such as abundance, distribution and character displacement (Connell, 1961; Schoener, 1983; Grant & Grant, 2006; Wisz et al., 2013). By definition, competition mechanism takes place if organisms have a negative effect over others, by consuming or controlling access to resources of limited availability (Keddy, 2001). Thus, the presence of a superior competitor may prevent a species of occupying part of its fundamental niche (Gause, 1934; Hutchinson, 1957; Connell, 1961;

Austin, 1999). Species occupying similar niches tend display similarity in ecological traits and resources required, increasing competition intensity, as suggested by the strength in competitive relationship between trait-similar close related species (Chase & Leibold, 2003; Violle et al., 2011; Verdú et al., 2012; Allan et al., 2013).

Pairwise competitive interactions between species may present varying outcomes. For instance, the competition effects may be symmetrical (reciprocal) if species suppress each other equally. However, when differing in competitive performance, the superior competitor induces stronger effects on the other, leading to asymmetric (non-reciprocal) competition (Keddy, 2001). This may generate differential exploitation of essential resources such as trophic and spatial ones. Moreover, competition interaction may be direct, such as through interference competition and predation, or indirect, through the depletion of the availability of a resource of common utilization (exploitation competition) (Hutchinson, 1957; Schoener, 1989; Keddy, 2001).

The costs and consequences of interspecific competition are relatively well understood in some taxa such as plants (e.g. Grace & Tilman, 1990; Craine & Dybzinski, 2013; Paradis et al., 2014; Sheppard & Burns, 2014) and ants (e.g. Parr & Gibb, 2010; Cerdá et al., 2013; Dáttilo et al., 2014). In other highly diverse groups, however, information on competition is scattered and undefined. For instance, in the species-rich group of spiders, investigation of the process is still incipient. Seminal studies present contrasting conclusions. Concerning web-building spiders, some suggested that it constitutes an underlying process in the structuration of spider communities (Spiller 1984 a,b; Nyffeler et al., 1986; Polis et al., 1989; Hann, 1990; Bednarski et al., 2010; Jakob et al., 2011; Lewis, 2013; Houser et al., 2014), while others advocate that it is weak or even absent (Wise, 1981; Riechert & Cady, 1983; Horton & Wise, 1983; Wise, 1984;

Hoffmaster, 1985; Wise, 1993). Putting aside this ambiguity, if the mechanism does commonly occur, it would very likely influence spider growth rates, reproductive output and spatio-temporal distribution.

Recently, Cardoso & Gonzaga (in prep.) described a system in which competition may be lying behind. The spider species *Helvibis longicauda* and *Chrysso intervalles* are phylogenetically related (Arnedo et al. 2004, 2007; Eberhard et al., 2008; but see Agnarsson, 2004) and occur sympatrically along the understory of a riparian tropical forest. These species share many life-history traits such as subsociality, infanticidal males (Gonzaga & Leiner, 2013; Gonzaga et al., in prep), moisture-dependence and web attributes (Gonzaga et al., 2006). Moreover, in niche occupation, they overlap in the exploitation of many resources, such as prey type and plant species used as support for web construction (Cardoso & Gonzaga, in prep.). However, *H. longicauda* population is distributed mainly close to river margins, while *C. intervalles* is more abundant a few meters away from the margins. This fine-scale horizontal spatial segregation in spiders has never been reported before. Cardoso & Gonzaga (in prep.) suggested that the peculiar spatial arrangement occurs due to the interaction and equilibrium between three main factors. In the horizontal scale, (1) environmental filtering apparently restricts *Helvibis longicauda* to cooler places, which are the areas close to river margins. The authors hypothesized that web adhesiveness is impaired due to a higher water evaporation from web droplets at hotter places, compromising prey capture. On the other hand, *C. intervalles* may occupy a wider horizontal range. In the vertical plane, these species present (2) interspecific functional trait differentiation, with *C. intervalles* specializing on lower microhabitats than *H. longicauda*. When horizontal and vertical arrangements are treated together, there is a fundamental niche overlap zone where

both species may potentially occupy, in river margins, at positions close to the soil. Apparently, through (3) competitive exclusion, due to its high populational abundances and motility in the environment, *H. longicauda* displaces the *C. intervalles* from the river margins through asymmetric exploitation competition for space. This set of mechanisms leads populations to become spatially arranged in two well-defined horizontal zones.

In addition to exploitation competition, agonistic interactions may be important to the final spatial configuration observed. Under this framework, we follow Cardoso and Gonzaga (in prep.) assumptions and hypothesised that *H. longicauda* is usually well succeed in confrontations on the microhabitats used to web placement. Herein, we investigated the outcomes of agonistic interactions between individuals of these two species. In addition, we experimentally test if the success of establishment and colonization of species differ, in both microhabitats. We hypothesise that *H. longicauda* establishment success and colonization of available sites are higher in the river margins, but lower in places away from it. On the other hand, *C. intervalles* establishment may be equivalent in both regions, while colonizations may be lower at regions close to the river due to the scarcity of potential colonizers.

Materials and Methods

Studied species

Helvibis longicauda and *Chryso intervalles* are restricted to riparian regions, occurring always in shaded, humid regions (Gonzaga et al. 2006). Webs of both species are composed entirely by viscid silk lines (i.e. adhesive droplets in all over the web extent),

and positioned underneath laminar leaves, which are apparently used as retreat (Gonzaga et al. 2006).

