Taxonomic diversity and functional redundancy of spider communities in African savannas

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1   ABSTRACT

The study compared the descriptive parameters of the araneofauna of six contiguous savannas in Franceville (Gabon) two months before traditional fire management to characterize a reference community. Two approaches were implemented: morphospecies identification (taxonomic approach) and functional group determination (functional approach) based on the measure of functional traits of female and male morphospecies. The taxonomic and the functional turnover between the six communities were analysed. Three main results emerged: (i) spider communities exhibit a high degree of morphospecific diversity accompanied by significant turnover (ii) for all savannas merged, the mean value of the sampling efficiency was 69.6% and 71.2% for females and males morphospecies, respectively, suggesting that the sampling effort was just about sufficient to characterize a global spider community of the savanna hills and (iii) spider communities are composed of morphospecies that are highly redundant which could be separate into four main functional groups. Savanna ecosystems are regularly subjected to fire management which modifies the microhabitat conditions on which spiders depend. This work reveals that a community of reference can be characterized before burning by taking the communities of the six merged savannas into account. Because functional redundancy between savannas is high, future studies on the resilience capacities of savanna after burning can also be considered for each savanna independently by referring to functional groups.

2   INTRODUCTION

Due to their diversity and high abundances in many ecosystems, spiders have long been considered as excellent indicators of microhabitat environmental changes induced by human habitat management or disturbances (see for instance Marc *et al.,* 1999). Regarding the African savannas, spiders form a very diverse and dominant taxon (Whitmoore *et al.*, 2002; Foord *et al.,* 2011, 2013, Haddad *et al.,* 2018, Joseph *et al.*, 2018) and occupy a wide range of spatial niches (Blandin & Célérier, 1981; Russell Smith, 2002; Whitmore *et al.,* 2002). However, estimating the impact of anthropogenic disturbances on African savanna spider communities face major taxonomic gaps: to the notable exception of South Africa, most of the savanna spider species are not described, (especially in Gabon, Jocqué *et al.,* 2013, World spider Catalog, 2022). To overcome this problem, two different approaches can be implemented to analyse communities and their evolution in response to natural or anthropogenic habitat modifications. The first one aims to characterize spider communities based on the identification of morphospecies. Morphospecies constitute a good estimate of

spider diversity and may be used as surrogates for species in tropical field studies in assessment of turnover between sites (Oliver & Beattie, 1996). This approach can partially circumvent the lack of taxonomic knowledge on savanna spiders and in tropical areas in general (Privet *et al.,* 2018). The second approach attempts to characterize communities based on the use of functional traits of species that must account for important structural properties of communities while pointing to certain key dimensions of biodiversity not taken into account by a purely taxonomic approach (Vandewalle *et al.,* 2010). In temperate zones, spiders have been used as models in many functional diversity studies to asses land-uses changes from global (Cardoso *et al.,* 2011) to regional (Morel & al. 2019) scale. To our knowledge, studies on the functional diversity of African savanna spider communities have received little attention so far (Joseph *et al.,* 2018). Based on these two approaches, the main objective of the present study is to describe the structural and functional components of the spider communities of a large savanna site distributed on the eastern and western slopes of three contiguous savanna hills two months before annual traditional fire management. In addition to the comparison of the composition of the communities using an approach based on the morphospecies, this study sought to analyse the functional composition of the communities based on measurable traits on the morphospecies. Given the configuration of the site selected for the study, two hypotheses can be made: (i) if the rate of morphospecies shared by the three contiguous hills is high, the structural and functional composition of the community can be characterized by considering the whole complex as a single entity; (ii) if taxonomic or functional turnover between hill is important, each savanna hill should be considered independently in the future assessment of the impact of fire management. The following questions were asked to analyse these hypotheses: (i) is the sampling plan representative of a reference community for this sampling period? (ii) Based on morphospecies analysis, what is the turnover of communities on the sampled plots? (iii) Given that little information is available on the biology of the sampled morphospecies, can we select and measure relevant functional traits on these morphospecies to characterize the functional groups? (iv) Can we highlight taxonomic or functional redundancy between hills?

3   MATERIALS AND METHODS

3.1   Sampling protocol: Sampling took place in three contiguous savanna hills of identical physiognomy, located near the village of Benguia (Haut-Ogooué, Gabon, 1°37'33"S, 13°30'40"E). The vegetation cover was similar in all six savanna hills, and dominated by herbaceous plants of the *Poaceae* and *Cyperaceae* type, annually and partially burned as part of traditional management. Ninety pitfall traps were spread across the three eastern and western slopes of each of the three savanna hills. Sampling took place over a six week period, from June 6 to July 18, 2019, just before the burning period at the end of July 2019. The traps were organized in three transects of five traps per slope and spaced apart by more than 10 m to avoid interference (Topping & Sunderland, 1992). Each trap consisted of a plastic cylinder (14 cm height; 8 cm diameter) topped with a funnel and a rainproof structure. The traps were filled up to one third of their volume with a brine solution at a concentration greater than 265 g.L^{-1} to kill and preserve the trapped specimens. An unscented detergent was added to the brine solution to break the surface tension (Schmidt *et al.,* 2006). The weekly collected specimens were stored in 70 ° alcohol.

