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## Small and large spatial scale coexistence of ctenid spiders in a neotropical forest (French Guiana)

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While spiders constitute the most abundant and diverse arthropods in many habitats, they remained under-studied, especially in tropical rainforests. The goal of this study is to assess the spatial distribution of the spider family Ctenidae by assessing associations of species diversity and population traits among different habitat conditions. Fieldwork was carried out during 2013 in habitats varying in flooding frequency (plateau vs. flooded forest) and elevation (inselberg vs. lowland) in the Nouragues National Natural Reserve, French Guiana. Assemblage composition, population structure, and trait measurements of one dominant species were assessed using hand collection in replicated quadrats. We found strong effects on ctenid assemblages attributable to both elevation and flooding, with changes in relative abundance of species among habitats, but few correlated densities between species. At the population level, main differences in species distribution between and within habitats were detected only when juveniles were taken into account. No effect of elevation was found on the measurements of traits of the dominant species, but legs were proportionally shorter in flooded habitats, suggesting reduced active dispersal in these habitats. Our study highlights the value of complementary measures of diversity and traits at different biological scales in Ctenidae.

**Keywords:** Araneae; Guianese shield; flooding; inselberg; juveniles

### Introduction

Understanding natural ecosystem functioning represents a central issue in ecology, especially for tropical forests that hold up to 80% of the total terrestrial biodiversity (Lamarre et al. 2016). Although numerous studies documented the role of primary producers, or autotrophs (Fortunel et al. 2014) and some on primary consumers (e.g. Novotny et al. 2006), few have studied the next trophic level of secondary consumers (but see Coddington et al. 2009). Because these organisms represent most of animal species richness and because of the increasing recognition of the ecosystem services they provide (e.g. Werling et al. 2014), the number of ecological studies focused on arthropods has increased exponentially for the last decade (Basset et al. 2013; Lamarre et al. 2014). Yet, and despite the huge taxonomic

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and functional diversity they represent, the role of most arthropods in community function remains little understood (Lawes et al. 2005; Basset et al. 2013).

In conservation biology, an increasing number of studies are now incorporating assemblage-level metrics, in order to balance conclusions that would emerge from individual case, population or species-based studies (e.g. Leroy et al. 2012, 2014). Several challenges have emerged in adopting this approach and mainly concern the definition of an ad hoc protocol taking into account varying scales of time, space, and organization (e.g. Cardoso et al. 2008; Vedel and Lalagüe 2013; Sereda et al. 2014; Vedel et al. 2015), as well as the identification of species or even morpho-species (e.g. Oliver and Beattie 1996). The identification step is especially challenging in tropical regions, where most biodiversity is concentrated, but also where a vast proportion remains undescribed (Gardner et al. 2008). For most arthropods in such regions, typically only adults (or imago) are identified with certainty through sexual organs and are therefore included in subsequent data analyses. This a priori simplification might be appropriate for field studies investigating insects that have different ecologies in larval and adult stages (especially for hemi- and holometabolous taxa). However, for arthropods where the juveniles occupy the same ecological niche, such as for those with incomplete metamorphosis like paurometabolous insects and spiders, it can be problematic to exclude juveniles from any population or community assessment without introducing a strong bias.

Among the secondary consumers, the most abundant and diverse arthropods in many habitats are spiders (Marc et al. 1999; Cardoso et al. 2004; Nyffeler and Birkhofer 2017). In this study, we focused on the polyphyletic spider family Ctenidae (Polotow and Brescovit 2014; Polotow et al. 2015) because (i) ctenids have morphological characteristics that allow a good differentiation among species (or by morpho-species) based on their single habitus (Gasnier and Höfer 2001), and (ii) they are dominant ground-dwelling predators in tropical forests (Gasnier et al. 1995). The goal of this study is to investigate the species diversity and traits (from assemblages to individuals) among different habitats. The habitats ranged from lowlands to an inselberg (a habitat island with a particular climate that contrasts with the surrounding forest, Parmentier 2005). We compared plateau vs. flooded forest habitats to investigate the effects of flooding in shaping assemblage composition, population density, and individual size (for general effects on spiders, see Döbel et al. 1990; Lafage et al. 2015). More precisely, we tested the following hypotheses.

At the scale of species assemblages, differences in habitat selection among species should result in (i) different species composition over the range of habitats studied, and (ii) negative correlations in species densities among habitats. Due to inter-specific competition occurring in closely related species (Schaefer 1974), we expect opposite trends of densities among ctenid species (Gasnier and Höfer 2001). At the population scale, we expect differences in habitat selection between stages, both among (Lycosidae: Kessler and Slings 1980) and within habitats (Ctenidae: Schuster et al. 1994). Within species, we expect larger individuals at higher elevations because of longer development cycle (Bergmann rule; e.g. Chown and Gaston 2010; although the opposite pattern is frequently found: Blanckenhorn and Demont 2004), and proportionally longer legs in flooded habitats associated with selection for higher dispersal abilities, Lambaerts et al. (2008). These hypotheses were tested in French Guiana by comparing habitats that varied in elevation and flooding frequency.

## Material and methods

### *Study site and field sampling*

The sampling was conducted in the research station Les Nouragues, French Guiana, South America (4°04'18"N, 52°43'57"W). This research station is in the middle of pristine undisturbed neotropical rain forest. Les Nouragues can be divided into two parts, the Inselberg (400 m asl), which is close to a granitic mountain, and Pararé (altitude close to sea level), which is on the edge of the Arataye River at lowest altitude.

We collected spiders from two distinct habitats (plateau and flooded forest) in each of the two elevations (lowland and inselberg). Vegetation structure was quite similar between both flooded forests, whereas the two non-flooded forests also had the same dominant plants (Poncy et al. 2001). The main differences between lowland and inselberg were the occurrence of a more complex and diversified flora at lower elevations, where pH and humidity are higher (see also Sarthou et al. 2017).

