

Spider assemblage structure in a neotropical rainforest-inselberg complex: ecological and methodological insights from a small-scale intensive survey

KAÏNA PRIVET^{1,#,*}, CYRIL COURTIAL¹, THIBAUD DECAENS², EL AZIZ DJOUDI¹,
VINCENT VEDEL^{3,4}, FREDERIC YSNEL¹ & JULIEN PÉTILLON^{1,#}

¹*Univ Rennes, G-Tube (Géoarchitecture: Territoires, Urbanisation, Biodiversité, Environnement)
EA 7462, F-35000 Rennes, France*

²*Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS–Univ Montpellier–Univ
Paul-Valéry–EPHE–SupAgro Montpellier–INRA–IRD, Montpellier, France*

³*Laboratoire d'entomologie Entobios, 97310 Kourou, Guyane Française*

⁴*UMR CNRS 8175 Écologie des Forêts de Guyane, Université Antilles-Guyane,
Kourou, Guyane Française*

Abstract: Despite the huge diversity tropical arthropods represent, factors shaping their communities are still poorly known, especially at small spatial scales. In this study, we aimed at providing ecological and methodological insights from a short and intensive field sampling of spiders, a highly diverse group of predators. We investigated how sampling methods, habitat type and day-time affect diversity and composition of spider assemblages. The standardized sampling protocol was applied in a tropical rainforest in French Guiana, where both ground- and vegetation-dwelling (up to 2.5 meters) assemblages were sampled during day and night using supposedly complementary methods at low and high (granitic hills called inselbergs) elevations. Observed and estimated richness of vegetation-dwelling spiders, as well as their species composition, did not differ between methods (sweep netting *vs.* beating). Species richness was much lower in pitfall traps than in litter samples, which suggests a low mobility of ground-dwelling spiders and reveals the inadequacy of the former method compared to the latter. Spider assemblage in the vegetation of inselberg was two times poorer than in lowland forests and dominated by different families, probably due to harsher habitat conditions there. Strongly different patterns were here highlighted between vegetation and ground-dwelling spider assemblages, the latter being less diversified than in the vegetation which deserves further attention.

Key words: Araneae, composition, day-time, French Guiana, non-parametric estimators, richness, sampling method.

Introduction

Assessing spatial patterns in organisms' diversity, and understanding their ecological determinants, is still one of the most fundamental topics in modern ecology. Yet our knowledge derives

primarily of vertebrates and plants studies; much less is known about the structure of terrestrial arthropod communities despite they represent the most diversified taxa with highest species richness. Arthropods are especially speciose in tropical rainforests where nearly 1.5 million species have

*Corresponding Author; e-mail: kprivet@hotmail.fr

#Current Address: Univ Rennes, CNRS, Ecobio (Écosystèmes, biodiversité, évolution) - UMR 6553, F-35000 Rennes, France

been currently described out of an estimated number of 3 to 11 million tropical rainforests could host (Hamilton *et al.* 2010, 2013).

Among terrestrial arthropods, spiders are one of the most diversified group of arthropod predators worldwide (Nentwig 2013), with high bio-indicative values (*e.g.* Marc *et al.* 1999). Indeed, spiders are abundant occupying a wide range of spatial niches (Kremen *et al.* 1993) and inhabit almost every terrestrial habitat. Numerous studies have investigated the driving factors of spider assemblages in temperate habitats, such as vegetation structure, or habitat management (*e.g.* Hatley & Macmahon 1980; Lafage *et al.* 2015; Prieto-Benitez & Mendez 2011; Scharff *et al.* 2003). However, we still know much less regarding the factors that drive spider assemblages in tropical forests, where most of the studies have been carried out with inventory objectives or at the population level (Azevedo *et al.* 2014; Coddington *et al.* 1991; Dias *et al.* 2009; Scharff *et al.* 2003; Sereda *et al.* 2014; Sørensen *et al.* 2002). This is particularly true in French Guiana where spider assemblages have been the subject of several inventory surveys (see Vedel & Lalagüe, 2013; Vedel *et al.* 2015) and where a list of spiders have been recently updated (Vedel *et al.* 2013) but where the determinants of assemblages are still misunderstood. Tropical rainforests of the Guiana Shield are characterised by the existence of different and contrasting forest habitats. They differ in their ground texture and fertility, their seasonal water stress and the associated forest structure (Baraloto *et al.* 2011). These habitats included “terra firme” to seasonally flooded lowland rainforest and sometimes rocky outcrops named inselbergs, which rise abruptly from the surrounding landscape. Lowland rainforests lie in low-lying areas near rivers where episodic flooding often submerges ground surfaces during periods of high precipitation (Baraloto *et al.* 2007). At the opposite, inselbergs exhibit very particular ground and microclimate conditions: alternation of heavy rain and severe drought with air temperature and insolation that regularly reach values that are considerably higher than average values in surrounding forests (Kounda-Kiki *et al.* 2004). Then, inselbergs are considered as “xeric island” or “microclimatic desert” (Porembski 2007). Vegetation of inselbergs is starting to be known, and studies highlighted that these habitats host a characteristic vegetation mosaic (Porembski 2007; Sarthou *et al.* 2003, 2010). In contrast, little research has been devoted to the fauna of inselbergs ecosystems, especially for invertebrates (Kounda-

Kiki *et al.* 2004; Lees *et al.* 2014; Sarthou *et al.* 2009; Vedel & Lalagüe 2013) and spiders (Vedel *et al.* 2013). Inselbergs are considered less rich than surrounding rainforest, but to date no direct study have compared their assemblage to that of other forest habitats.

Even in well studied tropical habitats, spider assemblages, as for arthropods in general, are larger than measured due to high frequencies of rare species (in average 32% of singletons; Coddington *et al.* 2009) whatever the sampling effort. Tropical forest sampling of spider is then a difficult task with the need of using a combination of different sampling methods (*e.g.* Cardoso *et al.* 2009; Jiménez-Valverde & Lobo 2005) and a high sampling effort to collect a significant part of the fauna (Coddington *et al.* 2009). Thus, it has been underlined that to get significant knowledge on the ecology of particular indicator taxa, quasi-optimal design (*sensus* Malumbres-Olarte *et al.* 2017) using complementary sampling methods is still needed. Moreover, comparisons based on observed species numbers are misleading and could have important implications in answering ecological questions. In addition, day *vs.* night period sampling seems to be an important factor influencing the composition of spider assemblages (Cardoso *et al.* 2009; Coddington *et al.* 1991; Sørensen *et al.* 2002) and could potentially explain part of singletons due to nocturnality (Coddington *et al.* 2009). In fact, spiders are known to be mostly active only at night and a smaller proportion is active only during the day (Foelix 2010).