3.2   Morphospecies distinction and measurements: Because of the lack of taxonomical knowledge about Gabonese spiders and key species identification, morpho-species (MS) were defined based on morphological traits, mainly by observing the genitalia and habitus. The morphospecies were identified using a Carl Zeiss Stemi-305 cam model Stand K LAB stereomicroscope and Zeiss Labscope for

Windows software (version 3.0.1 of 24-04-2020). The specimens were identified and classified according to their morphospecies. Males and females were considered separately in order not to artificially increase morphospecific richness. The analyses focused on adult specimens. To ensure reliable identifications whatever the intra-specific variations (Derraik *et al.,* 2002), the morphospecies were separated by experienced arachnologists.

3.3   Statistical analyses

3.3.1   Sampling effort and alpha-diversity analyses: The expected species richness were estimated by using different nonparametric estimators: the abundance-based coverage estimator (ACE) (Chao & Yang 1993), the incidence-based coverage estimator (ICE) (Lee & Chao 1994), Chao1 and Chao2 (Chao 1984, 1987), and Jackknife 1 and Jackknife 2 (Burnham & Overton 1978, 1979). Sampling efficiency, expressed in percentages, was calculated as the number of observed morphospecies divided by the number of estimated morphospecies. The mean values of morphospecific richness and abundance between transects and between slopes were tested using the non-parametric Kruskal-Wallis test (KW). Rank-abundance and UpSet diagrams (Lex *et al.,* 2014) were drawn to visualize the dominant morphospecies and the distribution of the morphospecific compositions sites, respectively.

3.3.2   Taxonomical beta-diversity analyses: β taxonomic diversity (e.g. diversity among communities) calculated with the Jaccard dissimilarity index was quantified by measuring the differences between each pair of transects (by summing the samples collected for each row of five traps). This index constitutes a common metric of taxonomic β diversity, and is suitable for a small dataset (Schroeder & Jenkins 2018). Both turnover and nestedness were calculated from this index to measure the extent of the differences in species composition between communities. A non-metric multidimensional scaling (NMDS) type analysis was performed to visualize taxonomic β diversity per transect. This ordination method represents the dissimilarity between several objects in a low-dimensional space with a high degree of robustness (Buttigieg & Ramette, 2014). Then, a multivariate analysis of variance by permutations (PERMANOVA; 10,000 permutations) was applied on the Jaccard dissimilarity matrices to verify whether the communities differed according to the hills, the orientation, the slopes or the transects, and to identify the main sources of variation by evaluating the part of the variance explained by each variable.

3.3.3   Functional beta-diversity analyses: Functional traits were selected so that they could be easily determined by non-specialists. Based on the previous works by Cardoso *et al.,* (2011), Gonçalves-Souza *et al.,* (2015) and Joseph *et al.,* (2018), a set of four functional traits including response traits and effect traits were considered, i.e., body compression (continuous variable: length of the prosome multiplied by its width), velocity (continuous variable: length of the longest paw divided by body length), guild (categorical variable: ground hunters, other hunters, sheet web weavers, space web weavers, ambush hunters), and ocular dimorphism (categorical variable: present, absent). These traits can provide information on the dispersal activity, velocity, hunting strategy, the type and size of consumed prey and microhabitat selection. For continuous data, all available character values were averaged per morphospecies. For discontinuous data, the dominant category of each trait for each morphospecies was used. Gower's metric was chosen to measure the functional dissimilarity between morphospecies from the previously cited traits because it allows the use of qualitative traits and tolerates missing values (Podani & Schmera, 2006). The functional groups were partitioned according to the k-means method, and the optimal number of functional groups was obtained by a consensus between the techniques of Gap statistic (Tibshirani *et al.,* 2001), of the silhouette coefficient (Kaufman & Rousseeuw, 1990) and elbow. Two dendrograms were constructed using functional distances according to the Ward method (Ward2 algorithm; Murtagh & Legendre, 2014). Once the functional groups were determined,

functional β diversity was quantified using the same methods as those used for taxonomic β diversity (Jaccard dissimilarity index decomposed into turnover and nestedness NMDS and PERMANOVA). All analyses were performed using R software (R Core Team, 2020). Sampling efforts were assessed with the "fossil" package (Vavrek, 2011). The handling of trait matrices and identification of functional groups were done using the package "cluster" (Maechler *et al.,* 2019). The measures of beta diversity were made with the "vegan" package (Oksanen *et al.,* 2017) and the "betapart" package (Baselga and Orme 2012).