Five plots (5 m \* 5 m) were chosen randomly in each habitat. In each plot, every spider belonging to the family Ctenidae was collected on the ground and on low vegetation by two collectors (the same for all habitats) equipped with headlamps for 15 min. Our approach favored sampling intensity over long-term sampling effort, as both components are not equivalent (Lövei and Magura 2011; see also Coddington et al. 2009).

The spider family Ctenidae includes average to large-sized hunting spiders, which mainly live in the leaf litter stratum and low vegetation. They are mainly active at night and were, thus, collected by the well-established method of nocturnal hand collecting (Cardoso et al. 2008; Azevedo et al. 2014). Sampling was conducted between 20:00 and 23:00 from 8 to 15 December 2013. This season is at the beginning of the rainy season and has been shown to be the best period to document ctenid assemblages (Gasnier and Höfer 2001).

### *Identification and measurements*

Spiders were placed in tubes filled with ethanol (70%) and separated by site, habitat, and plot. For each sample, we sorted and identified individual spiders to the species level, defining morpho-species only when the individuals did not match a published description of species. Juvenile spiders were included and identified following the description of Gasnier and Höfer (2001). When their identification was not possible, they were noted as "juveniles" in the data-set. Unidentified juveniles represented only 11.3% of the total individuals (83 unidentified juveniles out of 720 individuals). Individuals were also classified on a numerical scale representing their life stage (without considering their molt numbers): 4, adult individuals with fully developed genitalia; 3, sub-adults (genital organs visible but not fully developed); 2, average-sized juveniles (25–75% of adult size); and 1, small-sized juveniles (around 10–20% of the adult).

Biometry was done on a dominant, widely distributed species with an accurate identification possible even for early instars, i.e. *Cupiennius bimaculatus* Taczanowski, 1873. Length and width of prosoma, as well as length of right femur on leg IV, were measured on all individuals ( $N = 90$ , four individuals could not be properly measured) from pictures taken with a camera on a dissection microscope (precision = 0.01 mm).

### *Data analysis*

Expected differences in habitat use among species were tested both using a  $\chi^2$  test on relative abundances of ctenids in the four studied habitats and by calculating the Spearman

correlations on densities of all species in all quadrats ( $N = 20$ ; for an example of such paired-species densities, see e.g. Pétilion et al. 2014).

Expected differences in habitat use between juveniles and adults were tested using a GLM (Vincent and Haworth 1983; O'Hara and Kotze 2010) on mean densities of all dominant species (at least 30 individuals) per habitat and per stage, with elevation (inselberg vs. lowland), flooding, and their interaction as fixed factors. A Poisson error structure was first modeled, and in case of overdispersed data (residual deviance larger than residual degrees of freedom), a quasi-Poisson error was used. Spatial distribution of juveniles and adults was investigated within habitats using a  $\chi^2$  test.

Effects of elevation and flooding on mean size were tested using a Linear Model on mean prosoma length and width of one dominant species (*C. bimaculatus*) per habitat with elevation, flooding, and their interaction as fixed factors. If the covariate-by-factor interaction was not significant (homogeneity of slopes in full model), a standard ANCOVA (model 2) was used to test significant differences in dependent variables between habitats (i.e. differences in intercept using the adjusted mean prosoma width). We also performed a  $\chi^2$  test on 1 mm size classes (Torres-Sánchez and Gasnier 2010) in lowland vs. inselberg to test more precisely for an effect of elevation on body size (hypothesis 3). Effects of elevation and flooding on relative leg length were tested using an ANCOVA with elevation, flooding, and their interaction as fixed factors, and the width of prosoma (as a proxy of body size in spiders: Jakob et al. 1996) as covariate.

In models,  $p$ -values of fixed factors are either those of the additive model if the interaction was not significant, and not provided if the interaction was significant. All analyses were conducted in the R 3.2.3 statistical platform (R Development Core Team 2015), using packages *vegan* (Dixon 2003; Oksanen et al. 2013) and *Rarity* (Leroy 2017).

## Results

A total of 720 ctenids representing 12 morpho-species were collected. The dominant species was *Ctenus crulsi* Mello-Leitao, 1930 (257 individuals), followed by *Ctenus* sp. 1, *Cupiennius bimaculatus*, *Ctenus* sp. 2, *Ctenus manauara* Höfer, Brescovit & Gasnier, 1994, *Ctenus amphora* Mello-Leitao, 1930 and *Ctenus inaja* Höfer, Brescovit & Gasnier, 1994 (126, 94, 83, 73, 40, and 32 individuals, respectively). The other species being represented by one (*Phoneutria fera* Perty, 1833, *Phoneutria reidyi* F.O. Pickard-Cambridge, 1897 and *Ancylometes rufus* Walckenaer, 1837), two (*Ancylometes bogotensis* Keyserling, 1877), and 10 (*Ctenus villasboasi* Mello-Leitao, 1949) individuals.

### Assemblages

Ctenid species had different habitat affinities ( $\chi^2$  test,  $\chi^2 = 264.30$ , 21 df,  $p < 0.001$ ), with e.g. *C. crulsi* dominant in the flooded lowland habitat and *C. manauara* and sp. 1 more frequent in the non-flooded lowland habitat (Figure 1). Most species were independently distributed (Figure 2). We detected only one negative relationship between the abundances of *C. crulsi* and *C. manauara*. In addition, we detected one positive relationship between the abundances of *C. manauara* and *C. sp. 1* (see Spearman correlation plots, and associated Rho and  $p$ -values: Figure 2).