Study site

We performed the study in the Intervales State Park (24°16'S, 48°25'W), Ribeirão Grande, São Paulo State, Brazil, during July 2014. The area is part of a protected continuum of Atlantic Forest wherein the weather is subtropical with two well-defined seasons, a cold-dry (April to September) and a warm-wet (October to March) (Chelini et al., 2011). Our study site comprises the “site 7” described in the study of Gonzaga et al. (2006), a 200 m transect on the Mirante river margins (see details in Gonzaga et al., 2006).

Procedures

Web-invasion experiments

We induced spiders to directly interact with each other by simulating intra and interspecific web invasion events in an interference competition context. In this sense, four different treatment categories were set: *H. longicauda* introduced in webs of *H. longicauda*, *C. intervalles* in webs of *C. intervalles* (intraspecific invasions), *H. longicauda* in webs of *C. intervalles* and *C. intervalles* in webs of *H. longicauda* (interspecific invasions). For each category, we conducted 40 *in situ* essays, comprising 160 interactions. Since the reproductive status of spiders could influence interaction outcomes, for both, intruder and resident, we only selected adult females without egg sacs or spiderlings. Intruder spiders were collected in their webs and kept in separated vials for 15 min before introduction. Intruder spider was always placed in one of the

support threads, located above the web centre and connecting the upper leaf to the lower. After being left in the resident's web, the intruder immediately began to climb toward the centre (Fig. 1A). Each interaction was observed during a maximum period of 20 min. Afterwards, the event was categorized as one of the following behavioral outcomes: (1) resident spider wins the contest and stays in the web (Fig. 1B, C); (2) intruder spider wins the contest and takeover the web; (3) resident runs away without fighting; (4) intruder runs away without fighting (Fig. 1 D); (5) both spiders stay in the web and (6) both spiders leave the web. In order to investigate if spider's biomass influenced interaction outcomes, after each event, contestants were captured and weighted in an analytical balance (readability of 0.0001g).

To evaluate if the presence of the resident spider influences behavioural outcomes of interactions, we performed the same experimental protocol described above, with the same sample size, but removing the web owner before intruder placement. Thus, the alien spider was entering an empty web. After 20 min, we recorded if (1) the intruder left resident's empty web or if (2) the intruder remained in the web. Individuals were weighted in order to investigate if biomass plays a role in these outcomes as well.

Spider establishment and colonization

In order to investigate the establishment success of both species in the two different microhabitats, near and far away from the river margins, individuals were transplanted between them. Colonization was evaluated by monitoring potential web-building sites over time. Thereby, 180 individuals of *Calathea communis* (Marantaceae) were selected in a 200 × 5 m transect immediately parallel to the riverbank. At 20 m far

away from the riverbank and parallel to the first transect, a second transect was delimited and other 180 *C. communis* selected. Plants were at least 3m away each other. We chose *C. communis* because it is an abundant species, occurring far and near the river and occupied by both species (Cardoso & Gonzaga, in prep). On each plant, we selected one leaf without herbivory marks, which was positioned above other leaf to allow thread attachment. In the leaves selected near the river, 70 had *H. longicauda* placed, 70 *C. intervalles*, and other 70 were left empty. Far away from the river, we performed the same procedure with equivalent sample size. We introduced spiders by carefully placing them in the adaxial surface of the leaf. Immediately, the spider began moving and then, reached the leaf lower surface. Some spiders inspected the abaxial surface and others remained motionless. After introduction, we waited for 10 min in order to investigate if the spider left the site in this first moment. When it occurred, the spider was replaced by a conspecific and not used anymore. Leaves with spiders were used to evaluate establishment while leaves without spiders, colonization. We inspected leaves every day during five days.

Statistical analysis

A G test with Williams correction was carried out in each category of interaction to compare the frequency of behavioral outcomes during introduction experiments in webs with resident spiders. We attributed equal expected frequency for each of the six possible results. With the purpose of investigating contest success of resident spiders, on each interaction category, we grouped the outcomes indicating that resident remained solely on its web (“resident spider wins the contest and stays in the web” and

“intruder runs away without fighting”) and compared these values to the sum of the remaining outcomes through Chi-square tests.

Afterwards, we grouped the outcomes “intruder species wins the contest and stays in the web”, “resident runs away, without fighting” and “both spiders stay in the web” and classified them as a unique behaviour: “intruder remains in the resident’s web”. The remainder outcomes were considered as “intruder left resident’s web”. We used this data to calculate the probability of the intruder remain in the web according to the biomass difference between intruder and resident (intruder minus resident body weight). We expected that size-advantaged intruders present an increase in the probability of remaining in resident’s web. We test this through logistic regression applied to the different treatment categories. In empty webs introductions experiments, the outcome “intruder left resident’s web” presented less than five occurrences, so due to this data paucity, we did not perform Chi-square tests neither logistic regressions (see results). We grouped overall 480 spiders weighted and used this data to compare body mass between species through a Student’s t-test.

Spider abundances were compared along time through survival analysis. First, we compared the four curves of spider establishment: *H. longicauda* placed (1) near and (2) far from the river and *C. intervales* placed (3) near and (4) far from the river. For this purpose, we performed Logrank (Mantel-Cox) and Gehan-Breslow-Wilcoxon tests. The basic difference between these two tests is that the Gehan-Breslow-Wilcoxon test weight “deaths” occurring in the curve beginning. Statistical differences obtained in both tests indicate that the curves analysed are not similar in the overall populations. These same tests were used to compare the four curves related to colonization by both spider species, near and far from the river.