In this study, we applied an intensive quasi-optimal protocol by day and night on vegetation and ground-dwelling spider assemblages from inselberg and lowland rainforest at the Nouragues National Nature Reserve in French Guiana. We focused on species richness and assemblage composition as the main response variables (*e.g.* Azevedo *et al.* 2014; Coddington *et al.* 1996; Lafage & Pétilion 2016; Prieto-Benitez & Mendez 2011) with the aim of investigating the effect of habitat type on diversity and composition of spider assemblages

We focused on spider assemblages of the two more accessible strata: understorey vegetation and ground leaf litter. In understorey stratum, the two sampling methods known to be the most efficient are the sweep net and beating tray. These methods target different microhabitats with sweep net targeting lower understorey vegetation and the beating tray higher understorey vegetation (Coddington *et al.* 1991; Vedel & Lalagüe 2013).

Regarding the ground stratum, pitfall traps remains one of the most widely used methods for studying ground-dwelling macro-arthropods in general (Spence & Niemelä 1994) and especially spiders, while depletion quadrat with litter sifting, despite being time-consuming, also seems to represent an interesting complementary method (*e.g.* Baars 1979; Mantzouki *et al.* 2012). As we used two different and supposedly complementary methods on each stratum, during two periods of the day, we also aim at bringing some new methodological insights on spider sampling in tropical rain forests, particularly in inselberg forests.

More specifically, we tested the following hypotheses. (i) Microhabitat influence the diversity of vegetation-dwelling spider assemblages. We thus expect species richness and composition to be different between both sampling methods targeting understorey vegetation. Moreover, these two sampling methods sampled different volumes of habitat (*i.e.* sweeping sampled twice the volume of habitat of beating). Thus, we expected spider species richness to follow changes in the volume of habitat sampled by the different methods. (ii) Pitfall trap sampling can be considered as a surrogate of other, time-consuming, sampling methods like litter sifting (*e.g.* Baars 1979; Mantzouki *et al.* 2012) for ground-dwelling spiders. Thus we expected species richness, abundances (caught by pitfall traps) and densities (caught by litter sifting) to be correlated, whereas composition was expected to differ slightly between methods, with more mobile species caught by pitfall traps. (iii) Diversity of spider assemblage changes along with the type of tropical forest habitat. We expected vegetation and ground-dwelling spider assemblages' species richness to be less rich in inselberg forests compared to lowland forest due to harsh climate conditions and less depth of ground layer found on inselbergs (Kounda-Kiki *et al.* 2004). In the same way, we expected the species composition of spider assemblages to be significantly different between inselberg and the nearby lowland forests, as it has been found for vegetation (Porembski 2007; Sarthou *et al.* 2010). (iv) Daytime influences the activity of vegetation and ground-dwelling spiders. Thus, night assemblages were expected to be richer than day ones (Foelix 2010) and to have different species composition (Cardoso *et al.* 2011).

Materials and methods

Study site

The fieldwork was carried out in the Nouragues

national nature reserve (French Guiana; 4°04'18"N; 52°43'57"W). Sampling was done during nine consecutive days and nights early during the rainy season (6–15 December 2013), which is considered by Vedel & Lalagüe (2013) as the best sampling period. It was achieved in two rainforest habitats: (i) lowland seasonally flooded rainforest located in the Pararé area, and (ii) low forest located on the top of the Nouragues inselberg (411 m above sea level). Lowland vegetation is typical of primary lowland rainforest, with few inclusions of different vegetation types: palmito-swamp forests, liana forests and bamboo forests. Canopy height varies between 30 and 50 m. The Nouragues inselberg is a rocky outcrop isolated from the rest of the forest where the ground is washed away and the ground granitic. Hence, only a few but specialized species survive in this harsh environment (Porembski 2007). The low forest found nearby the top of this inselberg is rich in Myrtaceae with many endemic plants. It is characterized by a significant number of shrubby species or small bushy shrub with multiple stems and trees with leaning stems. Other trees have tapering trunk. Canopy height ranges from 8 to 15 m high.

Sampling design and field work

A standardized protocol was established to assess differences between lowland and inselberg habitats on spider rainforest assemblages inhabiting the ground and understorey vegetation, and to compare assemblages observed during day *vs.* night collecting for both strata. This protocol is described, tested and criticized for the first time in this study.

Two surface-standardized active sampling methods targeting understorey vegetation species were selected. First, sweep netting was carried out in the lower herb layer or shrubby vegetation with a sweep net along 20 m long and one meter wide (arm length plus sweep handle) transects, representing a sampling volume of 50 m³ each. Twelve stratified transects were conducted per period (day and night) by the same two persons.

The second method consisted in vegetation beating to collect spiders living in the shrub, high herb vegetation, bushes, and small trees. A stout stick was used to hit branches or other vegetation in order to collect falling specimen on a beating tray placed underneath. These samples were conducted in 9 × 9 m quadrats where the vegetation was beat to a height of 2.5 m allowing to sample about 22.5 m³. Twelve stratified quadrats were conducted per period (day and night) by two duos concurrently (six quadrats per duo).

As in our protocol, sweep netting sampled twice the volume-habitat of beating, we investigate if species richness of assemblage collected followed the same pattern, i.e. being two times richer by sweep netting than by beating.

Two methods were used to sample ground-dwelling assemblages. First, pitfall traps constituted by circular, 10 cm diameters, plastic traps containing ethylene glycol as a preservative were used. Fifteen pitfalls have been arranged along a line, spaced 10 m apart (Topping & Sunderland 1992), and were set over a period of two days (days plus nights) in each habitat. They allow to estimate the abundance of ground-dwelling spiders. The second method consisted in litter sifting conducted by using a Winkler extractor as a depletion method to estimate the density of spiders on 1 m² as in Groc *et al.* (2009), hereinafter called 'litter sifting'. Hand sorting of these samples were conducted in lab. Fifteen 1 m² litter samples were spatially pair-matched with pitfall traps and conducted per day and per night (total thirty). Pitfall traps and litter samples were spatially paired to test if pitfall traps can be considered as surrogate of litter sifting.

A total of 156 samples were collected from the Nouragues Nature Reserve, 96 from vegetation and 60 from ground, with 78 samples from each habitat (see Table 1).

Sorting and identification

Samples were fixed and preserved in 70% ethanol. Individuals were first sorted and identified to family following to Dippenaar-Schoeman & Jocqué (1997), Adis (2002), and Jocqué & Dippenaar-Schoeman (2006). Because of the lack of taxonomical knowledge about tropical spiders we defined morpho-species (MS) based on morphological traits, mainly by observation of genitalia and habitus. Under a 65 microscope, we realized a side-by-side comparison of specimens to determine distinct morphological entities. Both juveniles and adults were identified at the family level. Because only adults are identifiable at species level, no morpho-species was defined based on juveniles. Juveniles were then excluded of the richness measures, although they represented ~60% of the specimens. When it was possible, sexes were matched based on color patterns and physical characteristics. For each identified morpho-species a unique code was assigned and a reference individual was designated to take images of dorsal and ventral body views and genitalia. All

individuals are deposited at the University of Rennes 1 (Rennes, France).

