SHORT COMMUNICATION

The African weaver ant has no negative impact on spiders in mango orchards of Senegal

Thibault Nève de Mévergnies^{1,2} | Anaïs Chailleux^{1,3,4} | Claire Detrain²¹Biopass, Cirad-ISRA-UCAD-IRD, Dakar, Senegal²Unit of Social Ecology, Université Libre de Bruxelles, Brussels, Belgium³Cirad, UPR HortSys, Dakar, Senegal⁴Cirad, Univ. Montpellier, Montpellier, France**Correspondence**Thibault Nève de Mévergnies, Biopass, Cirad-ISRA-UCAD-IRD, Dakar, Senegal.
Email: tneve@hotmail.fr**Funding information**

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1 | INTRODUCTION

Sustainable pest-control strategies aim to limit the abundance of pests through, for example, maintenance of their predators in the system. The use of multiple generalist predators can enhance pest control through additive or synergistic effects due to their complementarity (Letourneau et al., 2009). However, their presence can also lead to drawbacks such as off-target or intraguild predation (Rosenheim et al., 1995).

In many African agroecosystems, top predator effects on sympatric communities still await to be disentangled and effective sustainable control of invasive pests is lacking (de Bon et al., 2014; Grzywacz et al., 2014). In Senegal, mango production is devastated by an invasive pest, the oriental fruit fly *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), which is responsible for important economic losses (Vayssières et al., 2014). A solution has been implemented through the presence of the arboreal weaver ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) in large parts of Sub-Saharan Africa, including Senegal. Indeed, this generalist predator exerts aggressive control over its territories, which include multiple host trees such as mango and citrus, reducing the fly pest densities through predation and repellence (Diamé et al., 2015; Vayssières et al., 2016; Way, 1954). As dominant generalist predators, weaver ants are however responsible for negative interactions towards beneficial organisms such as some pollinators (Tsuji et al., 2004), parasitoids (Migani et al., 2017; Tanga et al., 2015) and a lynx spider (*Oxyopes* sp.) (Peng & Christian, 2013). While the positive impact of weaver ants on fruit yields suggests that the benefits they provide to crops usually outweigh the costs (Diamé et al., 2017; Thurman et al.,

2019), there is still a lack of knowledge about their interactions with other organisms within their trophic guild.

We thus investigated the interactions between *O. longinoda* and the Araneae community in Senegalese mango orchards. Indeed, spiders are abundant generalist predators (Nyffeler & Birkhofer, 2017) that naturally regulate arthropod pest populations and as such have been effectively used as control agents in many agroecosystems worldwide (Rajeswaran et al., 2005; Riechert & Lockley, 1984). We hypothesised that certain spider families suffer from competition and/or intraguild predation from the weaver ants in their overlapping territories. In particular, we expected that actively hunting spiders such as jumping spiders (Salticidae), or sac spiders (Clubionidae) would see their population numbers decrease as they potentially share the same hunting grounds and prey as the weaver ants.

2 | MATERIALS AND METHODS

2.1 | Study site and spider sampling

The Niayes region of Senegal is under Sahelian climate with unimodal rainfall (250–350 mm per year) from July to September. We sampled 10 mango orchards in this zone with similar characteristics (Appendix 1) in February 2020, during the dry season when trees are flowering. In each, we randomly selected three non-contiguous mango trees bearing distinct *O. longinoda* ant colonies, and three trees without ants. We evaluated the density of ants on each tree by counting the number of ants on trails on a 1 m portion of the main branches, following Pinkalski et al. (2015). We made sure that the

Ants	Habitat	N	S	Median s (Q1–Q3)	D	H
Yes	Canopy	297	53	12.5 (11.00–15.75)	0.928	3.170
	Ground	153	55	8.5 (8.00–12.75)	0.965	3.672
	Total	450	95	11.5 (8.75–14.2)	0.959	3.842
No	Canopy	280	51	12.5 (12.00–15.50)	0.950	3.358
	Ground	131	52	7.0 (5.25–9.50)	0.941	3.443
	Total	411	99	11.5 (6.75–14)	0.970	3.984

TABLE 1 Diversity indices for the spider communities depending on the habitat and the presence of the weaver ant

Note: "N" represents the total abundance of sampled spiders. "S" is the total morphospecies richness for each habitat when grouped for all sites. "Median s" is the median number of spider morphospecies per site with first (Q1) and third (Q3) quartiles. "D" is the GiniSimpson index and "H" is the Shannon-Wiener index for the overall sampled spider communities.