Results

The frequency of behavioral outcomes is apparently not random, once there were significant differences in interactions frequencies for all groups (*H. longicauda* intruder – intraspecific: $G = 18.08$, $df = 5$, $p = 0.002$; interspecific: $G = 24.14$, $df = 5$, $p = 0.0002$; *C. intervalles* intruder – intraspecific: $G = 18.69$, $df = 5$, $p = 0.002$; interspecific: $G = 17.39$, $df = 5$, $p = 0.003$; Fig. 2). For all analyzed categories, the most common outcome was “intruder left without fighting”, followed by “resident spider won the fight” (Fig. 1 B - D). In this sense, the resident condition is apparently an advantage over intruders, regardless of spider identity. The frequency of outcomes is summarized in table 1, arranged according to intruder biomass in relation to the resident (larger or smaller). During interactions, we observed that exclusively resident spiders present a series of agonistic vibratory behaviors during web invasion, which probably drives away intruders. When invasive spiders are still far from the web upper region, climbing the threads, the resident perceives the movement and position itself facing the stimuli source. Regardless of the invader identity, *H. longicauda* promotes vibratory stimuli on threads with the first pair of legs. On the other hand, *C. intervalles* perform warning stimuli by hitting the abdomen consecutively in the web threads. Intruder permanence was the most common outcome observed when spiders were placed on empty webs, regardless of intruder species or web type (Fig. 3). The frequency of residents success was higher than the frequency of remaining outcomes in all interactions categories (*H. longicauda* intruder – intraspecific: $\chi^2 = 10.00$, $df = 1$, $p = 0.0016$; interspecific: $\chi^2 = 10.00$, $df = 1$, $p = 0.0016$; *C. intervalles* intruder – intraspecific: $\chi^2 = 8.10$, $df = 1$, $p = 0.0044$; interspecific: $\chi^2 = 10.00$, $df = 1$, $p = 0.0016$).

In all performed categories, the larger the intruder mass compared to the web owner, the higher the probability of this alien spider remaining in the web (*H. longicauda* intruder – intraspecific: $\chi^2 = 4.86$, $df = 1$, $p = 0.027$; interspecific: $\chi^2 = 9.18$, $df = 1$, $p = 0.002$; *C. intervalles* intruder – intraspecific: $\chi^2 = 12.29$, $df = 1$, $p = 0.0004$; interspecific: $\chi^2 = 4.37$, $df = 1$, $p = 0.036$, Fig. 4). Overall spiders analyzed demonstrated that *C. intervalles* (mean \pm SD: 4.04 ± 1.86 mg) is significantly heavier than *H. longicauda* (2.9 ± 1.03) ($t = 8.26$, $df = 478$, $p < .0001$; Fig. 5).

There is no difference in establishment curves of both species, in both microhabitats, according to Log-rank ($\chi^2 = 3.92$, $df = 3$, $p = 0.26$) and Gehan-Breslow-Wilcoxon ($\chi^2 = 3.86$, $df = 3$, $p = 0.27$) tests. Colonization curves, however, were different (Log-rank: $\chi^2 = 14.19$, $df = 3$, $p = 0.002$; Gehan-Breslow-Wilcoxon: $\chi^2 = 14.11$, $df = 3$, $p = 0.002$) (Fig. 6).

Discussion

Many costs are associated with web takeover for the resident spider. By losing the web, its time and energy consuming for the dislodged spider searching for a new site and building a new web (e.g. Jakob et al. 2001, Venner et al. 2003; Leclerc, 1991). For instance, energetic investment in web corresponds to approximately four days of foraging activity in a pholcid spider (Jakob, 1991). Webs of theridiid spiders are built gradually over a period of many days and present long life span (Benjamin & Zschokke 2003). Thus, web losing may represent an impairment of several days of previously time and energetic investment. In addition, losing the web represents potential predation risk during the searching process to locate another suitable site for web construction and the risk of establishment in new site with lower food intake (Leclerc, 1991). In this sense,

resident spiders are expected to defend their valuable webs due to costs related to lose it. On the other hand, as a new web is costly, in many circumstances, a webless spider attempts to take over webs of others with similar traits instead of building its own (Wise, 1993; Enders, 1974; Spiller, 1984b; Bednarski et al., 2010; Houser et al., 2014). Moreover, as spiders concentrate in prey-rich areas, a pre-existing web indicate a suitable foraging site (Harwood et al., 2001, 2003; Schuck-Paim & Alonso, 2001). Overall, for resident and intruder spiders, risk injury or predation may exist due to physical contest. In this sense, there might be costs and benefits in competition for webs and sites related.

The outcomes of agonistic interactions were similar and followed the same pattern in all species interactions categories. Body mass difference explained the behavior of intruder remain in the alien web. Effective web takeover occurred in most of these cases (Intruder won + Resident left) and these separated results were also related to the mass difference (results not shown). Body size is an important trait in species interactions and in the structuration of animal assemblages (Werner & Gilliam, 1984). Although in some isolated cases one spider species may be dominant over other (Houser et al., 2014; Fischer et al., 2014), in general, large-bodied individuals are more successful in intra (Riechert, 1978; Wise, 1983; Samu et al., 1996) and interspecific web takeover (Enders, 1974; Wise, 1993; Eichenberger et al., 2009; Fischer et al., 2014). Our results are in agreement with the tendency observed in literature, suggesting that *H. longicauda* is not competitively superior in interference competition for webs. Likewise, outcomes indicate that *C. intervalles* displacement to further river regions is not a product of direct behavioral conflicts between species.