Statistical analyses

Correlation between pitfall traps and litter sifting

To test if pitfall sampling can be considered a surrogate of litter sifting, we used correlation to compare pair-matched data using log(x+1) transformed data. Litter sifting, and especially pitfall trap, collected few adult spiders (Table 1). There was no significant difference between abundances (pitfall traps) and densities (litter sifting) (Generalized Linear Model, abundances ~ methods, $F_{1,0.2} = 1.57$, $P = 0.21$) and there were either not significantly correlated (Spearman correlation test, $r = -0.17$, $P = 0.38$, $n = 30$). Hence data from pitfall traps were omitted from subsequent analyses.

Influence of methods, habitat, daytime and strata on morphospecies richness

To test if habitat, daytime, methods and strata influence observed species richness, generalized linear models (GLM) were carried out. First, a model comprising all factors and their interaction was carried out. Type of error (Poisson *vs.* Quasi-Poisson) was selected by comparing residual deviance and denominator freedom degree (O'Hara & Kotze 2010). A second model was calculated if interaction was not significant. We estimated the expected species richness by using different non-parametric estimators: Abundance-based Coverage Estimator (ACE) (Chao & Yang 1993), Incidence-based Coverage Estimator (ICE) (Lee & Chao 1994), Chao1 and Chao2 (Chao 1984 1987), Jackknife 1 and Jackknife 2 (Burnham & Overton 1978, 1979), which determined the least number of species present in the assemblage (Mao & Colwell 2005). Such estimators do not show dependence to unequal sampling effort between modality (Basset *et al.* 2012) and they show little dependence to number of rare species, however a minimum sampling effort is needed to produce a reliable estimation (Chao *et al.* 2009). Richness estimators were compared using species rarefaction curves (Gotelli & Colwell 2001). Sample coverage was calculated for each sample according to Chao & Jost (2012) method and sampling intensity was calculated as the ratio of adult number on species richness (Coddington *et al.* 1996).

Table 1. Summary of spider sampling by each method, for both lowland and inselberg habitats. Nb.: number, ad.: adults, prop.: proportions.

	Inselberg				Lowland				Total
	Pitfall	Litter	Beat	Sweep	Pitfall	Litter	Beat	Sweep	
Nb. replicates	15	30	48	48	15	30	48	48	-
Nb. individuals (ad.)	35 (21)	51 (15)	196 (66)	205 (64)	23 (4)	77 (20)	270 (101)	404 (129)	1261 (420)
Nb. morpho-species	12	14	44	38	4	17	66	80	216
Prop. singletons (%)	67	93	80	71	100	82	74	71	67
Prop. doubletons (%)	25	0	9	8	0	18	11	15	18

Influence of methods, habitat and daytime on assemblage composition (morpho-species)

To test for differences in assemblage composition between methods (beating *vs.* sweeping and pitfall *vs.* sifting), habitat (inselberg *vs.* lowland forest) and daytime (day *vs.* night samples), we conducted an analysis of similarities using PERMANOVA (PERmutational Multivariate ANalysis Of VAriance, 9999 permutations) on the corrected Bray-Curtis index (Clarke *et al.* 2006).

Analyses were made using R software (R Development Core Team 2013), except richness estimators that were calculated with EstimateS software (Colwell 2013)

Results

A total of 1261 spiders were collected belonging to 35 families and 216 morpho-species. Among them, 1075 vegetation-dwelling spiders (17% adults) and 186 ground-dwelling spiders (32% adults) were collected with a high proportion of singletons (67%; Table 1). The intensity of this sampling was 5.5.

Influence of methods, habitat and daytime on species richness

Despite the difference in sampled habitat volume between both vegetation sampling methods, sampling intensity was nearly the same with 1.5 and 1.7 for beating and sweeping on the inselberg and 1.5 and 1.6 in lowland, respectively. Observed richness was not significantly different between methods used to sample vegetation-dwelling spiders (Table 2). Non-parametric richness estimators did not highlight high differences between beating and sweeping methods (Table 3). Estimators never stabilized with the increase of number of individuals sampled as neither of species rarefaction curves reached an asymptote (Fig. 1).

Observed species richness was significantly higher in lowland than in inselberg for vegetation-

dwelling spiders (Table 1; Fig. 2), but not for ground-dwelling spiders collected by litter sifting where there was no difference between both habitats (Table 2). The different non-parametric richness estimators did not show an asymptote with the increase of sample set (Fig. 3). These curves showed that the expected richness was higher in lowland than in inselberg over both ground and vegetation assemblages. Moreover, the sample coverages were very small for all samples with 46% of the estimated fauna diversity sampled by beating, 58% by sweeping, 63% by pitfall trap and 14% by litter sifting on the inselberg, and 52%, 55%, 0% and 32%, respectively, in lowland rainforest.

There was no significant difference in species richness between day and night for both vegetation and ground-dwelling spider assemblages (Table 2).

The sampling intensity was nearly the same for both strata with an average of 1.12 for the ground and 1.54 for the vegetation. Vegetation-dwelling species richness was significantly higher than that of ground (Generalized Linear Model, richness \sim strata, $F_{1,36} = 160.76$, $P < 2.2e^{-16}$; Table 1), which was confirmed by the rarefaction curves showing that estimated species richness was higher for vegetation-dwelling spiders than ground-dwelling ones.

Influence of methods, habitat and daytime on composition

Difference in morpho-species composition between sweeping and beating was non-significant (PERMANOVA, $R^2 = 0.01$, $P = 0.51$).

Significant difference in morpho-species composition per family was found between inselberg and lowland vegetation-dwelling assemblages (PERMANOVA, $R^2 = 3.14$, $P = 1e^{-4}$). There were 176 morpho-species identified in vegetation samples (Table S1). Among them, only 19 were shared by inselberg and lowland assemblages (*i.e.* 11%), 51 were specific to inselberg (*i.e.* 29%) and 106 to low-

Table 2. Effects of methodological and ecological factors on spider species richness (GLM).

Strata tested	Variable tested	Source of variation	<i>F</i>	df	<i>P</i>
Vegetation	Richness	Model 1 (test for interaction)			
		Method	0.7	1	0.391
		Habitat	30.7	1	3.079e-7
		Period	0.7	1	0.391
		Method x habitat	2.1	1	0.152
		Method x period	0.7	1	0.394
		Habitat x period	0.2	1	0.650
		Method x habitat x period	0.2	1	0.652
		Model 2 (no interaction)			
		Method	0.7	1	0.389
		Habitat	30.8	1	2.73e-7
		Period	0.7	1	0.389
		Ground (litter)	Richness	Model 1 (test for interaction)	
Habitat	0.3			1	0.613
Period	0.3			1	0.613
Habitat x period	0.2			1	0.641
Model 2 (no interaction)					
Habitat	0.3			1	0.61
Period	0.3			1	0.61
Ground <i>vs.</i> vegetation	Richness	Model 1 (no interaction)			
		Strata	160.8	1	<2.2e-16

land (*i.e.* 60%). Morpho-species belonging to the families Mimetidae and Uloboridae were only found on the inselberg while those belonging to Ctenidae and Linyphiidae were found only in lowland (Fig. 4). But the main morpho-species difference between both habitats was primarily due to four of the richest families: Theridiidae, Salticidae, Thomisidae and Araneidae. In fact, 78% of Theridiidae were specific to lowland, 11% shared to both habitats and 11% specific to inselberg. As well as 63% of Salticidae were specific to lowland, 13% common and 25% specific to inselberg; and respectively 60%, 29%, 13% of Thomisidae and 57%, 12%, 31% of Araneidae. On the contrary, there was no significant difference in morpho-species composition of ground-dwelling samples (PERMANOVA, $R^2 = 0.045$, $P = 0.21$), but only one morpho-species was common to lowland and inselberg litter ground samples (Table S2).