4   RESULTS
4.1   Sampling effort: A total of 345 adult spiders (215 females and 130 males) was collected, belonging to 12 families and 97 morphospecies (66 female morphospecies; 31 male morphospecies). About 50% of the morphospecies were collected with a high proportion of singletons (33 female singletons; 15 male singletons). The most abundant families were *Lycosidae* (54.2 %), *Gnaphosidae* (18 %), *Salticidae* (9.6 %) and *Corinnidae* (5.8 %). The six morphospecific accumulation curves calculated for the six slopes (Fig. 1) show a constant increase of the number of morphospecies, with a higher rate of accumulation of female morphospecies in all cases. For all slopes merged, the mean value of the sampling efficiency was 69.6% and 71.2% for females and males, respectively, suggesting that the sampling effort was just about sufficient to characterize a global spider community of the savanna hills. However, the completeness rates showed a significant variation among slopes (table 1) with minimum values of 13% (slope 5) and 25%

(slope 6) and maximum values of 80% (slope 6) and 81 % (slope 5) for females and males, respectively, suggesting that sampling completeness was very uneven depending on the slope.

3.2   Morphospecific approach: No statistical difference was observed between the mean numbers of female and male morphospecies per trap per transect (KW test: 9 ± 0.71, df = 17, p> 0.005, and KW test: 5 ± 0.50, df = 17, p> 0.005, respectively) or according to the slope (KW test: 23 ± 1.72, df = 5, p> 0.005, and KW test: 11 ± 0.79, df = 5, p> 0.005, respectively). Eight out of 66 morphospecies (5 *Lycosidae*, 1 *Gnaphosidae*, 1 *Corinnidae*, 1 *Scytotidae*) represented nearly 50% of the total abundance of females, while three out of 31 morphospecies (1 *Gnaphosidae*, 2 *Lycosidae*) represented nearly 50% of the total abundance of males (Fig. 2). Except for one *Scytodidae*, these morphospecies belonged to three of the most abundant families (*Lycosidae, Gnaphosidae, Corinnidae*).

Table 1. Observed morphospecific richness (MSR); minimum, mean and maximum values of completeness (expressed in %) per slope (1 to 6) and for all slopes merged together (total).

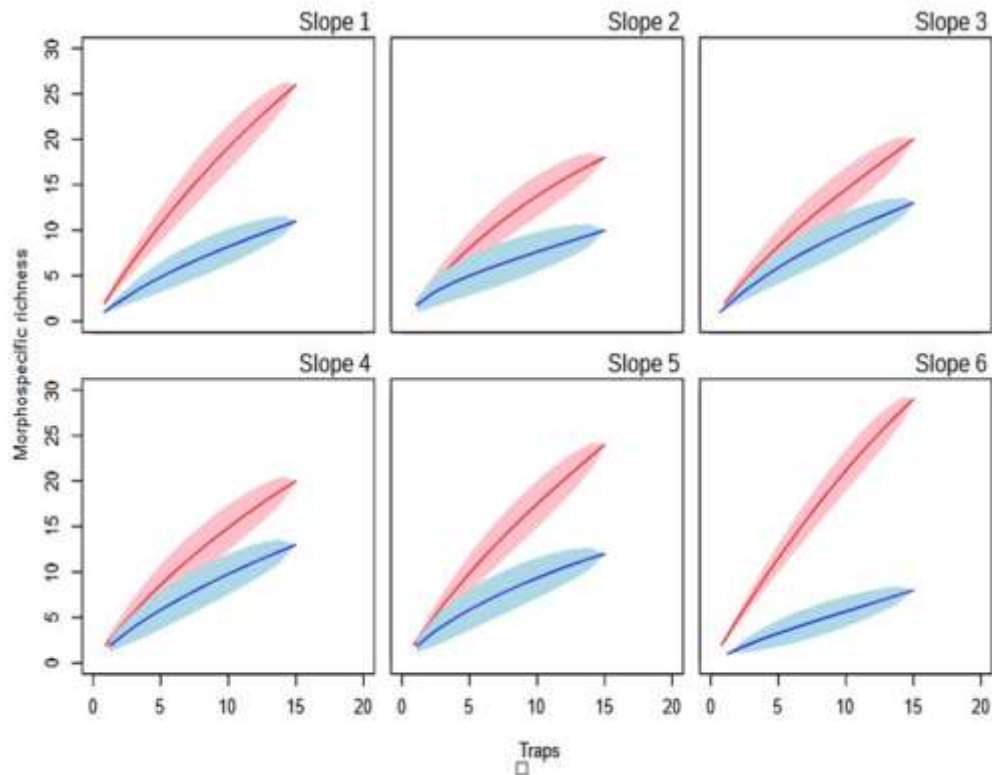|	Slopes	MSRobs	Minimum	Mean	Maximum
Females	1	26	33	50	78
	2	18	53	63	80
	3	20	14	44	77
	4	20	47	58	79
	5	24	13	46	78
	6	29	27	49	78
	Total	66	55	70	83
Males	1	11	42	53	78
	2	10	34	59	80
	3	13	26	53	79
	4	13	41	56	79
	5	12	54	67	81
	6	8	25	42	76
	Total	31	58	71	83