### Populations

When all species were pooled, many more individuals belonged to the juvenile stages (stage 1-2-3) than adults (Stage 4) for each habitat. The proportion of adults were lower

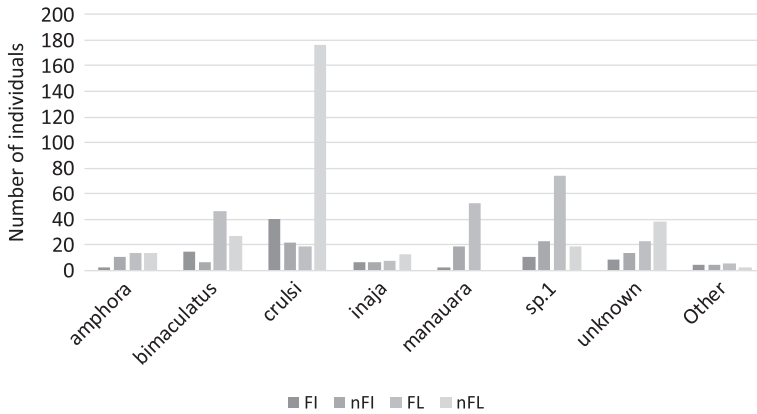


Figure 1. Total densities (number of individuals collected in quadrats) of ctenid species under the four habitat conditions (FI = Flooded Inselberg, nFI = non-Flooded Inselberg, FL = Flooded Lowland, nFL = non-Flooded Lowland).

in flooded forests of both sites (2.3–3.1%) compared to non-flooded forests of both sites (3.3–3.9%). The most abundant stage was stage 2, with a proportion of 52.3% on the hill-top of the site Inselberg and 58.95% on the flooded forest of the site Inselberg. Stages 1 and 3 represented, respectively, from 19.6 to 29.4% and from 10.2 to 22.9% of the density per habitat.

Juveniles were far more abundant (representing 96% of total numbers) than adults for all species collected at every site and every habitat. Overall, differences in species distribution among habitats are significant only when juveniles were taken into account ( $\chi^2$  test,  $\chi^2 = 228.31$ , 15 df,  $p < 0.001$ ), and not when they were excluded ( $\chi^2$  test,  $\chi^2 = 16.41$ , 15 df,  $p = 0.356$ ).

When testing for the effects of flooding and altitude on the six dominant species (Unknown ctenids were not tested because only represented by juveniles), more significant or nearly significant effects were found in juveniles than in adults (13 vs. 5, respectively: Table 1). Altitude\*Flooding interactions were significant for the juveniles of three species, indicating one preferred habitat of the four studied (see e.g. *crulsi*: Figure 3). Lastly, adults of *C. inaja* were significantly influenced by elevation (in the sense of higher densities at lower elevations) whereas the juveniles of this species had no preferred habitat type (Table 1).

### Individuals

When testing the effect of altitude and flooding on prosoma length and width of *C. bimaculatus*, the interaction term was not significant in both full models ( $F_{1,86} = 1.74$ ,  $P < 0.086$  and  $F_{1,86} = 1.73$ ,  $P = 0.088$ , respectively). Neither prosoma length nor width was significantly influenced by altitude ( $F_{1,87} = -0.32$ ,  $P < 0.751$  and  $F_{1,87} = -0.09$ ,  $P = 0.929$ , respectively) and flooding ( $F_{1,87} = 0.81$ ,  $P = 0.422$  and  $F_{1,87} = 0.54$ ,  $P = 0.589$ , respectively) factors. Frequency of size classes of *C. bimaculatus* were not different between lowland vs. inselberg habitats ( $\chi^2$  test,  $\chi^2 = 0.42$ , 2 df,  $p = 0.811$ ).

When testing for the effect of altitude, flooding, and body size on femur length of *C. bimaculatus*, all four interaction terms (with  $P$ -values ranging from 0.262 to 0.808 in the full model), as well as altitude ( $P = 0.982$ ) were not significant. Both flooding and prosoma width had a strong significant effect on femur length ( $F_{1,83} = 2.70$ ,  $P < 0.001$  and

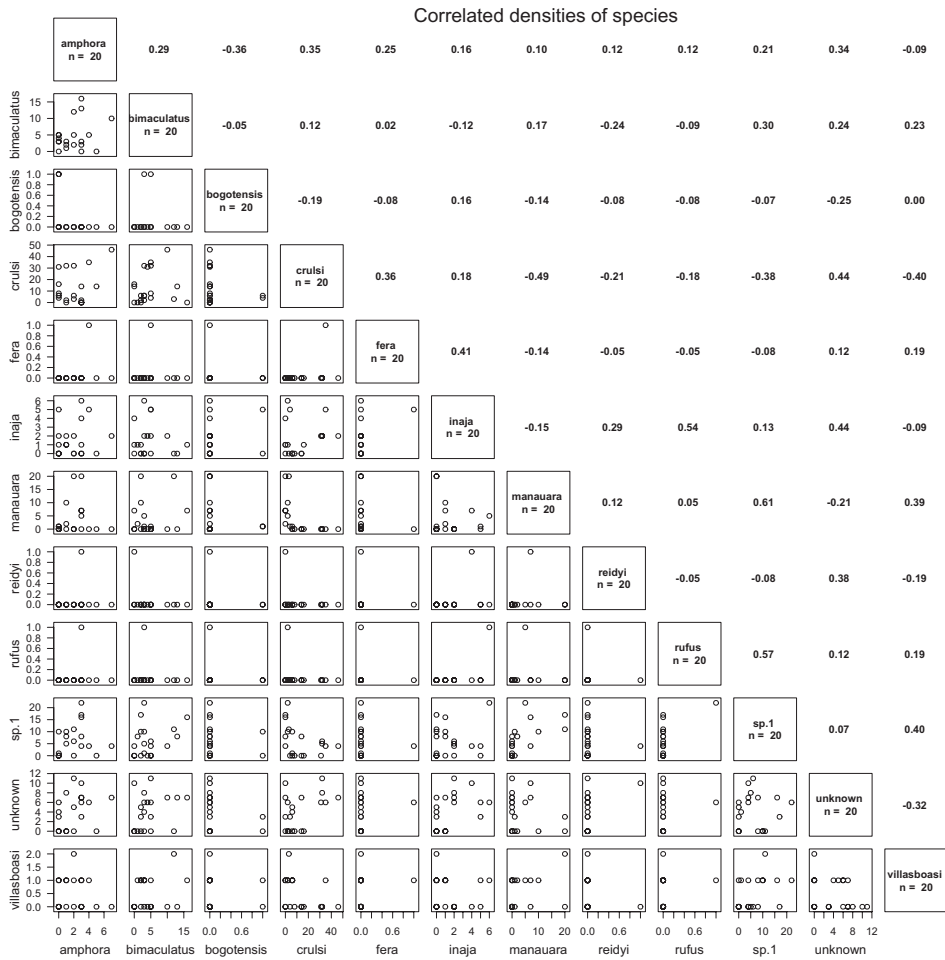


Figure 2. Correlation plots of the densities of ctenid spiders per quadrat (all habitats). The lower half shows the scatter plots of number of individuals. The upper half shows values of Spearman's rho (significance: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ ,  $p$  values corrected for false discovery rate). The diagonal shows the different ctenid species measured, and the number of quadrats considered.