There was no significant difference between day and night morpho-species abundances (*i.e.* composition) between day and night for vegetation-dwelling (PERMANOVA, $R^2 = 0.01$, $P = 0.52$) and ground-dwelling assemblages (PERMANOVA, $R^2 = 0.05$, $P = 0.11$).

Discussion

The present study is the first application of a quasi-optimised protocol developed to answer ecological questions about tropical arthropod assemblage, particularly to compare unknown inselberg's assemblage to the little better described lowland's. Thanks to an intensive field survey, we can bring both ecological and methodological insights by using a highly diversified group, spiders, as a model. Despite a high sampling effort, the sampling intensity is still low and the proportion of singletons is high (*sensu* Coddington *et al.* 2009). This typically shows the difficulty to reach exhaustive inventory, which was not our objective, when targeting mega-diverse taxa like spiders.

Comparison of sampling efficiency between methods

When doubling the volume of habitat sampled (here two times higher by sweeping than by beating), the observed species richness of vegetation-dwelling spiders did not significantly increase. Sweeping

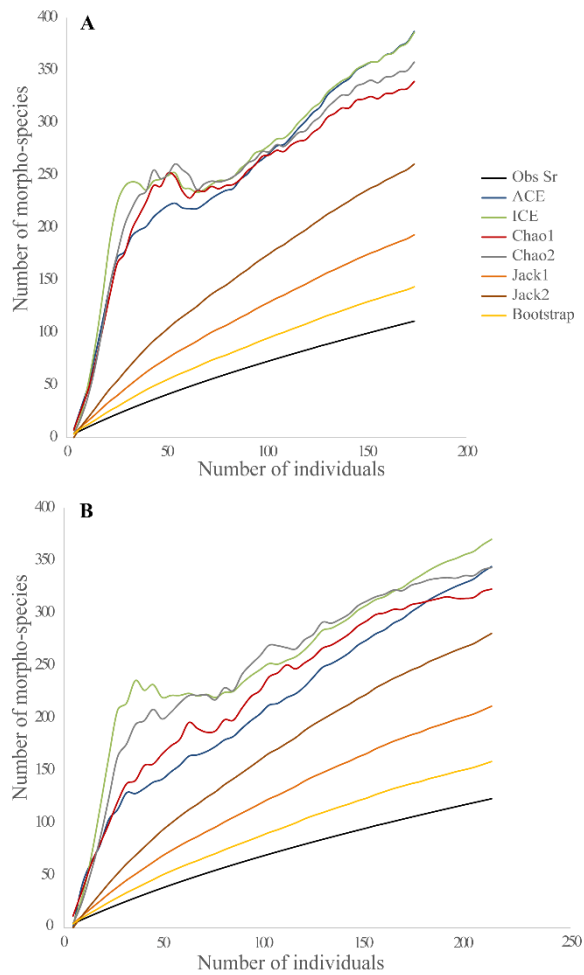


Fig. 1. Comparison of species rarefaction curves between beating (A) and sweep netting (B) obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap). Obs. Sr: observed species richness.

allowed to collect more individuals, but not more species. Instead, a doubled habitat volume did not increase the sampling efficiency. That is invalidating our first hypothesis: species richness does not linearly increase with the volume of habitat sampled. According to Rosenzweig (1995), species richness can logarithmically increase with sampling area. Hence, it would probably be necessary to increase the volume of habitat sampled more than expected to get a significant increase in species richness. Moreover, none of the species rarefaction curves reached an asymptote, which shows that the sampling effort was not sufficient for both methods to collect a representative part of the spider fauna. Further-

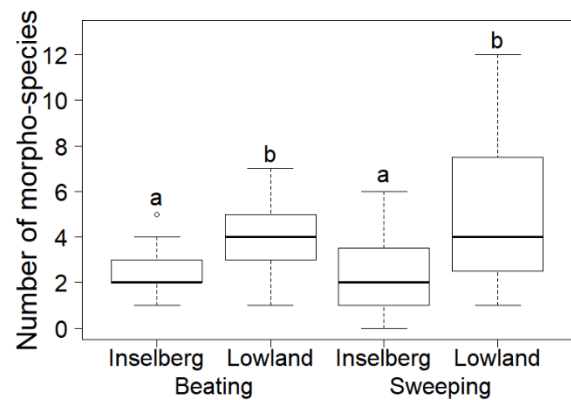


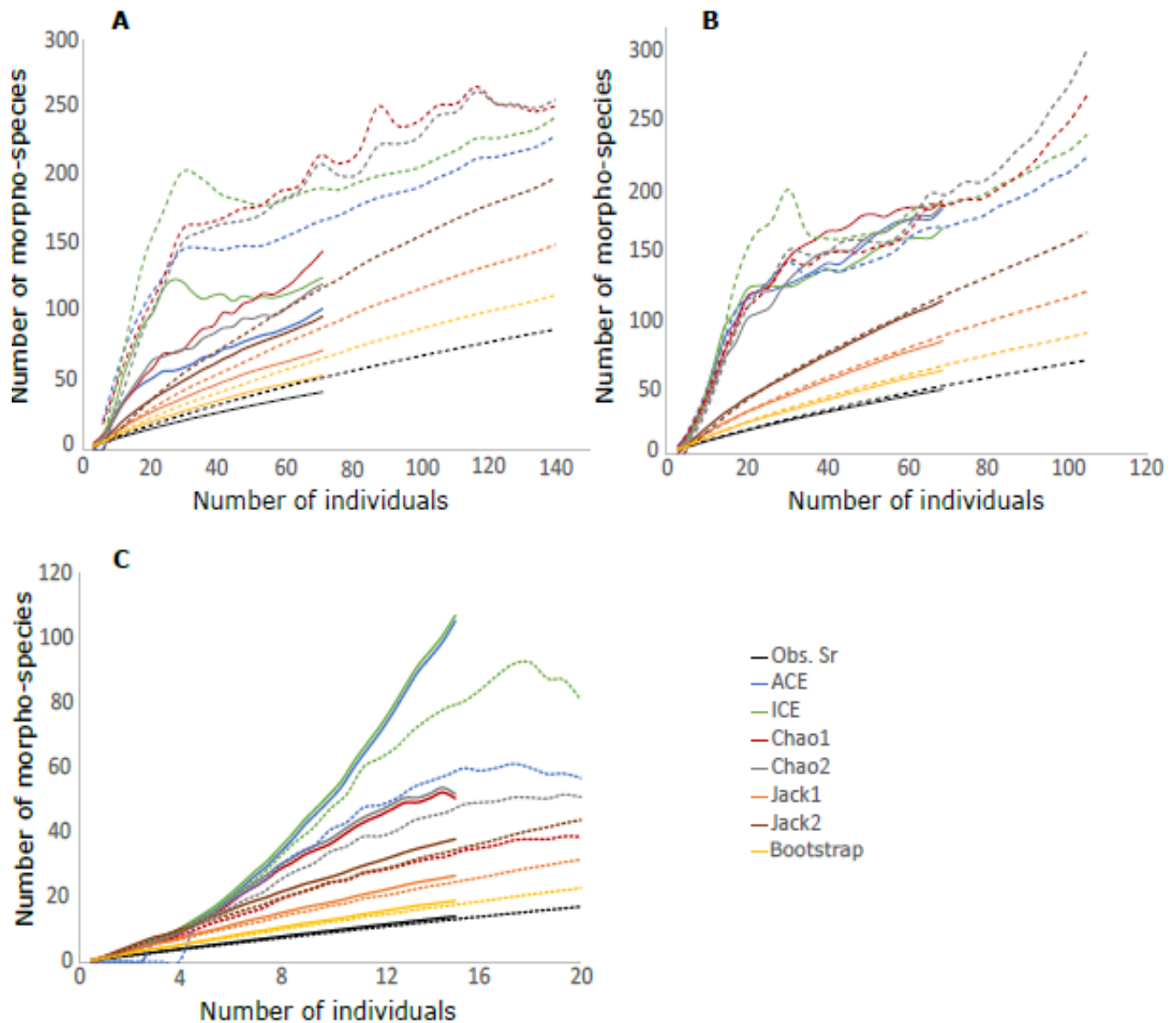
Fig. 2. Comparison of mean observed species richness between lowland and inselberg habitats, for each vegetation sampling method.