The intensity of interference agonistic interactions between arachnids may be viewed as a continuum from nonlethal interactions (such as the use of repellent chemicals), nonlethal fighting, or even intraguild predation (Reitz & Trumble, 2002). Despite it is likely to occur in web invasion contexts (e.g. Enders, 1974; Eichenberger et al., 2009; Houser et al., 2014), and the studied species may prey on spiders (Cardoso & Gonzaga, in prep.), we did not observe cannibalism or intraguild predation between *H. longicauda* and *C. intervalles*. In addition to nonlethal fighting during interactions, we also witnessed ritualized displays that apparently mediate communication between intruder and web owner, as observed in other experiments involving agonistic interactions (Riechert, 1978; Fischer et al., 2014). For instance, by investigating intruder-resident contests on *Metepeira labyrinthea*, Wise (1983) recorded that winners usually displayed a greater behavior variety, such as web shaking. In our system, vibratory stimuli were only performed by resident spiders and may be interpreted as a pre-fight warning behavior. Vibrations on the web may offer a cue for weight assessment between distinct spider individuals interacting (Riechert, 1984). It is likely that the resident's performance is related to the high rates of intruder fleeing behavior, reducing risk injury due to a forthcoming larger opponent.

Although the resident status does not influence the context outcomes in other systems (e.g. Wise, 1983), apparently, the web owning condition is an advantage in intra and interspecific contests involving *H. longicauda* and *C. intervalles* (and in other systems, e.g. Schuck-Paim, 2000; Fischer et al., 2014), since resident spiders remained in the web solely in approximately $\frac{3}{4}$ of all interactions, in all categories. For instance, most common outcomes were "Intruder left the web" followed by "resident won the fight". Moreover, resident spiders won contests even against larger intruders,

suggesting that intruders with small mass advantage may still lose contests and withdraw from residents' web. The mere presence of the resident spider associated to the vibratory signals are important in determining interaction outcomes, as suggested by empty web introductions experiments, in which most of intruders remained in the invaded web. Even though, we still do not know if these intruder spiders are prompt to remain in the web for long periods, performing foraging and reproductive activities, though this is expected due to the costs involved in spinning a new web.

Chrysso intervales average biomass is higher than that of the heterospecific. Since biomass is a determinant of dispute outcomes, this difference could confer *C. intervales* a competitive advantage over the heterospecific. However, we do not have information about spiders motility and web abandonment rates. It is likely that undernourished individuals leave their sites more often due to unfavorable local conditions. For instance, by comparing abdomen volumes, Enders (1974) observed that web invader spiders are usually undernourished. Moreover, younger adults leaving the mothers web may not be as heavier as older spiders, and it's known that juveniles are disadvantaged in taking over alien webs (Fischer et al., 2014). As ownership is an advantage, the difference between *C. intervales* invaders and *H. longicauda* residents might not be enough to confer successful takeovers to the intruders.

Results concerning colonization by both species corroborate our hypothesis that each species is more able to colonize available sites on the respective region it is abundant. Transplant experiments did not pointed differences in establishment of spiders in the microhabitats. This goes against the thermal limit proposed by Cardoso & Gonzaga (in prep.) which states that *H. longicauda* is not able to thrive in distal river environments due to higher temperatures. However, it is too soon to refute this

hypothesis. First, the experiment occurred only in five days and this might not be enough time to detect differences. Secondly, in the same days we performed this experiment, the local temperature did not present significant differences between the sites analyzed in the current study (Cardoso & Gonzaga, in prep). Differences in maximum temperature were restricted to summer (Cardoso & Gonzaga, in prep). These authors suggest that during winter, the period of low temperatures is not enough to cause population mixing, especially because individuals are less abundant.

Regardless of species identity, our results indicate that biomass differences along with ownership condition are the main determinants of success in contests involving occupation of profitable microhabitats for web construction. However, the lack of a dominant-subordinate relationship indicates that indirect mechanisms such as exploitation competition may underlie the fine-scale horizontal segregation pattern. Further research is needed to elucidate the spatial distribution pattern, especially retesting establishments in summer, with long-term experimentation also concerning spiders reproductive output.