Figure 1. Accumulation curves for female (red) and male (blue) morphospecies. 95% confidence intervals are represented by the blue and red areas.

No statistical difference was found between the mean abundance of males per trap per transect (KW test: 0.047 ± 0.03, df = 17, p> 0.005) or according to the slope (KW test: 0.047 ± 0.03, df = 5, p > 0.005). The mean abundance of females did not differ per trap or per transect (KW test: 0.036 ± 0.02, df = 17, p> 0.005) or according to the slope (KW test: 0.036 ± 0.02, df= 5, p > 0.005). The community composition of the six slopes varied strongly (Fig. 3). The communities of slopes 5 and 6 included the greatest number of unique female morphospecies, i.e., sampled only on one slope. The community of slope 1 included the greatest number of unique male morphospecies (four morphospecies). A few morphospecies were common to certain slopes (1 to 3 for females; 1 or 2 for males) or to all slopes (3 for females; 2 for males).
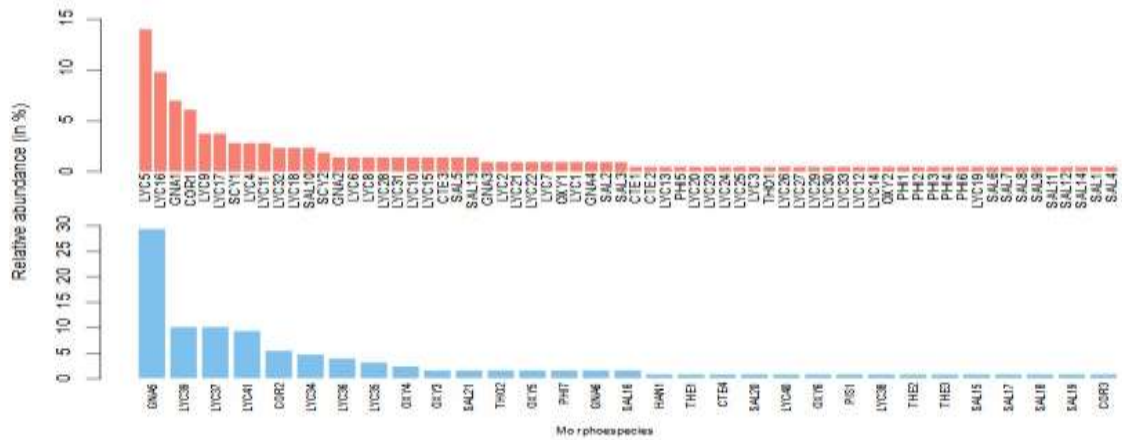
Figure 2. Rank-abundances of female (pink) and male (blue) morphospecies. COR = *Corinnidae*;
CTE = *Ctenidae*; GNA = *Gnaphosidae*; HAN = *Hahniidae*; LYC = *Lycosidae*; OXY = *Oxyopidae*;
PHI = *Philodromidae*; PIS = *Pisauridae*; SAL = *Salticidae*; SCY = *Scytodidae*; THE = *Theridiidae*; THO = *Thomisidae*.
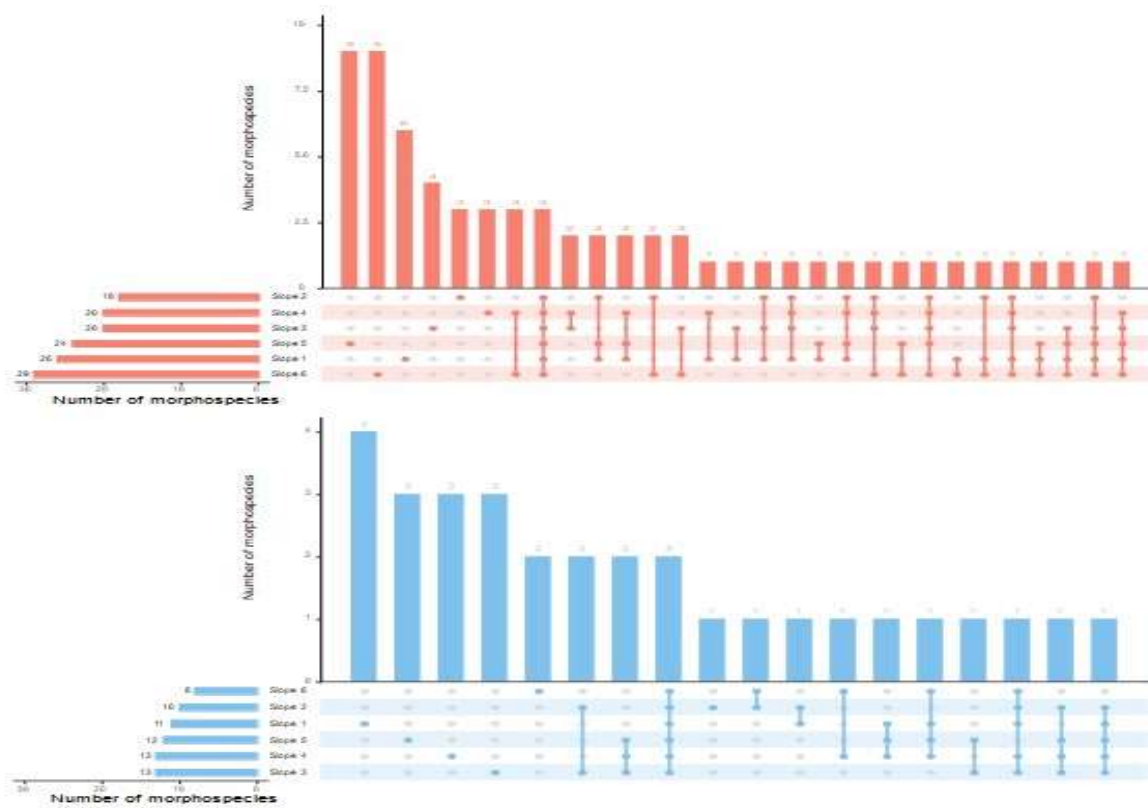