more, beating and sweeping sampled different subsets of spider assemblages, *i.e.* lower understory vegetation for sweep netting and higher for beating (Cardoso *et al.* 2008; Scharff *et al.* 2003; Vedel & Lalagüe 2013). However, we found no difference of composition between these two sampling methods. In addition to the low abundance of most of the morpho-species collected, this suggests that the scale at which sedentary tropical arthropods should be sampled is frequently underestimated (Chao *et al.* 2009; Coddington *et al.* 2009), probably due to aggregate patterns of fauna in tropical forests.

Pitfall traps collected only few ground-dwelling spiders while litter sifting collected much more. We found no correlation between species richness by pitfall traps and spatially paired litter sifting samples and no correlation between number of individuals by both methods, *i.e.* abundances (pitfall traps) and densities (litter sifting). Thus, pitfall sampling cannot be considered as a surrogate of litter sifting. Pitfall traps seems to be not suitable to estimate abundance and diversity of ground-dwelling predators like spiders in tropical rainforests, which conforms few previous studies on spiders (Azevedo *et al.* 2014; Luff 1975; Maelfait & Baert 1975; Malumbres-Olarte *et al.* 2017) and on neotropical harvestmen (Tourinho *et al.* 2014). Three alternative explanations can be proposed to explain this result. (i) Pitfall traps samples collected less spiders because they do not capture cursorial spiders. But then densities by litter sampling would have been even higher: thus, this explanation is considered unlikely. (ii) Another explanation is that pitfall traps are less efficient than active ground

Table 3. Observed and estimated species richness for the four sampling methods in both habitats. Obs.: observed.

		Obs.	Chao1	Chao2	Jack1	Jack2	ACE	ICE	Bootstrap
Inselberg	Beat	44	190	186	84	115	184	169	62
	Sweep	38	146	121	73	98	103	126	54
	Pitfall	12	22	22	19	23	35	33	15
	Litter	14	50	52	27	38	105	107	19
Lowland	Beat	66	269	303	122	166	223	239	91
	Sweep	80	252	257	150	199	230	244	113
	Pitfall	4	9	10	8	11	9	10	5
	Litter	17	39	51	32	44	57	81	23

**Fig. 3.** Comparison of species rarefaction curves between inselberg (solid line) and lowland (dotted line) habitats obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap) for 3 different sampling methods: sweep netting (A), beating (B) and litter sifting (C). Obs. Sr: observed species richness.

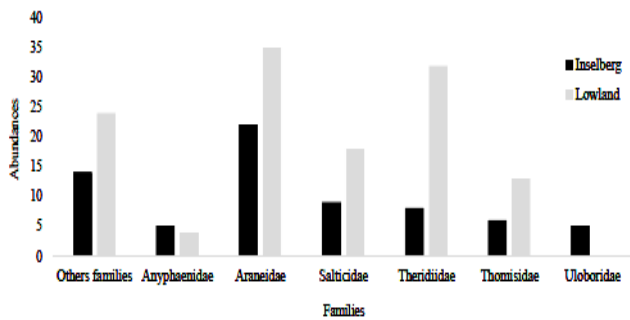


Fig. 4. Comparison of abundances by spider family between inselberg and lowland forest (vegetation samples only).

sifting method because ground-dwelling spiders have a low mobility. This has been suggested in temperate forests by Siewers *et al.* (2014) for small, web-building species. (iii) It has been previously suggested that systematic and standardized designs may not adequately reflect the abundance and composition of spider assemblages because of environmental gradients and microhabitats (*e.g.* presence or absence of herb layer) that are not correctly encompassed by pitfall sampling (Cardoso *et al.* 2009; Sereda *et al.* 2014). Our results showed that pitfall traps do not allow to collect high number of spiders in tropical habitats, and we thus consider this method as unsuitable for tropical habitats (to the difference of temperate, arctic and Mediterranean habitats where it is more effective and commonly used: see *e.g.* Cardoso *et al.* 2008; Scharff *et al.* 2003). This lack of efficiency should be considered to standardize further samplings of tropical ground-dwelling spiders.

Comparison of spider assemblages between inselberg and lowland forests

Inselberg forests are isolated on a rocky outcrop, characterized by harsh microclimatic conditions, poor and shallow ground, and the vegetation found there is poorer than that of surrounding, lowland, rainforests (Porembski 2007). Although the importance of inselberg forest biodiversity has been shown for vertebrates and plants (*e.g.* Fredericksen *et al.* 2003; Girão *et al.* 2010; Porembski 2007), we found only three studies that investigated the difference of arthropod richness and composition between lowland tropical rainforest and low forests located on the top of adjacent inselbergs (canopy spiders: Russell-Smith & Stork 1994; ground-dwelling Scarabaeidae: Feer, 2013; ground and understory spiders: Vedel & Lalagüe 2013). In their study, Vedel & Lalagüe (2013) compared abundance, richness and diversity

of spiders between one inselberg forest plot and three lowland forest plots. They found greater species richness in lowland forests spiders than in the low inselberg forest, which was explained by the differences in local habitat conditions (mainly higher moisture in lowland forests) between habitats. Feer (2013) observed the same pattern regarding the ground-dwelling Scarabaeidae. However, Vedel & Lalagüe's work was a pilot study with methodological and inventory objectives undertaken with non-optimal conditions (*i.e.* low sampling effort, sampling during periods of low abundance for arthropods), with no spatial replication and the authors did not perform statistical tests on their data. In some Indomalayan rainforests, Russell-Smith & Stork (1994) found an increase in canopy spider abundance and richness with increasing altitude. Yet the fact that the spiders they studied were located another biome and in the canopy make their results hard to compare to ours.