$F_{1,83} = 44.83$ ,  $P < 0.001$ , respectively). Femur length was positively influenced by prosoma width, and was proportionally larger in non-flooded compared to flooded habitats (Figure 4).

## Discussion

### Assemblages

Differences in patterns of habitat selection among the different species of Ctenidae suggest that different mechanisms are jointly responsible for species assemblage. For example, two species showed inverse patterns of densities across habitats, while several species co-occurred within single habitats, with also some species being positively associated.



Table 1. Result of the GLM analysis (Poisson with associated  $\chi^2$  Wald statistics or Quasi-Poisson with associated  $F$ -ratio statistics) of the effect of altitude and flooding factors on mean densities (number of individuals per quadrat) for the most abundant ctenid species (i.e. represented by at least 30 individuals, both juveniles and adults).

Stage	Species	Interaction		Altitude		Flooding	
		Test	$P$	Test	$P$	Test	$P$
Juvenile	<i>C. amphora</i>	$F_{1,16} = 3.26$	<u>0.090</u>	$F_{1,18} = 3.73$	<u>0.070</u>	$F_{1,17} = 0.30$	0.593
	<i>C. bimaculatus</i>	$F_{1,16} = 0.21$	0.650	$F_{1,18} = 13.80$	<b>0.002</b>	$F_{1,17} = 4.16$	<u>0.057</u>
	<i>C. crulsi</i>						<b>0.002</b>
	<i>C. inaja</i>	$F_{1,16} = 0.50$	0.490	$F_{1,18} = 0.34$	0.565	$F_{1,17} = 0.68$	0.422
	<i>C. manauara</i>						<b>0.048</b>
	<i>C. sp. 1</i>	$F_{1,16} = 5.45$	<b>0.003</b>	$F_{1,18} = 6.90$	<b>0.018</b>	$F_{1,17} = 3.31$	0.090
Adult	<i>C. amphora</i>						<b>0.019</b>
	<i>C. bimaculatus</i>	$\chi^2_{1,16} = 6.44$	1	$\chi^2_{1,18} = 6.44$	<u>0.096</u>	$\chi^2_{1,17} = 6.44$	1
	<i>C. crulsi</i>	$\chi^2_{1,16} = 11.00$	0.105	$\chi^2_{1,18} = 14.31$	<u>0.088</u>	$\chi^2_{1,17} = 13.63$	0.410
	<i>C. inaja</i>	$\chi^2_{1,16} = 9.66$	0.999	$\chi^2_{1,18} = 10.00$	<b>0.041</b>	$\chi^2_{1,17} = 9.66$	0.560
	<i>C. manauara</i>	$\chi^2_{1,16} = 3.21$	1	$\chi^2_{1,18} = 4.46$	0.239	$\chi^2_{1,17} = 3.22$	0.239
	<i>C. sp. 1</i>	$\chi^2_{1,16} = 6.44$	<u>0.096</u>	$\chi^2_{1,18} = 9.21$	1	$\chi^2_{1,17} = 9.21$	1

Notes:  $P$ -values of fixed factors are those of the additive model if the interaction is not significant and not given if the interaction is significant. Underlined and bold  $p$ -values indicate, respectively, nearly significant ( $0.05 < P < 0.10$ ) and significant ( $P < 0.05$ ) effects of fixed factors and their interaction.

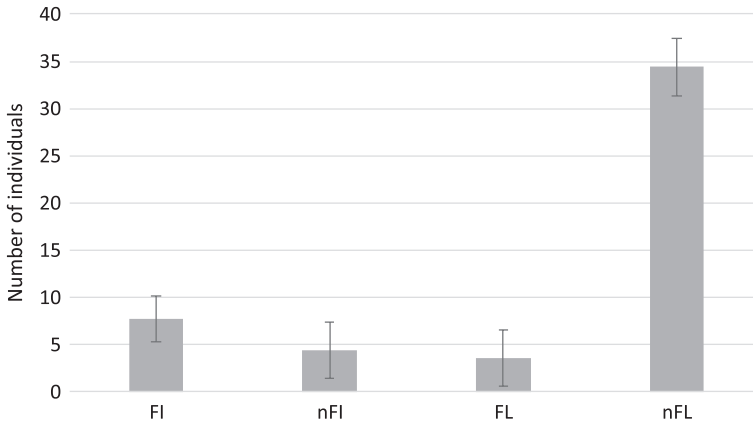


Figure 3. Mean densities (number of individuals  $\pm$  s.e.,  $N = 5$  quadrats per habitat) of *crulsi* in the four habitat types (FI = Flooded Inselberg, nFI = non-Flooded Inselberg, FL = Flooded Lowland, nFL = non-Flooded Lowland).