Figure 3. UpSet diagrams of females (pink) and males (blue). The matrix indicates whether the
morphospecies are common to several slopes (several points connected by a line) or specific to one slope (one
isolated point), while the vertical bars represent the number of morphospecies specific (one point) or common
to several slopes (several points connected by a line) . The horizontal bars represent the number of
morphospecies determined per slope.

3.3   Determination of functional groups:
After partitioning, four functional groups including different morphospecies were determined among females (Fig. 4). They were composed of four morphospecies from two families (*Philodromidae, Scytodidae*) for group A, five morphospecies from two families (*Corinnidae, Gnaphosidae*) for group B, 24 morphospecies from five families (*Ctenidae,*

Oxyopidae, Philodromidae, Salticidae, Thomisidae) for group C, and 33 morphospecies (*Lycosidae*) for group D. Four functional groups were determined among males: group E included eight *Lycosidae,* group F included one *Pisauridae* and two *Theridiidae,* and group G included eight morphospecies (*Corinnidae, Gnaphosidae, Hahniidae, Philodromidae, Theridiidae*).
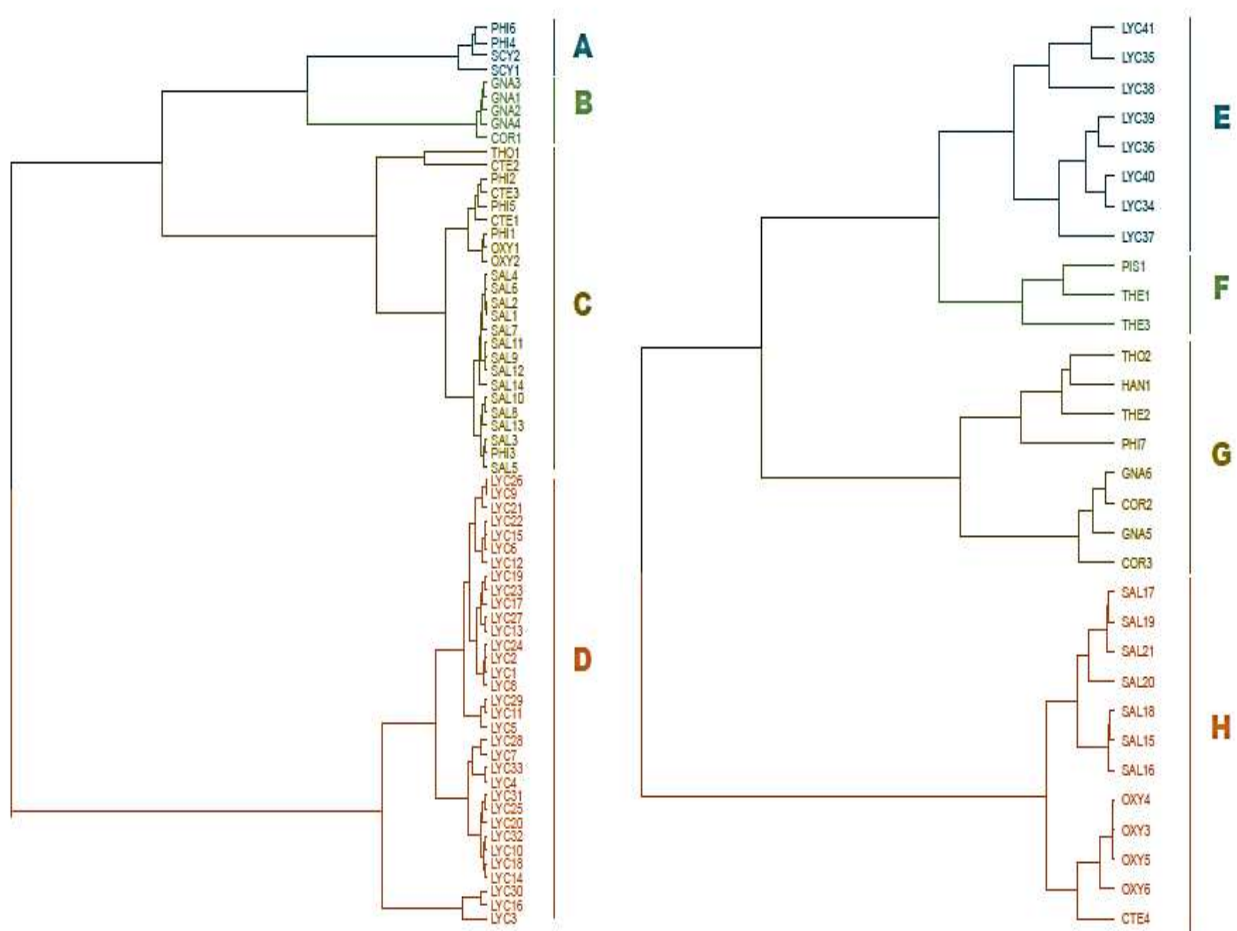