The present study partially confirmed Vedel & Lalagüe (2013) results, and supplemented them in terms of assemblage composition, also indicating contrasted results between strata. As a matter of fact, observed and estimated species richness of vegetation-dwelling spiders were higher in lowland forests than on the top of inselberg while the opposite pattern was found on ground-dwelling spiders using quadrat sampling. It is known that litter depth has generally direct and positive effects on spider assemblages (Uetz 1979), as well as for the ground-dwelling arthropods of tropical lowland rainforests (Ashford *et al.* 2013). This is overall consistent with a bottom-up control of spider density and diversity (*e.g.* Bennett 2010). However, we found that ground-dwelling spiders were richer on inselberg where the ground is shallow. We assumed three alternative and non-exclusive explanations for this pattern: (i) ground hygrometry and periodic flooding could be a more limiting for the ground-dwelling spiders of lowland forests than the harsh climatic conditions and shallow ground on the Inselberg and (ii) flooding in lowland forest is a factor of litter homogenization (Adis & Junk 2002; Decaëns *et al.* 2016; Lafage & Pétilion 2016), which could result in decreased spider abundance and richness there. Moreover, (iii) inselberg are considered as functional islands (Prance *et al.* 1996; Sarthou *et al.* 2017) and low forests growing are more seen as ecotone (Sarthou *et al.* 2010) that would generate rainforest biodiversity thanks to environmental heterogeneity (Smith *et al.* 1997). While the species composition was studied in Vedel

& Lalagüe (2013) only in lowland tropical rainforests, our study gives for the first time knowledge about spider assemblage composition on an inselberg, and its comparison to the spider composition of an adjacent lowland forest provided. The change in morpho-species composition observed in vegetation-dwelling spiders supports the idea that inselbergs act as a habitat very distinct from the surrounding forests. These tropical forest habitats host different spider assemblages, with for example less Theridiidae than in lowland suggesting that the vegetation structure complexity is lower in this habitat (Hatley & Macmahon 1980). However, morpho-species occur in low numbers. Accordingly, further studies are needed to investigate a gradual shift in composition from lowland to the top of inselbergs. Furthermore, no difference between habitats was found for ground-dwelling spiders, probably because the number of individuals were too low. Nonetheless, another study conducted at the same place on ground-active Ctenids found differences in spider densities between elevations using hand-collections in depletion quadrats (Pétillon *et al.* 2018).

Influence of day-time collecting

Several tropical studies revealed a higher spider richness at night (Coddington *et al.* 1991; Green 1999; Sørensen *et al.* 2002) and change in species composition between day and night (in tropical: Malumbres-Olarte *et al.* 2017; Sørensen *et al.* 2002; temperate: Cardoso *et al.* 2008). It has consequently been argued that spiders should be sampled both day and night in temperate and tropical forests (see Cardoso *et al.* 2009 and Vedel & Lalagüe 2013, respectively).

Conforming few other studies, our results showed no difference in spider species richness (see Coddington *et al.* 1996; Dobyms 1997 and Vedel *et al.* 2015 for temperate and tropical forests, respectively) and composition (see Cardoso *et al.* 2008 & Sørensen *et al.* 2002; Malumbres-Olarte *et al.* 2017 for temperate and tropical forests, respectively) between sampling times. Vedel *et al.* (2015) suggested that collecting spiders at only one time during the day was enough to estimate the diversity of spider assemblages across vegetation types. However, the lack of consensus emerging from the different studies on species composition implies that it is necessary to collect spiders during both day and night to confirm that period has no significant influence on the composition. Further-

more, sampling during both periods is still necessary to describe and inventory the diversity of spider assemblages (Malumbres-Olarte *et al.* 2017).

Due to the poor abundances collected by pitfall traps, comparison during both periods has only been conducted on assemblage collected by litter sifting. Ground-dwelling assemblages were then not significantly different between sampling periods. Litter sifting can only catch spiders when they are out of their refuge. Unlike what is usually reported on spider species inhabiting the leaf litter (Vedel *et al.* 2015), our results showed that these spiders are not more active (*i.e.* foraging) at night.

However, we cannot rule out the possibility that the absence of difference can be due to the low numbers of individuals collected here and generally in tropical samples because it probably had a direct influence on the assemblage composition.

Comparison of spider assemblages between ground and vegetation strata

Estimated species richness was much lower at ground surface compared to the surrounding vegetation (data from the same sampling stations by beating and sweep-netting). Such a difference between ground and vegetation strata is surprising because their diversities are likely correlated in arthropods (Donoso *et al.* 2010, but see Mathieu *et al.* 2009 with low spider densities in an Amazonian grassland). Moreover, ecological comparisons of ground- and vegetation-dwelling spider assemblage conducted in this study highlighted that ground and vegetation patterns in species richness are different. Vegetation-dwelling spider richness was indeed lower on the inselberg compared to the lowland forest and composition changed between both habitats, whereas species richness and composition did not change between habitats for ground-dwelling. These results suggest that species richness are probably not correlated between ground- and vegetation-dwelling spiders. Considering that the number of species living together reflects the richness of adaptive opportunities, species richness is the result of inter-specific competition and factors that conditioned productivity, as well as niche size, quantity of resources (Ricklefs 1979). Hence, lowered abundances and species richness of ground-dwelling spiders would reflect a high competition with other predators such as ants, one of the most diverse taxa on tropical ground and low available resources due to a high rate of recycling (due to ants or environmental conditions) (Ashford *et al.* 2013;

Malumbre-Olarte *et al.* 2017). Accordingly, ground and vegetation samples are not redundant and both are essential to fully understand the influence of ecological factors in shaping spider assemblages.

Overall, we showed that differences in the volume of sampled vegetation did not significantly influence spider species richness probably due to differences in spider assemblages sampled by both methods used. This study showed that pitfall trap-based method is uncorrelated to litter sifting and, unknotted suitable to sample ground-dwelling spiders, probably due to a too high (large spiders) or too low (small species) mobility. The habitat type (*i.e.* lowland vs. inselberg) influenced the species richness and composition of tropical vegetation-dwelling spiders, probably due to harsher conditions on inselberg (no pattern was found for ground-dwelling spiders). This study is, to our knowledge, the first to compare composition of spider assemblages between lowland and inselberg forests using a standardized and statistically robust protocol. We showed the originality of inselbergs when compared to adjacent, lowland, assemblages, and bring out the basis for further studies on inselberg spider assemblages. The sampling period did not significantly influence the species richness of vegetation and ground-dwelling spiders, not more than the composition of assemblages, the latter being inconsistent with usually defined hunting guilds. Finally, by comparing vegetation and ground-dwelling spider assemblages, we showed that their diversities were not correlated, and that they differently responded to ecological factors such as habitat type. Further studies are needed to understand inselberg spider diversity, test some better standardized ground sampling in tropical rainforest, and assess the importance of other ecological factors such as vegetation structure, biomass, litter depth or prey density. Finally, this study suggests some particularities of spider assemblage structure and composition compared to the literature which is largely based on temperate habitats. It is thus urgent to compare factors shaping arthropod diversity and composition between tropical and habitats and using similar protocols.