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Figures and Tables

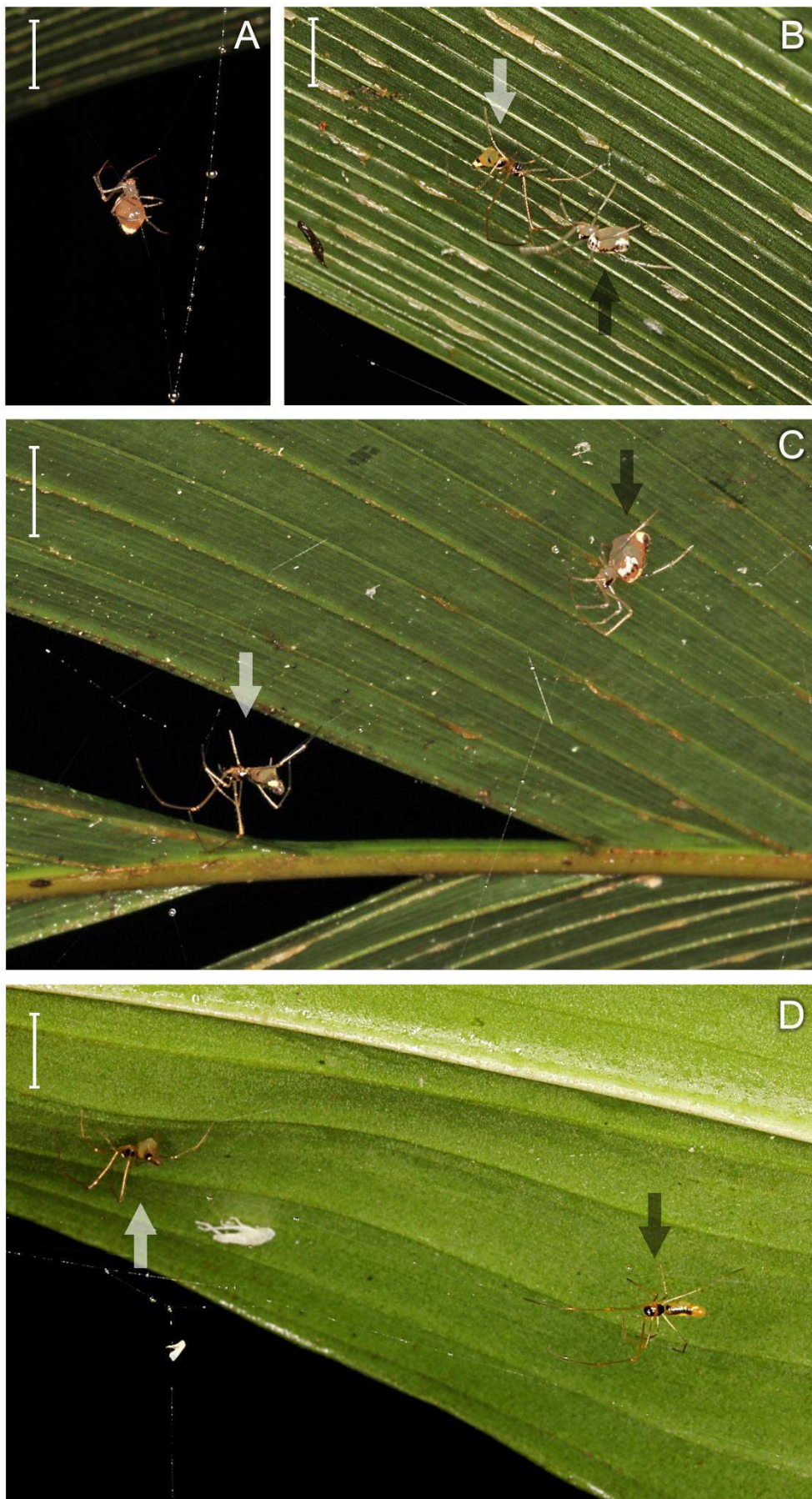


Fig. 1 - Interactions between resident and intruder spiders. (A) *Chrysso intervalles* individual climbing on a support thread towards the web hub of a conspecific. As soon as intruder spiders were placed on support threads, they began climbing. (B) *Helvibis longicauda* intruder fighting against a *C. intervalles* resident. In this specific interspecific contest, intruder lost and left the web (C). (D) Intraspecific contest between *H. longicauda* individuals in which the intruder fled the web (without fighting). White arrows: intruder spiders; Black arrows: resident spiders; Scale bar: 5 mm.