The significant patterns in species densities can be explained either by high inter-specific competition or by a similar habitat selection. Competition and intra-guild predation in spiders have been much debated (e.g. Schaefer 1974; Wise 2006), but likely occurs mostly in simple habitats (Marshall and Rypstra 1999; Pétilion and Garbutt 2008). By contrast, there are a great number of abiotic variables likely to influence ground-running



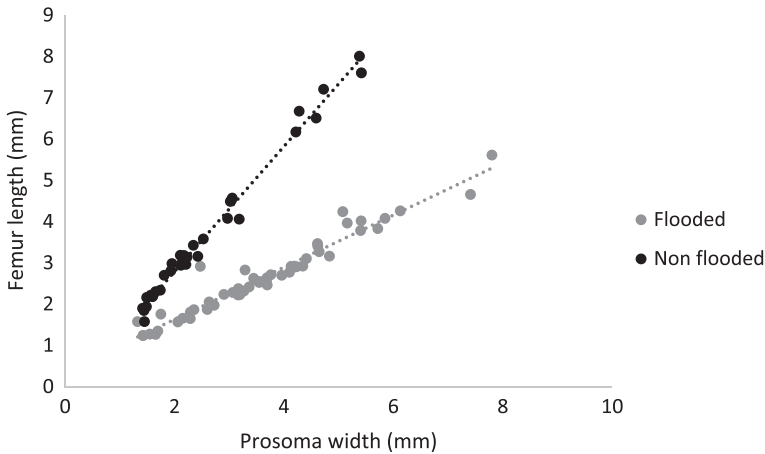


Figure 4. Length of right femur (mm) vs. prosoma width (mm) in *Cupiennius bimaculatus* ( $N = 90$  individuals). Black and gray circles: data from non-flooded and flooded habitats, respectively. Black and gray lines: linear regression in non-flooded and flooded habitats, respectively.

spiders like ctenids. Among habitat characteristics likely to vary among the habitats studied, some are “classical”, such as litter depth or habitat structure (Uetz 1979; Hatley and Macmahon 1980), but also less obvious characteristics, such as soil grain size (Portela et al. 2013, see also Řezáč et al. 2007 on Eresids). Biotic interactions may also play a role in shaping ctenid distribution and abundance, as ctenids can be both prey for larger animals (including frogs: Caldwell and Araújo 1998) as well as predators or competitors of other arthropods (e.g. ants: Gasnier et al. 1995; Schuldt and Staab 2015). Lastly, some of the studied habitats experienced disturbances strong enough to select for more specialized species and/or to disfavor generalist ones. Flooding is, indeed, well known to shape arthropod assemblages (Adis and Junk 2002) and to filter spider species able to withstand or to avoid immersion (e.g. Pétilion et al. 2010). Spiders have not been well-studied on inselbergs (in contrast to studies of plants, see e.g. Sarthou et al. 2017), but the thinner litter layer of inselbergs (Bourguignon et al. 2011) likely is a constraint for some ground-dwelling spiders like ctenids. Because ctenids are generalist opportunistic predators like most wandering spiders (Pekár and Toft 2015), additional investigations of feeding habitats of ctenids would be of interest.

Co-occurrence of different ctenid species within a single habitat can possibly be explained by niche partitioning (Torres-Sánchez and Gasnier 2010). Such partitioning has been reported for ctenids over both time (Gasnier and Höfer 2001) and in space, at a micro-habitat scale (Gasnier et al. 2002), and for other tropical spiders (Lapinski and Tschapka 2013). Micro-habitat partitioning over small-scale abiotic gradients has similarly been reported in lycosids (mainly for humidity, temperature, and salinity: DeVito et al. 2004; Frick et al. 2007; Pétilion et al. 2011). The observed high densities of sympatric ctenid species is similar to that reported for lycosids in several temperate or polar habitats (see e.g. Pétilion et al. 2005; Høye et al. 2009, respectively). Ctenidae could consequently be considered as functional equivalent of Lycosidae in tropical forests (such a functional equivalence was already reported for other spider families: Cardoso et al. 2011). The occurrence of agonistic behaviors, already reported in lycosids (e.g. Nosssek and Rovner 1984),

should probably be examined in ctenid spiders because they are likely to reduce predation risks within and among species and could explain the co-occurrence of sympatric species.

### **Populations**

Juveniles and adults showed different distributions between and within habitats, suggesting different micro-habitat selection (see e.g. *C. inaja*), and/or spatial patterns of adults masked by their low numbers. Micro-habitat selection is likely driven by predation risk avoidance and differential distributions of prey (e.g. Wise 1993). Differences in habitat between stages were found in several species that had one particular preferred habitat. Two alternative, non-exclusive, mechanisms might explain aggregated distributions: strong habitat selection and limited spider dispersal. Habitat selection was not directly quantified in this study, but instead estimated by the preferential use of habitat types (see above).

This study also showed that the numbers of juveniles is far greater than the number of adults for each species of Ctenidae for the two elevations of tropical rainforest and for the two habitats varying in flooding frequency (plateau and flooded forest). The juvenile stage the most commonly collected is stage 2, which is just before being a sub-adult and can probably be longer than previous stages. This stage has a very similar ecology to the adult and only slightly smaller size suggesting stage 2 has quite a similar impact on the ecosystem as predator and also as prey. In this situation, excluding the juvenile stages in an ecological study because one cannot identify species with certainty causes one to lose or ignore over 95% of the abundance data. This strong “under-sampling” error would otherwise bias any study of the distribution and impact of important predators in the ecosystem.

The proportion of juveniles and adults over all species did not differ between habitats and sites. Differences in (micro-)habitat selection are rarely reported for spiders (but see e.g. in a lycosid species, Kessler and Slings 1980). However, within species significant differences were found in the proportion of juveniles and adults between habitats and sites. In other words, there is a different ratio of juveniles/adults for one given species on a specific habitat and another ratio for another species. Again, not taking into account the diversity and abundance of juveniles gives a misleading picture of abundance and diversity from the population to the community level. In addition, at some seasons or in some micro-habitats, only juveniles might be present, but not adults. If the sampling occurs at this season or only at this place and cannot be repeated in other conditions and juveniles are excluded, some species would not be recorded at all.

As one of the most diverse and abundant arthropod predators, spiders (Araneae) are now recognized as important components of ecological communities, with implications for both ecology and conservation (Cardoso et al. 2008). However, almost all spider studies actually exclude immatures from the data analyzed (either during the sampling or identification process; but see Jocqué et al. 2005), because only sexual characters allow an accurate identification of species. However, although this may be true for many cryptic species, many species can be accurately distinguished as immatures. These species, when already identified and confirmed using sexual characters in a pilot study, can then be observed and identified morphologically without using sexual characters. Taking juveniles into account in ecological sampling is possible in ctenid species (Steyn et al. 2002; Portela et al. 2013; this study), but also in other spider (e.g. Gasteracanthinae in Araneidae, Oxyopidae) or insect families.