FIGURE 1 Rank-abundance curve (Whittaker plot) ranking the sampled spider morphospecies S in the canopy (a) or on the ground (b) by their abundance depending on the presence (black triangles) or absence (grey circles) of weaver ants

ants belonged to different colonies by assessing the characteristic aggressive behaviour they show towards alien conspecifics.

Per tree, three randomly chosen branches of similar volume, bearing foliage and flowers were beaten five times with a standardised stick over a hand-held 1 m² catching sheet. Spiders were caught on the sheet using a mouth aspirator and subsequently killed in 70% alcohol for further identification. Two pitfall traps (≈500 ml) were randomly placed under the canopy of each of the selected trees to sample the epigeic spider community. These were filled with water, 30% ethylene glycol and a drop of detergent to lower surface tension (Schmidt et al., 2006), then left on site for 72 h. Traps were emptied in the field through a sieve (2 mm mesh) to discard soil particles. All spiders were collected and placed in a 70% ethanol solution,

and then brought to the laboratory for identification. Due to the lack of literature about Senegalese spiders, specimens were identified to family level and placed in morphospecies categories based on keys from Jocqué and Dippenaar-Schoeman (2007).

2.2 | Statistical analysis

We discarded families with a total sum of individuals per habitat (arboreal or epigeic) of less than six individuals. In addition to the morphospecies richness (S) and the abundance of spiders per family and morphospecies, we calculated two standard diversity indices to evaluate the impact of the presence of ants in each orchard: first,

the GiniSimpson (D) index that quantifies the probability that two individuals taken randomly in a sample belong to two different species (the higher the D value the more diverse the community), and second, the Shannon index (H) that quantifies the equitability of the distributions of the sampled morphospecies (the higher H the more uniform the distribution of relative abundance of morphospecies). To compare these diversity indices grouped per orchard and per habitat depending on the presence of ants, we used non-parametric Wilcoxon rank-sum tests due to non-Gaussian data distribution. Generalised linear mixed models with a Poisson distribution and a log link were implemented to investigate whether the presence of weaver ants (as a fixed factor) influenced the total abundance of the spiders. Then, we carried out permutational multivariate analyses of variances (PERMANOVA) to detect possible effects of weaver ants on the composition of spiders when being considered at the family level. These PERMANOVA analyses were made separately for the canopy and for the ground communities of spiders. Finally, we generated GLMMs to further study the impact of the weaver ant on the abundances of certain spider families or morphospecies of potential interest for their role in biological control. The variable orchard was set as a blocking random factor in all the models. For the spider abundances at family and morphospecies level, we presented results only when a significant difference was detected linked to the presence of weaver ants. All analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the RStudio interface (RStudio Team, 2020) and the packages ggplot2 (Wickham, 2016), lme4 (Bates et al., 2015), BiodiversityR (Kindt & Coe, 2005) and vegan (Oksanen et al., 2019). All results are statistically significant at a 95% confidence level ($\alpha = 0.05$).

3 | RESULTS

All sampled trees bearing ants ($n = 30$) were colonised with an average of 6254 (± 6237 SD) major workers per m^3 of canopy. We sampled 577 spider individuals from the mango canopies, and 284 in the pitfalls, to a total of 861 individuals. The spiders belonged to 133 morphospecies representing 17 families. Ninety-five different morphospecies were found in areas where weaver ants were present and 99 in areas where they were absent (Table 1). The most represented families were the jumping spiders Salticidae (25 morphospecies out of 114 sampled individuals). These included *Myrmarachne* spp. ant mimics. This was followed by the crab spiders Thomisidae (22 morphospecies out of 224 sampled individuals) and the orb weavers Araneidae (19 morphospecies out of 133 sampled individuals) (Appendix 2).

The rank-abundance curves showed no difference linked to the presence of weaver ants (Figure 1a,b). Two morphospecies (Thomisidae_4 and Clubionidae_2) were dominant in the canopy regardless of ant presence (Figure 1b). On the ground, one morphospecies of Gnaphosidae followed by another Lycosidae morphospecies were dominant both in the presence and absence of the weaver ant (Figure 1).

The presence of weaver ants had no significant impact on the total abundance of spiders that were collected per mango tree. This was true in the canopy and on the ground (Table 1. GLMM, p -values $> .05$). The diversity indices of the spider community showed no significant differences between orchards relating to the presence of ants, neither in the canopy nor on the ground (Table 1. $n = 10$; Wilcoxon, p -values $> .05$). At the family level, the composition of the spider communities was not impacted by the presence of the weaver ant whether in the canopy (PERMANOVA, $F = 0.641$, p -value $> .05$) nor on the ground (PERMANOVA, $F = 1.086$, p -value $> .05$).