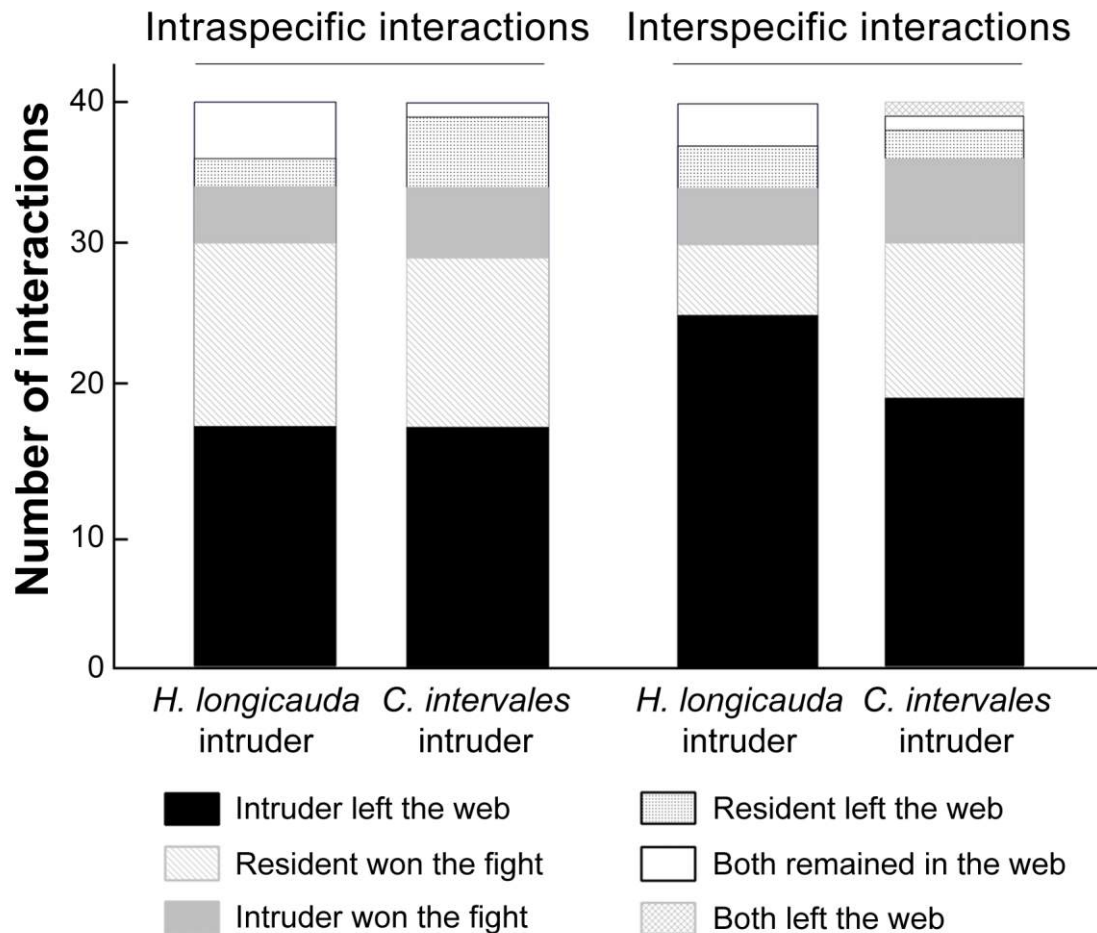


Fig. 2 – Frequency of behavioral outcomes from web invasion simulation experiments in webs with resident spider presence. Relative proportion of these events does not fit in a random expectation frequency distribution.

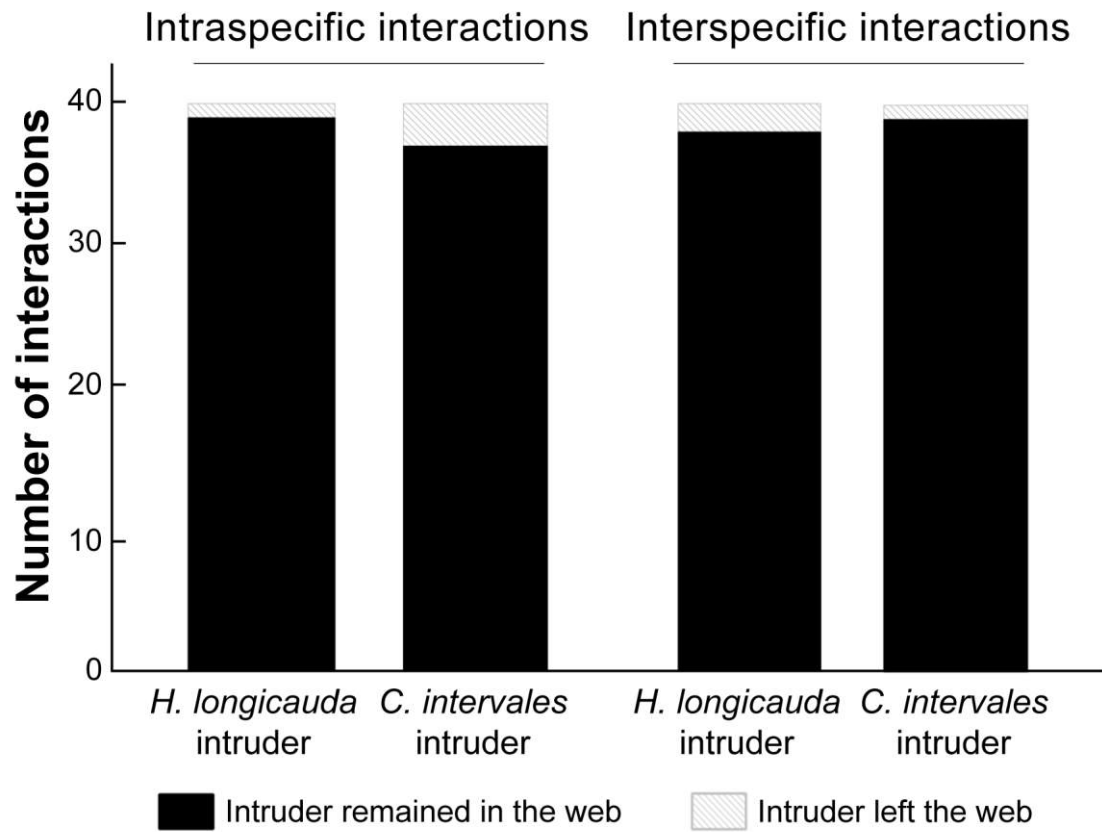


Fig. 3 – Frequency of behavioral outcomes from web invasion simulation experiments in webs without resident spider presence.