### **Biometry**

Smaller body sizes were initially expected at high elevation. No such effect was found for the abundant species *C. bimaculatus*, either for prosoma length and width, nor for femur length and size classes. It has also been shown that both habitat quality and temperature positively acts on spider body size (see Jocqué 1981; Vollrath 1988, respectively), which should have reinforced possible effects of altitude. We hypothesize that effects of elevation may be less under tropical conditions (mainly because of a reduced temperature range: Overgaard et al. 2011). Another explanation could be that effects of altitude on spider size (increase in spider size: e.g. Hein et al. 2015) might be balanced by soil succession resulting in reduced prey (see Kounda-Kiki et al. 2004). A high correlation was found between femur length and width of prosoma, as repeatedly shown in other spider families (e.g. lycosids: Puzin et al. 2014).

We found that legs were proportionally shorter in flooded habitats, which suggests either reduced need for active mobility in these habitats or the existence of two distinct species. Selection for relatively longer legs has been previously reported in web-building (Foellmer and Fairbairn 2005), free-running (Framenau 2005), and cave-living (Miller 2005) species. Longer legs proved to increase speed in steep ground (Prenter et al. 2012), but not for all species (Moya-Laraño et al. 2008). The last authors actually found that certain species moved slower with longer legs, which could argue for a selection of shorter legs in flooded habitats where fast dispersal is required (e.g. Adis and Junk 2002; Lafage et al. 2015). Another explanation for relatively shorter legs in flooded habitats could be reduced litter (Döbel et al. 1990), such that ground-dwelling spiders with longer legs would be more easily displaced. This hypothesis would be more strongly supported if it were the case that longer legs are selected for in complex habitats. A last possible explanation lies in reduced active (short-distance) dispersal in flooded habitats, whereas passive dispersal can be achieved by transport on water (see e.g. Lamberts et al. 2010). It is worth noting that this study is one of few to examine differences in biometrics regression slopes between individual spiders from ecologically distinct, but spatially close, habitats (Hendrickx et al. 2003; Pétilion et al. 2009; see also Torres-Sánchez and Gasnier 2010 for differences in size classes between habitats). Whether this difference results from plasticity in one single population or from local adaptation from two cryptic species remains to be studied further.

In conclusion, this study illustrates that the abundance and distribution of species and individuals of the spider family Ctenidae are a good indicator of different habitat conditions in a rainforest-inselberg ecotone. Further, the work highlights the complementary value of metrics measured at different biological scales from individuals to assemblages, and the importance in ecological studies of considering juveniles, and not solely adults, whenever their assignment to morpho- or genetic species level is possible.

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### **Disclosure statement**

No potential conflict of interest was reported by the authors.

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## References

- Adis J, Junk WJ. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshwater Biology*. 47:711–731.
- Azevedo GH, Faleiro BT, Magalhães ILF, Benedetti AR, Oliveira U, Pena-Barbosa JPP, Santos MTT, Vilela PF, de Maria M, Santos AJ. 2014. Effectiveness of sampling methods and further sampling for accessing spider diversity: a case study in a Brazilian Atlantic rainforest fragment. *Insect Conservation and Diversity*. 7:381–391.
- Basset Y, Eastwood R, Sam L, Lohman DJ, Novotny V, Treuer T, Miller SE, Weiblen GD, Pierce NE, Bunyavejchewin S, et al. 2013. Cross-continental comparisons of butterfly assemblages in tropical rainforests: implications for biological monitoring. *Insect Conservation and Diversity*. 6:223–233.
- Blanckenhorn WU, Demont M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology*. 44:413–424.
- Bourguignon T, Leponce M, Roisin T. 2011. Beta-diversity of termite assemblages among primary French Guiana rain forests. *Biotropica*. 43:473–479.
- Caldwell JP, de Araújo MC. 1998. Cannibalistic interactions resulting from indiscriminate predatory behavior in tadpoles of poison frogs (Anura: Dendrobatidae). *Biotropica*. 30:92–103.
- Cardoso P, Pekár S, Jocqué R, Coddington JA. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*. 6:e21710.
- Cardoso P, Scharff N, Gaspar C, Henriques SS, Carvalho R, Castro PH, Schmidt JB, Silva I, Szüts T, De Castro A, et al. 2008. Rapid biodiversity assessment of spiders (Araneae) using semi-quantitative sampling: a case study in a Mediterranean forest. *Insect Conservation and Diversity*. 1:71–84.
- Cardoso P, Silva I, de Oliveira NG, Serrano ARM. 2004. Higher taxa surrogates of spider (Araneae) diversity and their efficiency in conservation. *Biological Conservation*. 117:453–459.
- Chown SL, Gaston KJ. 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews*. 85:139–169.
- Coddington JA, Agnarsson I, Miller JA, Kuntner M, Hormiga G. 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*. 78:573–584.
- DeVito J, Meik JM, Gerson M, Formanowicz DR Jr. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat distributions. *Canadian Journal of Zoology*. 82:1119–1125.
- Dixon P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*. 14:927–930.
- Döbel HG, Denno RF, Coddington JA. 1990. Spider (Araneae) community structure in an intertidal salt marsh: effects of vegetation structure and tidal flooding. *Environmental Entomology*. 19:1356–1370.
- Foellmer MW, Fairbairn DJ. 2005. Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. *Oecologia*. 142:653–662.
- Fortunel C, Paine CET, Kraft NJB, Fine PVA, Baraloto C. 2014. Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*. 102:145–155.
- Framenau W. 2005. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae). *Journal of Arachnology*. 33:334–346.
- Frick H, Kropf C, Nentwig W. 2007. Laboratory temperature preferences of the wolf spider *Pardosa riparia* (Araneae: Lycosidae). *Arachnology*. 14:45–48.
- Gardner TA, Barlow J, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM, et al. 2008. The cost effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*. 11:139–150.
- Gasnier TR, de Azevedo CS, Torres-Sanchez MP, Höfer H. 2002. Adult size of eight hunting spider species in Central Amazonia: temporal variations and sexual dimorphisms. *Journal of Arachnology*. 30:146–154.