Figure 4. Dendrogram showing the functional group compositions of females (left) and males (right). Each letter designates a separate functional group.
COR = *Corinnidae* ; CTE = *Ctenidae*; GNA = *Gnaphosidae*; HAN = *Hahniidae*; LYC = *Lycosidae*;   OXY = *Oxyopidae*; PHI = *Philodromidae*; PIS = *Pisauridae*; SAL = *Salticidae*; SCY = *Scytodidae*;   THE = *Theridiidae*; THO = *Thomisidae*.

3.4 Taxonomic and functional β diversity: The values of the Jaccard dissimilarity index were 0.956 and 0.946 for morphospecies females and males, respectively. Likewise, the turnover rates were very high (0.943 and 0.918, respectively) for very low nesting rates (0.013 and 0.028, respectively). These results imply very strong dissimilarities in the taxonomic composition of communities on all slopes, in line with the large number of singletons and the low proportion of morphospecies in common between slopes. Based on the stress values given for each sex, the NMDS showed a clear separation of the spider communities of the different transects and slopes in terms of morphospecific composition (Fig. 5): none of the 18 sampled transects was markedly distant,

but none of them overlapped or clustered either. These results corroborate those of the Jaccard dissimilarity index and the UpSet plots (Fig. 3), as well as those of the turnover and nesting rates. For functional groups, the NMDS showed less marked separation of communities in males and females with some overlapping transects (Fig. 6). The values of the jaccard dissimilarity were 0,879 and 0,795 for functional groups females and males respectively. Rates of functional turnover (0.739 and 0,467 respectively for females and males) were lower than the ones of the taxonomic turnover. Nesting rates of functional groups (0.140 and 0.328 respectively for females and males) were higher than nesting rate for morphospecies.
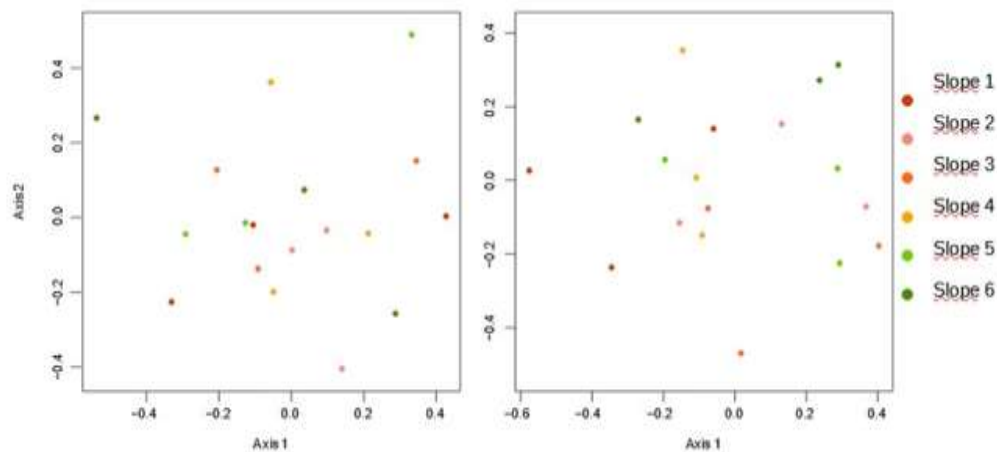