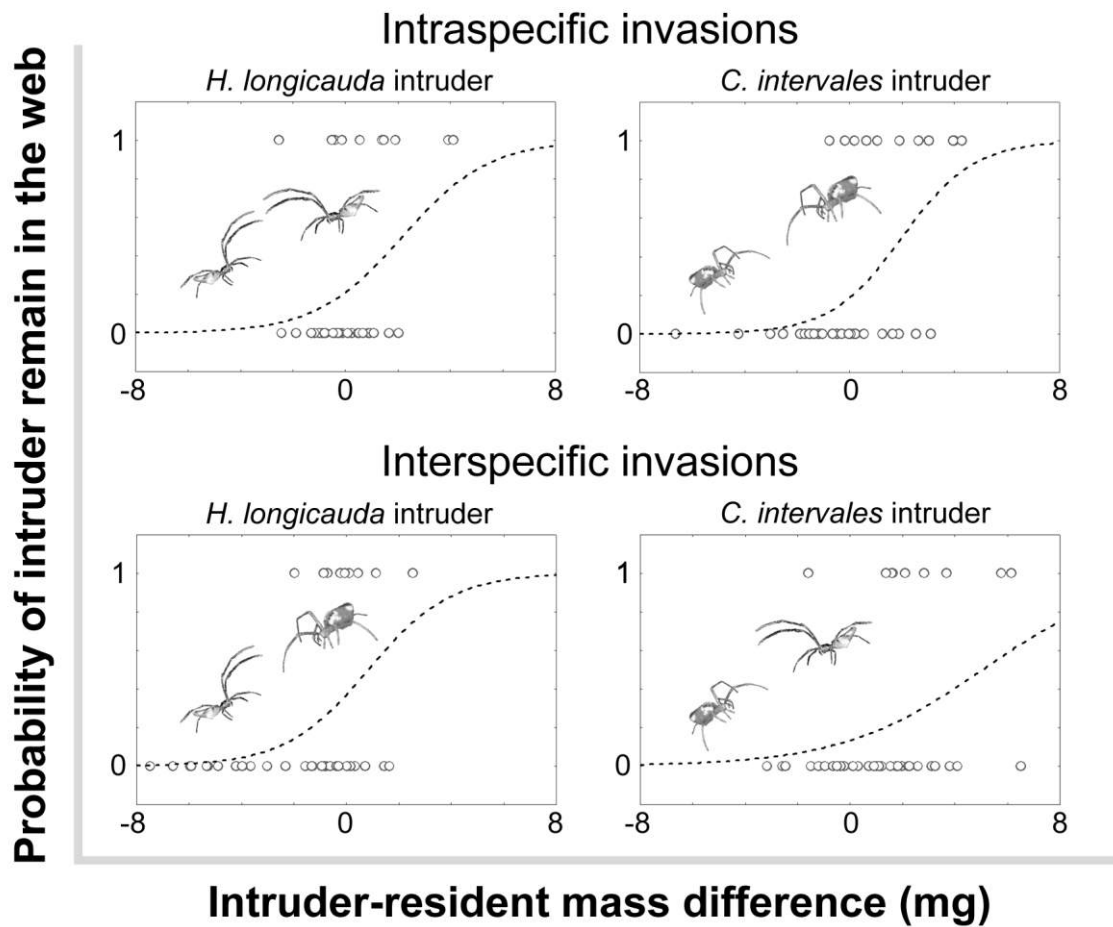


Fig. 4 – Logistic regression curves demonstrating the probability of intruder spider remain in resident's web (1) for the different interaction categories analyzed according to the body weight difference between the opponents. Positive values indicate a larger intruder and negative a smaller one. Dashed lines express predicted probability and dots, observed events.

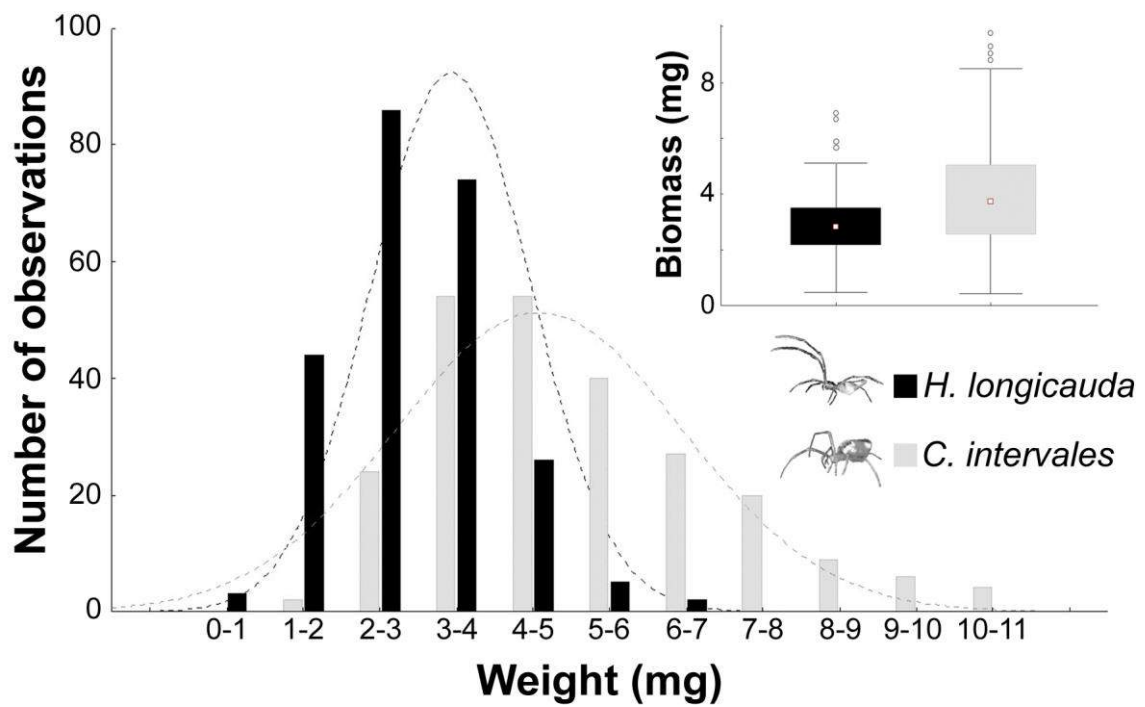


Fig. 5 – Histogram demonstrating *H. longicauda* and *C. intervalles* body mass differences (divided every 1 mg). In the right top, box plots indicate median, quartiles and extreme values of data.