- Gasnier TR, Höfer H. 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in Central Amazonia. *Journal of Arachnology*. 29:95–103.
- Gasnier TR, Höfer H, Brescovit AD. 1995. Factors affecting the activity density of spiders on tree trunks in an Amazonian rainforest. *Ecotropica*. 1:69–77.
- Hatley CL, Macmahon JA. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology*. 9:632–639.
- Hein N, Feilhauer H, Löffler J, Finch O-D. 2015. Elevational variation of reproductive traits in five *Pardosa* (Lycosidae) species. *Arctic, Antarctic, and Alpine Research*. 47:473–479.
- Hendrickx F, Maelfait JP, Speelmans M, Van Straalen NM. 2003. Adaptive reproductive variation along a pollution gradient in a wolf spider. *Oecologia*. 134:189–194.
- Høye TT, Hammel JU, Fuchs T, Toft S. 2009. Climate change and sexual size dimorphism in an Arctic spider. *Biology Letters*. 5:542–544.
- Jakob EM, Marshall SD, Uetz GW. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*. 77:61–67.
- Jocqué R. 1981. On reduced size in spiders from marginal habitats. *Oecologia*. 49:404–408.
- Jocqué R, Samu F, Bird T. 2005. Density of spiders (Araneae: Ctenidae) in Ivory Coast rainforests. *Journal of Zoology (London)*. 266:105–110.
- Kessler A, Slings R. 1980. Microhabitat selection in adults and juveniles of *Pardosa purbeckensis* F.O.P.-Cambridge (Araneae, Lycosidae). In: Gruber J, editor. Proceedings of the 8th International Congress of Arachnology. Wien (Austria): Verlag H. Egermann; p. 151–154.
- Kounda-Kiki C, Vaçulik A, Ponge J-F, Sarthou C. 2004. Soil arthropods in a developmental succession on the Nouragues inselberg (French Guiana). *Biology and Fertility of Soils*. 40:119–127.
- Lafage D, Sibelle C, Secondi J, Canard A, Pétilion J. 2015. Short-term resilience of arthropod assemblages after spring flood, with focus on spiders (Arachnida: Araneae) and carabids (Coleoptera: Carabidae). *Ecohydrology*. 8:1584–1599.
- Lamarre GP, Héroult B, Fine PVA, Vedel V, Lupoli R, Mesones I, Baraloto C. 2016. Taxonomic and functional composition of arthropod assemblages across contrasting Amazonian forests. *Journal of Animal Ecology*. 85:227–239.
- Lamarre GP, Mendoza I, Fine PVA, Baraloto C. 2014. Leaf synchrony and insect herbivory among tropical tree habitat specialists. *Plant Ecology*. 215:209–220.
- Lambeets K, Breyne P, Bonte D. 2010. Spatial genetic variation of a riparian wolf spider *Pardosa agricola* (Thorell, 1856) on lowland river banks: the importance of functional connectivity in linear spatial systems. *Biological Conservation*. 143:660–668.
- Lambeets K, Vandegheuchte ML, Maelfait JP, Bonte D. 2008. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*. 77:1162–1174.
- Lapinski W, Tschapka M. 2013. Habitat use in an assemblage of Central American wandering spiders. *Journal of Arachnology*. 41:151–159.
- Lawes MJ, Kotze DJ, Bourquin SL. 2005. Epigaeic invertebrates as potential ecological indicators of afro-montane forest condition in South Africa. *Biotropica*. 37:109–118.
- Leroy B. 2017. Rarity: calculation of rarity indices for species and assemblages of species. R package version 1.3-7. Available from: <https://cran.r-project.org/package=Rarity>.
- Leroy B, Le Viol I, Pétilion J. 2014. Complementarity of rarity, specialisation and functional diversity metrics to assess responses to environmental changes, using an example of spider communities in salt marshes. *Ecological Indicators*. 46:351–357.
- Leroy B, Pétilion J, Gallon R, Canard A, Ysnel F. 2012. Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect Conservation and Diversity*. 5:159–168.
- Lövei GL, Magura T. 2011. Can carabidologists spot a pitfall? The non-equivalence of two components of sampling effort in pitfall-trapped ground beetles (Carabidae). *Community Ecology*. 12:18–22.
- Marc P, Canard A, Ysnel F. 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture Ecosystems and Environment*. 74:229–273.
- Marshall SD, Rypstra AL. 1999. Spider competition in structural simple ecosystems. *Journal of Arachnology*. 27:343–350.
- Miller JA. 2005. Cave adaptation in the spider genus *Anthrobia* (Araneae, Linyphiidae, Erigoninae). *Zoologica Scripta*. 34:565–592.