A closer examination of the ants' impact on each family of spiders revealed an abundance of clubionids in the canopy that was significantly higher when weaver ants were present (Figure 2a GLMM, $\chi^2 = 8.69$, p -value = .003). Similar results were found on the ground (Figure 2b GLMM, $\chi^2 = 4.32$, p -value = .038). Ants had no significant impact on the abundances of the other families, whether in the canopy or on the ground (Figure 2 GLMM, p -values $> .05$).

When considering each morphospecies in the tree canopy, the presence of weaver ants led to a significant increase in the abundance of one morphospecies of araneid (Araneidae_7) (Figure 3a GLMM, $\chi^2 = 4.32$, p -value $< .001$) and of one clubionid (Clubionidae_2) (Figure 3b GLMM, $\chi^2 = 10.8$, p -value $< .001$). On the ground, there was a significant decrease in the abundance of a Lycosidae (Lycosidae_12) when in the presence of the weaver ant (Figure 3c GLMM, $\chi^2 = 5.86$, p -value = .015). For the other morphospecies, no significant differences in their abundances were detected relating to the presence or absence of the weaver ant (GLMM, p -values $> .05$).

4 | DISCUSSION

We expected a general decline of sympatric spiders due to resource competition (Vayssières et al., 2015) and intraguild predation (Rosenheim et al., 1995) from the weaver ants, since they are highly aggressive, territorial and able to hunt prey of a similar size range as the spiders' ones (Hölldobler, 1979; Hölldobler & Wilson, 1990; Wojtusiak et al., 1995). Furthermore, the occurrences of top predators similar to the weaver ants who affect the global composition of a community are commonly reported, for instance with the fire ant (Porter & Savignano, 1990) or with carpenter ants (Mody & Linsenmair, 2004). However, in mango orchards of Senegal, our preliminary study reveals that weaver ants do not deter spiders whose total abundance remains unaltered by their presence. Neither had weaver ants any impact on the global composition of the spider families whether in the canopy or on the ground. When considering separately each spider family and morphospecies, we found no negative impact on their abundances linked to the presence of the weaver ant, apart for a small lycosid on the ground. More surprisingly, the presence of the ant in tree canopies even resulted in an increase in the abundance of araneid, clubionid and salticid spiders, though not significant for the latter. A similar result, at a wider arthropod community scale, was found in Australia with their sister

FIGURE 2 Abundance per family of spiders in each canopy (a) or ground (b) sample depending on the presence (white bars) or absence (black bars) of the weaver ant. Values and bars represent mean abundances per sample for each spider family. Error bars represent standard error SE. $n = 30$ observations per group. The asterisk indicates significant differences between the abundances of spider families when in the presence or absence of the weaver ant after a GLMM. p -value $< .001 = **$, p -value $< .05 = *$

species *Oecophylla smaragdina* (Fabricius) (Peng & Christian, 2013). Likewise, in coffee agroecosystems, abundance and diversity of spiders were higher when the ant *Azteca instabilis* (F. Smith) was present (Marín & Perfecto, 2013). The reasons behind this neutral to positive impact are probably multifactorial.

First, spiders can evade ant predation due to their multiple escape strategies (Cloudsley-Thompson, 1995). For instance, araneids add alkaloids in their silk, deterring ants from foraging on their webs (Zhang et al., 2012). Different day-night cycles of activities, such as in the nocturnal clubionid spiders, reduce the probability of agonistic encounters with the mainly diurnal weaver ant (Dejean, 1990). In contrast, salticids possess efficient vision-based detection allowing early flight when in danger (Stankowich, 2009).

Second, competitive exploitation is probably limited due to resource partitioning between ants and spiders (Roughgarden, 1976). During the dry season, weaver ants essentially feed on honeydew produced by their hemipteran trophobionts (Vayssières et al., 2015), a resource that is usually of no interest to the spiders. Furthermore, ants cannot catch flying insects such as adult Diptera which are the main prey of many spiders such as web weavers or active hunters on the foliage (Michalko & Pekár, 2016).

Noticeably, some spiders can directly benefit from the presence of the ants through myrmecophagy (Cushing, 2012). This is the case for certain *Myrmarchne* spp. (see Figure 3d) that can

show specific hunting strategies towards Formicidae and that may behave as inquiline species, feeding on ant larvae inside their nests (Edmunds, 1978; Wanless, 1978). These salticids can also indirectly benefit from occurring in sympatry with the weaver ant, as they appear to be Batesian mimics and hence supposedly gain protection from predators in their vicinity (Collart, 1941; Wanless, 1978).