Acknowledgments

We are grateful to Boris Leroy, Alain Canard, Maxime Cobigo, Jennifer Devillechabrolle and Stéphane Icho for help during field work, and Marguerite Delaval for continuous support. Founding and technical help was provided by the 'Réserve Naturelle Nationale des Nouragues'

(Office National des Forêts / Association de Gestion des Espaces Protégés).

References

- Adis, J. (ed.). 2002. *Amazonian Arachnida & Myriapoda: Identification Keys to All Classes, Orders, Families, Some Genera and Lists of Known Terrestrial Species*. Pensoft Pub., Sofia-Moscow.
- Adis, J. & W. J. Junk. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshwater Biology* **47**: 711–731.
- Ashford, O. S., W. A. Foster, B. L. Turner, E. J. Sayer, L. Sutcliffe & E. V. J. Tanner. 2013. Litter manipulation and the soil arthropod community in a lowland tropical rainforest. *Soil Biology and Biochemistry* **62**: 5–12.
- Azevedo, G. H. F., B. T. Faleiro, I. L. F. Magalhães, A. R. Benedetti, U. Oliveira, *et al.* 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.
- Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* **41**: 25–46.
- Baraloto, C., F. Morneau, D. Bonal, L. Blanc & B. Ferry. 2007. Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology* **88**: 478–489.
- Baraloto, C., S. Rabaud, Q. Molto, L. Blanc, C. Fortunel, *et al.* 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology* **17**: 2677–2688.
- Basset, Y., L. Cizek, P. Cuenoud, R. K. Didham, F. Guilhaumon, *et al.* 2012. Arthropod diversity in a tropical forest. *Science* **338**: 1481–1484.
- Bennett, A. 2010. The role of soil community biodiversity in insect biodiversity. *Insect Conservation and Diversity* **3**: 157–171.
- Burnham, K. P. & W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* **65**: 625–633.
- Burnham, K. P. & W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* **60**: 927–936.
- Cardoso, P., N. Scharff, C. Gaspar, S. S. Henriques, R. Carvalho, *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., S. S. Henriques, C. Gaspar, L. C. Crespo, R. Carvalho, *et al.* 2009. Species richness and composition assessment of spiders in a Mediterranean

- scrubland. *Journal of Insect Conservation* **13**: 45–55.
- Cardoso, P., S. Pekár, R. Jocqué & J. A. Coddington. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS ONE* **6**: e21710.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**: 265–270.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**: 783–791.
- Chao, A., Colwell, R. K., Lin, C. W. & Gotelli, N. J. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* **90**: 1125–1133.
- Chao, A. & L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**: 2533–2547.
- Chao, A. & M. C. Yang. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. *Biometrika* **80**: 193–201.
- Clarke, K. R., P. J. Somerfield & M. G. Chapman. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* **330**: 55–80.
- Coddington, J. A., C. E. Griswold, D. Silva Davila, E. Peñaranda & S. F. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. pp. 44–60. *In*: E. Dudley (ed.) *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*. Dioscorides Press, Portland, OR, USA.
- Coddington, J. A., L. H. Young & F. A. Coyle. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest. *Journal of Arachnology* **24**: 111–128.
- Coddington, J. A., I. Agnarsson, J. A. Miller, M. Kuntner & G. Hormiga. 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology* **78**: 573–584.
- Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Decaëns, T., D. Porco, S. W. James, G. G. Brown, V. Chassany, *et al.* 2016. DNA barcoding reveals diversity patterns of earthworm communities in remote tropical forests of French Guiana. *Soil Biology and Biochemistry* **92**: 171–183.
- Dias, S. C., L. S. Carvalho, A. B. Bonaldo & A. D. Brescovit. 2009. Refining the establishment of guilds in Neotropical spiders (Arachnida: Araneae). *Journal of Natural History* **44**: 219–239.
- Dippenaar-Schoeman, A. S. & R. Jocqué. 1997. *African Spiders: An Identification Manual*. ARC-Plant Protection Research Institute, Biosystematics Division, National Collection of Arachnida. Agricultural Research Council, Pretoria.
- Dobyns, J. R. 1997. Effects of sampling intensity on the collection of spider (Araneae) species and the estimation of species richness. *Pest Management and Sampling* **26**: 150–162.
- Donoso, D. A., M. K. Johnston & M. Kaspari. 2010. Trees as templates for tropical litter arthropod diversity. *Oecologia* **164**: 201–211.
- Feer, F. 2013. Variations in dung beetles assemblages (Coleoptera: Scarabaeidae) within two rain forest habitats in French Guiana. *Revista de Biología Tropical* **61**: 753–768.
- Foelix, R. 2010. *Biology of Spiders*. 3rd ed. Oxford University Press, Oxford.
- Fredericksen, N. J., T. S. Fredericksen, B. Flores, E. McDonald & D. Rumiz. 2003. Importance of granitic rock outcrops to vertebrate species in a Bolivian tropical forest. *Tropical Ecology* **44**: 183–194.
- Girão, W., C. Albano & A. A. Campos. 2010. Inselbergs as habitat to the critically endangered Grey-breasted Parakeet (*Pyrrhura griseipectus*), an endemic species from northeastern Brazil. *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology* **18**: 130–132.
- Gotelli, N. J. & R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379–391.
- Green, J. 1999. Sampling method and time determines composition of spider collections. *Journal of Arachnology* **27**: 176–182.
- Groc, S., J. Orivel, A. Dejean, J. M. Martin, M. P. Etienne, B. Corbara & J. H. C. Delable. 2009. Baseline study of the leaf-litter ant fauna in a French Guianese forest. - *Insect Conservation and Diversity* **2**: 183–193.
- Hamilton, A. J., Y. Basset, K. K. Benke, P. S. Grimbacher, S. E. Miller, *et al.* 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. *The American Naturalist* **176**: 90–95.
- Hamilton, A. J., V. Novotný, E. K. Waters, Y. Basset, K. K. Benke, *et al.* 2013. Estimating global arthropod species richness: refining probabilistic models using probability bounds analysis. *Oecologia* **171**: 357–365.
- Hatley, C. L. & J. A. Macmahon. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology* **9**: 632–639.
- Jiménez-Valverde, A. & J. M. Lobo. 2005. Determining a combined sampling procedure for a reliable estimation