Figure 5. nMDS ordination plots of the morphospecies composition of female communities (left) and male communities (right) based on a Jaccard dissimilarity index with points identified according to transects. Stress values: 0.155 (females); 0.158 (males).
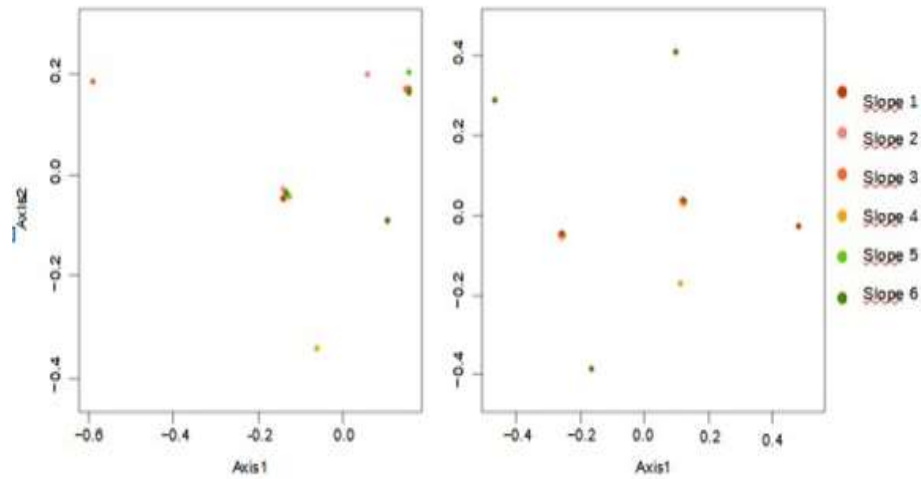
Figure 6. nNMDS ordination plots of the functional groups of female (left) and male (right) 250 communities based on a Jaccard dissimilarity index with points identified according to transects. Stress values: 0 (females); $4.75 10^{-5}$ (males).

The non-significant results of the PERMANOVA also revealed that there was no effect of the orientation of the slopes or of the slope itself on the taxonomic or functional composition of the spider communities of each transect line (table 2). Moreover, taxonomic β diversity did not differ for all the groups of females and males (table 3). Concerning functional β diversity, only the functional groups of males showed a heterogeneous dispersion (p = 0.04) possibly related to the orientation of the slopes.

Table 2. Effects of several variables on the taxonomic and functional β composition of spider communities (PERMANOVA; 10,000 permutations)

		Taxonomic				Functional			
		df	F	R²	P	df	F	R²	P
	Variables								
	Hills	2	0.88	0.10	n.s	2	0.63	0.08	n.s
Females	Orientation	1	1.15	0.07	n.s	1	0.50	0.03	n.s
	Slopes	5	0.84	0.26	n.s	5	0.54	0.18	n.s
	Hills	2	0.97	0.11	n.s	2	1.22	0.14	n.s
Males	Orientation	1	1.22	0.07	n.s	1	2.06	0.11	n.s
	Slopes	5	1.23	0.34	n.s	5	1.00	0.29	n.s

. df: degree of freedom; F: Fisher distribution; R²: explained part of the variance; P: p-value (significance level p = 0.05).

Table 3. Effects of several variables on taxonomic and functional β dispersal of spider communities (999 permutations; significance level p = 0.05).

	Variables	Taxonomic		Functional	
		F	P	F	P
Females	Hills	0.65	n.s	1.67	n.s
	Orientation	0.01	n.s	0.62	n.s
	Slopes	0.12	n.s	1.46	n.s
Males	Hills	0.65	n.s	1.40	n.s
	Orientation	0.01	n.s	5.17	0.04
	Slopes	0.12	n.s	1.26	n.s

ddf: degree of freedom; F: Fisher distribution; R²: explained part of the variance; P: p-value.

4 DISCUSSION

At regional or national spatial scales, spider communities in Afrotropical savannas show marked differences in taxonomic composition depending on the type of savanna or the land use (Russell-Smith, 2002; Muelelwa et al. 2010; Foord *et al.,* 2011, 2013; Joseph *et al.,* 2018). At a fine spatial scale, this study reveals a significant turnover of ground-dwelling spider communities in six contiguous and similar savanna plots. The functional structure of communities was characterized on the basis of functional traits measured on morphospecies. Therefore, we show that this two aspects of biodiversity can give two aspects of the spider communities, hence, the importance of using both taxonomic and functional group approaches to evaluate the effects of land-use change on biodiversity in savanna system. Despite the high turnover rate of morphospecies among savanna plots, our study shows significant functional redundancy across plots and across hillsides.