One should also consider possible indirect benefits for spiders derived from the weaver ant's mutualism with their hemipteran trophobionts (Way, 1963). Indeed, homopterans attract honeydew-feeding insects (Hung et al., 2015; Johnson & Stafford, 1985), thereby increasing prey abundance, ultimately attracting and favouring entomophagous predators including spiders (Harwood et al., 2003; Wise, 1993). Occasionally, the ant-mimicking *Myrmarchne* may even feed directly on honeydew, a diet perhaps not limited to this species (Nyffeler et al., 2016; Wanless, 1978).

Lastly, ants are important ecosystem engineers, generating new habitats that can host other organisms (Sanders & van Veen, 2011). Abandoned woven leaf nests of *O. longinoda* may become refuges to certain spiders, such as some salticids and clubionids (Nève de Mévergnies, pers. obs., February 15 2020).

In conclusion, our study shows that the presence of *O. longinoda* in mango tree canopies has no negative, but rather a positive impact on the arboreal spider community. Diversity of spider

FIGURE 3 Abundance per morphospecies of (a) Araneidae, (b) Clubionidae and (c) Lycosidae in the canopy (a and b) or on the ground (c) depending on the presence (white bars) or absence (black bars) of the weaver ant. Values and bars represent mean abundances per sample for each spider morphospecies. Error bars represent standard error SE. Only morphospecies with a total abundance of $N > 5$ were retained. $n = 30$ observations per group. The asterisk indicates significant differences between the abundances of spider morphospecies when in the presence or absence of the weaver ant following a GLMM. p -value $< .0001 = ***$, p -value $< .05 = *$. Picture insert represents a female (top) and a male of *Myrmarachne* sp. spider sampled in presence of the weaver ant. Scale bar represents 1 mm

morphologies and hunting strategies (web weavers, ambush hunters and active hunters) are therefore preserved and even reinforced. Co-occurrence of spiders and weaver ants in overlapping and/or adjacent trophic niches may thus extend and increase their predatory control over several pests, including *Bactrocera* flies which they prey upon (Kaspi, 2000; Picchi et al., 2015; Whitman et al., 1988). Further studies should investigate possible synergistic effects between spiders and weaver ants for the biological control of pests such as *B. dorsalis* fruit flies, with ants being more efficient at capturing *Bactrocera* at the egg or larval stage on the mango fruit (Vayssières et al., 2015), and spiders better regulating the winged adults on the foliage.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare in relation to this work.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

ORCID

Thibault Nève de Mévergnies <https://orcid.org/0000-0003-2608-7805>

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APPENDIX 1

TABLE A1 Localisation and description of the sampled orchards

Orchard	Location	Latitude, Longitude	Crop diversity
1	Keur Sega	14°48'25.14"N, 17° 7'8.43"W	Mango trees and citrus
2	Keur Moussa	14°46'24.35"N, 17° 6'31.00"W	Mango trees and citrus
3	Deni Biram Ndaw	14°50'26.05"N, 17°10'6.72"W	Mango trees, citrus and vegetables
4	Deni Biram Ndaw	14°50'24.10"N, 17°10'6.43"W	Mango trees, citrus and vegetables
5	Khaye	14°46'30.02"N, 17° 5'10.84"W	Mango trees, citrus and vegetables
6	Sangalkam	14°47'21.01"N, 17°13'37.76"W	Mango trees, citrus and vegetables
7	Sangalkam	14°47'26.80"N, 17°13'40.63"W	Mango trees, citrus and vegetables
8	Khaye	14°46' 35.48"N, 17° 5' 4.21"W	Mango trees and citrus
9	Bayakh	14°50'35.35"N, 17° 7'10.77"W	Mango trees
10	Bambilor	14°48'14.93"N, 17°12'34.80"W	Mango trees

APPENDIX 2

TABLE A2 Composition of the sampled spider families in terms of morphospecies and total abundance. "MS" is the total number of spider morphospecies, and *N* is the total abundance for each sampled family

Family	MS	<i>N</i>
Araneidae	19	133
Clubionidae	5	95
Ctenidae	3	16
Corinnidae	4	12
Dictynidae	2	5
Gnaphosidae	14	86
Lycosidae	13	70
Miturgidae	2	4
Oxyopidae	7	63
Palpimanidae	2	3
Philodromidae	2	12
Pholcidae	1	1
Salticidae	25	114
Scytodidae	1	5
Therididae	1	1
Thomisidae	22	223
Uloboridae	3	5
Unknown	9	13