- of Araneidae and Thomisidae assemblages (Arachnida, Araneae). *Journal of Arachnology* **33**: 33–42.
- Jocqué, R. & A. S. Dippenaar-Schoeman. 2006. *Spider Families of the World*. 1st ed. Koninklijk Museum Moor Midden-Afrika, Tervuren, Belgium; Pretoria, South Africa.
- Kounda-Kiki, C., A. Vaçulik, J. F. Ponge & C. Sarthou. 2004. Soil arthropods in a developmental succession on the Nouragues inselberg (French Guiana). *Biology and Fertility of Soils* **40**: 119–127.
- Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. A. Noss & M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**: 796–808.
- Lafage, D., S. Maugenest, J. B. Bouzillé & J. Pétilion. 2015. Disentangling the influence of local and landscape factors on alpha and beta diversities: opposite response of plants and ground-dwelling arthropods in wet meadows. *Ecological Research* **30**: 1025–1035.
- Lafage, D. & J. Pétilion. 2016. Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire. *Basic and Applied Ecology* **17**: 535–545.
- Lee, S. M. & A. Chao. 1994. Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* **50**: 88–97.
- Lees, D. C., A. Y. Kawahara, R. Rougerie, I. Ohshima, A. Kawakita, *et al.* 2014. DNA barcoding reveals a largely unknown fauna of Gracillariidae leaf-mining moths in the Neotropics. *Molecular Ecology Resources* **14**: 286–296.
- Luff, M. L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* **19**: 345–357.
- Maelfait, J. -P. & L. Baert. 1975. Contribution to the knowledge of the arachni and entomofauna of different wood habitats. Part I. Sampled habitats, Theoretical study of the pitfall method, survey of the captured taxa - Carabidae. *Biologisch Jaarboek Dodonaea* **43**: 179–196.
- Malumbres-Olarte, J., N. Scharff, T. Pape, J. A. Coddington & P. Cardoso. 2017. Gauging mega-diversity with optimized and standardized sampling protocols: A case for tropical forest spiders. *Ecology and Evolution* **7**: 494–506.
- Mantzouki, E., F. Ysnel, A. Carpentier & J. Pétilion. 2012. Accuracy of pitfall traps for monitoring populations of the amphipod *Orchestia gammarella* (Pallas 1766) in saltmarshes. *Estuarine, Coastal and Shelf Science* **113**: 314–316.
- Mao, C. X. & R. K. Colwell. 2005. Estimation of species richness: mixture models, the role of rare species, and inferential challenges. *Ecology* **86**: 1143–1153.
- Marc, P., A. Canard & F. Ysnel. 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems & Environment* **74**: 229–273.
- Mathieu, J., M. Grimaldi, P. Jouquet, C. Rouland, P. Lavelle, *et al.* 2009. Spatial patterns of grasses influence soil macrofauna biodiversity in Amazonian pastures. *Soil Biology and Biochemistry* **41**: 586–593.
- Nentwig, W. (ed.) 2013. *Spider Ecophysiology*. Springer-Verlag, Berlin.
- O'Hara, R. B., & D. J. Kotze. 2010. Do not log-transform count data. *Methods in Ecology and Evolution* **1**: 118–122.
- Pétilion, J., Leroy, B., Djoudi, E.A. & V. Vedel. 2018. Small and large spatial scale coexistence of ctenid spiders in a neotropical forest (French Guiana). *Tropical Zoology* **31**: 85–98.
- Porembski, S. 2007. Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. *Brazilian Journal of Botany* **30**: 579–586.
- Prance, G. T. 1996. Islands in Amazonia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **351**: 823–833.
- Prieto-Benítez, S. & M. Méndez. 2011. Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis. *Biological Conservation* **144**: 683–691.
- R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Ricklefs, R. E. 1979. Adaptation, Constraint, and Compromise in Avian Postnatal Development. *Biological Reviews* **54**: 269–290.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Russell-Smith, A. & N. E. Stork. 1994. Abundance and Diversity of Spiders from the Canopy of Tropical Rainforests with Particular Reference to Sulawesi, Indonesia. *Journal of Tropical Ecology* **10**: 545–558.
- Sarthou, C., J. F. Villiers, J. F. Ponge & J. Franklin. 2003. Shrub vegetation on tropical granitic inselbergs in French Guiana. *Journal of vegetation science* **14**: 645–652.
- Sarthou, C., C. Kounda-Kiki, A. Vaçulik, P. Mora & J. F. Ponge. 2009. Successional patterns on tropical inselbergs: A case study on the Nouragues inselberg (French Guiana). *Flora - Morphology, Distribution, Functional Ecology of Plants* **204**: 396–407.
- Sarthou, C., D. Larpin, É. Fonty, S. Pavoine & J. F. Ponge. 2010. Stability of plant communities along a tropical inselberg ecotone in French Guiana (South America). *Flora* **205**: 682–694.
- Sarthou, C., S. Pavoine, J. P. Gasc, J. C. de Massary & J. F. Ponge. 2017. From inselberg to inselberg:

- Floristic patterns across scales in French Guiana (South America). *Flora* **229**: 147–158.
- Scharff, N., J. A. Coddington, C. E. Griswold, G. Hormiga & P. de P. Bjørn. 2003. When to quit? Estimating spider species richness in a northern European deciduous forest. *Journal of Arachnology* **31**: 246–273.
- Sereda, E., T. Blick, W. H. Dorow, V. Wolters & K. Birkhofer. 2014. Assessing spider diversity on the forest floor: expert knowledge beats systematic design. *Journal of Arachnology* **42**: 44–51.
- Siewers, J., J. Schirmel & S. Buchholz. 2014. The efficiency of pitfall traps as a method of sampling epigeal arthropods in litter rich forest habitats. *European Journal of Entomology* **111**: 69–74.
- Smith, T. B., R. K. Wayne, D. J. Girman & M. W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. *Science* **276**: 1855–1857.
- Sørensen, L. L., J. A. Coddington & N. Scharff. 2002. Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an Afromontane forest. *Environmental Entomology* **31**: 319–330.
- Spence, J. R. & J. K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist* **126**: 881–894.
- Topping, C. J. & K. D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology* **29**: 485–491.
- Tourinho, A. L., L. de S. Lança, F. B. Baccaro & S. C. Dias. 2014. Complementarity among sampling methods for harvestman assemblages. *Pedobiologia* **57**: 37–45.
- Uetz, G. W. 1979. The influence of variation in litter habitats on spider communities. *Oecologia* **40**: 29–42.
- Vedel, V. & H. Lalagüe. 2013. Standardized sampling protocol for spider community assessment in the neotropical rainforest. *Journal of Entomology and Zoology Studies* **1**: 18–34.
- Vedel, V., C. Rheims, J. Murienne & A. D. Brescovit. 2013. Biodiversity baseline of the French Guiana spider fauna. *SpringerPlus* **2**: 361.
- Vedel, V., A. Cerdan, Q. Martinez, C. Baraloto, F. Petitclerc, J. Orivel & C. Fortunel. 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.

(Received on 26.06.2017 and accepted after revisions, on 03.04.2018)

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Relative abundance of morpho-species collected in vegetation in inselberg and lowland forests (sweeping and beating).

Table S2. Relative abundance of ground-dwelling morpho-species collected by litter sifting in inselberg and lowland.