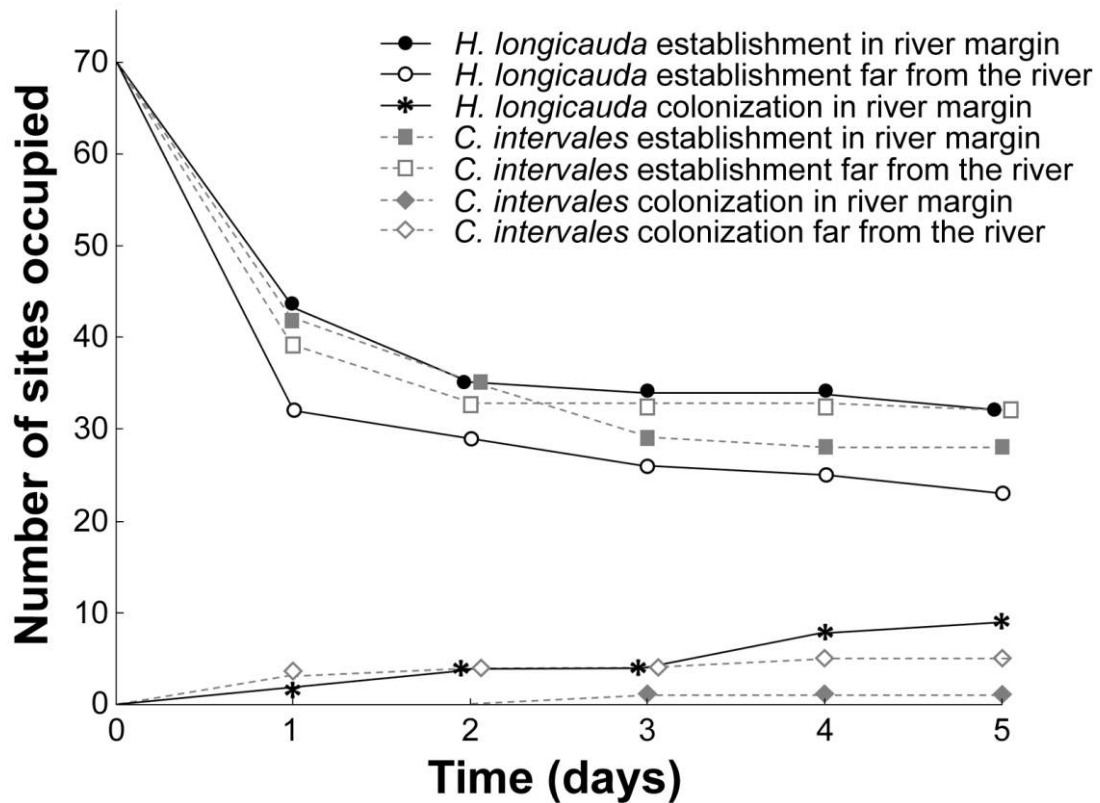


Fig. 6 – Survival curves demonstrating establishment and colonization successes of *H. longicauda* and *C. intervalles* along five days in both microhabitats: near (0 – 2 m distance) and far from the river (20 – 22 m). Colonization of *H. longicauda* far from the river is not shown due to the absence of occurrences in this event.

Table 1 – Relative proportion of behavioral outcomes according to interaction category and weight difference between intruder and resident (intruders smaller or larger than residents).

Outcome	Intraspecific				Interspecific			
	<i>H. longicauda</i> intruder		<i>C. intervalles</i> intruder		<i>H. longicauda</i> intruder		<i>C. intervalles</i> intruder	
	Smaller	Larger	Smaller	Larger	Smaller	Larger	Smaller	Larger
Intruder left the web	11	6	11	6	19	6	8	11
Resident won the fight	6	7	7	5	4	1	3	8
Intruder won the fight	1	3	1	4	3	1	—	6
Resident left the web	1	1	1	4	1	2	1	1
Both remained in the web	2	2	—	1	2	1	—	1
Both left the web	—	—	—	—	—	—	—	1
Total	21	19	20	20	29	11	12	28

CONCLUSIONS

In the present study, we reported the fine-scale horizontal spatial segregation between studied spiders. We confirmed our first assumptions that *Helvibis longicauda* populations are restricted to river margins regions while *Chysso intervalles* individuals are mainly found away from the river, after the populations of the heterospecific. Niche similarities were observed in many axis such as trophic and spatial. However, even being closely related, the species studied present niche differentiation in many resources, which may allow their syntopic coexistence. For instance, starting from spatial horizontally segregation, species also present vertical web-site differentiation and width of leaves occupied.

Despite the evidence that more *C. intervalles* reached river margins when fungi infested more *H. longicauda* individuals, further research is necessary to confirm that *H. longicauda* drives away the heterospecific through asymmetric exploitation competition for web-building sites. Our experimental procedures suggest that *C. intervalles* may thrive in river margins. They also indicate that direct behavioral constrains may be important in the spatial arrangement, once resident *H. longicauda* individuals are advantaged over *C. intervalles* intruders. Moreover, we observed that trophic niche specialization or competition apparently does not structure populations spatially. Future directions point to the replication of transplant experiments during summer, in order to investigate if higher temperatures indeed restrict *H. longicauda* to river margins. Ideally, experiments concerning long-term performances of both species in near and far river should corroborate our main findings.