- Moya-Laraño J, Vinković D, De Mas E, Corcobado G, Moreno E. 2008. Morphological evolution of spiders predicted by pendulum mechanics. *PLoS ONE*. 3:e1841.
- Nossek ME, Rovner JS. 1984. Agonistic behavior in female wolf spiders (Araneae, Lycosidae). *Journal of Arachnology*. 11:407–422.
- Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science*. 313:1115–1118.
- Nyffeler M, Birkhofer K. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *The Science of Nature*. 104:30.
- O’Hara RB, Kotze DJ. 2010. Do not log-transform count data. *Methods in Ecology and Evolution*. 1:118–122.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Henry MH, Wagner S, et al. 2013. Vegan: community ecology package.
- Oliver I, Beattie AJ. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications*. 6:594–607.
- Overgaard J, Kristensen TN, Mitchell KA, Hoffmann AA. 2011. Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? *American Naturalist*. 178:S80–S96.
- Parmentier I. 2005. Ecology and distribution of Melastomataceae in African rain forest inselbergs. *Biotropica*. 37:364–372.
- Pekár S, Toft S. 2015. Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). *Biological Reviews*. 90:744–761.
- Pétillon J, Garbutt A. 2008. Success of managed realignment for the restoration of salt-marsh biodiversity: preliminary results on ground-active spiders. *Journal of Arachnology*. 36:388–393.
- Pétillon J, Lambeets K, Montaigne W, Maelfait JP, Bonte D. 2010. Habitat structure modified by an invasive grass enhances inundation withstanding in a salt-marsh wolf spider. *Biological Invasions*. 12:3212–3226.
- Pétillon J, Lambeets K, Ract-Madoux B, Vernon P, Renault D. 2011. Saline stress tolerance partly matches with habitat preference in ground-living wolf spiders. *Physiological Entomology*. 36:165–172.
- Pétillon J, Potier S, Carpentier A, Garbutt A. 2014. Evaluating the success of managed realignment for the restoration of salt marshes: lessons from invertebrate communities. *Ecological Engineering*. 69:70–75.
- Pétillon J, Puzin C, Acou A, Outreman Y. 2009. Plant invasion phenomenon enhances reproduction performance in an endangered spider. *Naturwissenschaften*. 96:1241–1246.
- Pétillon J, Ysnel F, Canard A, Lefeuvre J-C. 2005. Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. *Biological Conservation*. 126:103–117.
- Polotow D, Brescovit AD. 2014. Phylogenetic analysis of the tropical wolf spider subfamily Cteninae (Arachnida, Araneae, Ctenidae). *Zoological Journal of the Linnean Society*. 170:333–361.
- Polotow D, Carmichael A, Griswold CE. 2015. Total evidence analysis of the phylogenetic relationships of Lycosoidea spiders (Araneae, Entelegynae). *Invertebrate Systematics*. 29:124–163.
- Poncy O, Sabatier D, Prévost MF, Hardy I. 2001. The lowland high rainforest: structure and tree species diversity. In: Bongers F, Charles-Dominique P, Forget PM, Théry M, editors. *Nouragues. Monographiae Biologicae*, vol 80. Dordrecht: Springer.
- Portela E, Willemart RH, Gasnier TR. 2013. Soil type preference and the coexistence of two species of wandering spiders (*Ctenus amphora* and *C. crulsi*: Ctenidae) in a rainforest in Central Amazonia. *Journal of Arachnology*. 41:85–87.
- Prenter J, Fanson BJ, Taylor PW. 2012. Whole-organism performance and repeatability of locomotion on inclines in spiders. *Animal Behaviour*. 83:1195–1201.
- Puzin C, Leroy B, Pétillon J. 2014. Intra- and inter-specific variation in size and habitus of two sibling spider species (Araneae, Lycosidae): taxonomic and biogeographic insights from sampling across Europe. *Biological Journal of the Linnean Society*. 113:85–96.
- R Development Core Team. 2015. R: a language and environment for statistical computing. Available from: <http://www.R-project.org>.
- Řezáč M, Řezáčová V, Pekár S. 2007. The distribution of purse-web *Atypus* spiders (Araneae: Mygalomorphae) in Central Europe is constrained by microclimatic continentality and soil compactness. *Journal of Biogeography*. 34:1016–1027.

- Sarthou C, Pavoine S, Gasc J-P, de Masary J-C, Ponge J-F. 2017. From inselberg to inselberg: floristic patterns across scales in French Guiana (South America). *Flora*. 229:147–158.
- Schaefer M. 1974. Experimentelle Untersuchungen zur Bedeutung der interspezifischen Konkurrenz bei 3 Wolfspinnen-Arten (Araneida: Lycosidae) einer Salzwiese. *Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere*. 101:213–235.
- Schuldt A, Staab M. 2015. Tree species richness strengthens relationships between ants and the functional composition of spider assemblages in a highly diverse forest. *Biotropica*. 47:339–346.
- Schuster M, Baurecht D, Mitter E, Schmitt A, Barth FG. 1994. Field observations on the population structure of three ctenid spiders (*Cupiennius*, Araneae, Ctenidae). *Journal of Arachnology*. 22:32–38.
- Sereda E, Blick T, Dorow WHO, Wolters V, Birkhofer K. 2014. Assessing spider diversity on the forest floor: expert knowledge beats systematic design. *Journal of Arachnology*. 42:44–51.
- Steyn TL, Van der Donckt J-F, Jocqué R. 2002. The Ctenidae (Araneae) of the rainforests in eastern Côte d'Ivoire. *Annales du Muséum royal de l'Afrique Centrale (Zoologie)*. 290:129–166.
- Torres-Sánchez MP, Gasnier TR. 2010. Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* (Araneae: Ctenidae) in a Central Amazonian rainforest. *Journal of Arachnology*. 38:433–440.
- Uetz GW. 1979. The influence of variation in litter habitats on spider communities. *Oecologia*. 40:29–42.
- Vedel V, Cerdan A, Martinez Q, Baraloto C, Petitclerc F, Orivel J, Fortunel C. 2015. Day-time vs. night-time sampling does not affect estimates of spider diversity across a land use gradient in the Neotropics. *Journal of Arachnology*. 43:413–416.
- Vedel V, Lalagüe H. 2013. Standardized sampling protocol for spider community assessment in the Neotropical rainforest. *Journal of Entomology and Zoology Studies*. 1:18–35.
- Vincent PJ, Haworth JM. 1983. Poisson regression models of species abundance. *Journal of Biogeography*. 10:153–160.
- Vollrath F. 1988. Spider growth as an indicator of habitat quality. *Bulletin of the British Arachnological Society*. 7:217–219.
- Werling BP, Dickson TL, Isaacs R, Gaines H, Gratton C, Gross KL, Liere H, Malmstrom CM, Meehan TD, Ruan L, et al. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences*. 111:1652–1657.
- Wise DH. 1993. Spiders in ecological webs. Cambridge (United Kingdom): Cambridge University Press.
- Wise DH. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology*. 51:441–465.