4.1 Sampling completeness: For most of the plots, estimated morphospecific richness was higher than observed richness. This reflects the over-representativeness of singletons in the surveys. This result is frequent in tropical ecosystems (Novotný & Basset, 2000) and classically reflects under-sampling (Coddington *et al.,* 295 2009). In tropical ecosystems, the low catchability of species by traps is probably linked to the low levels of movement of species within their habitats. Moreover, the density of adult individuals is generally much lower than in temperate habitats (Privet *et al.,* 2018). On the other hand, persistent local management by fire may have resulted in long-lasting disruption of the community structure by influencing species equity. Considering the characterization of communities from a purely taxonomic viewpoint, one of the major results of this study is that the trapping pressure, in relation with the large surface area of each plot, should be considerably increased during the period under consideration, and certainly also during the other seasons because individuals of a same species may be active several times a year. An increased sampling pressure could also help to determine whether the taxonomic community differences between slopes are real or linked to the low catchability of the species. However, the "cost / benefit" ratio of ground trapping sampling will always remain a limiting factor for achieving a satisfactory completeness rate. The combination of trapping with another sampling method such as harvesting by mowing through herbaceous layers could also increase the diversity and representativeness of the sampled spiders and limit the biases associated with passive soil sampling. However, Yekwayo *et al* (2019) have demonstrated that wandering spiders were good candidate surrogates for monitoring post-fire recovery for instance.

4.2 Taxonomic analyses: The four dominant families (*Lycosidae*, *Gnaphosidae*, *Salticidae* and *Corinnidae*) correspond to those found in other studies carried out by pitfall trapping in other Gabonese savannas (Nguéma *et al.,* 2020) or in southern or central African savannas (e.g., Whitmore, 2000; Russell-Smith 2002; Whitmore *et al.,* 2002; Foord *et al.,* 2011, 2013; Muelelwa *et al.,* 2010; Joseph et al. 2018). The present study shows no transect or slope effect on the average number of morphospecies or the average number of trapped individuals. In contrast, we found a high turnover rate among plots, hence a low level of nestedness. This insight into the biodiversity of savanna spiders supports the results of other authors (Whitmore *et al.,* 2002; Parr *et al.,* 2014) stating that savanna biomes are likely to constitute "hyperdiversified" ecosystems for arthropods in general and spiders in particular. Based on semi-annual survey in central south African grasslands, Haddad et al. (2018) suggested that exposure of grassland hillsides may have a strong influence on shaping spider assemblages. We did not find such a result and any significant similarity in the composition of the spider communities between similarly oriented slopes. This is probably due to the short period of sampling and to the high representativeness of singletons in the samples.

4.3 Functional analysis: The functional group approach overcame the problems associated with the large proportion of singletons without particular constraints and presented a group validation method allowing a fairly satisfactory definition of functional groups based on the analysis of morphospecies. Functional β diversity appeared statistically different according to the slope orientation (west or east) for the male functional groups. Once again, given the low significance level (0.04), this result was probably an artefact of the initial dataset that contained a high proportion of singletons for a low number of morphospecies. Despite the lack of information on the biology of the sampled morphospecies, the selected traits distinguished a total of eight functional groups (four for females, four for males). The representativeness of the functional groups was not statistically different according to the slope. Despite some redundancy in the provided information, each trait described a specific aspect of the biology of the identified morphospecies. Consequently, the choice of functional traits in this study turned out to be relevant because they made it possible to characterize the functional components of the spider communities associated with the six savanna plots.

5 CONCLUSION

The local management methods of savanna more specifically based on the regular use of fire for agriculture, rearing, or conservation of vertebrate biodiversity (Nieman *et al.,* 2021, Mboumba *et al.,* 2021) inevitably leads to modifications of the vegetation structure of the savanna (Nieman *et al.,* 2022), while arthropods assemblages strongly depend on savanna composition (Botha *et al.,* 2016). Concerning specifically the use of fire local management, the impacts on spiders remain poorly understood in African savannas or grasslands (Haddad *et al.,*

2015, Uys *et al.,* 2006) especially as fires as frequent as it is the case in the selected study site. Despite these facts, this particular example showed that the resilience capacities of savanna spiders after fire events will be able to be analysed at several reference scales (from the slope to the entire savanna complex) based on morphospecies functional group analysis because there is significant functional redundancy between the six sampled savanna plots.

6 ACKNOWLEDGMENTS

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