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Effects of 12 crops associated with plantain on arthropods trophic groups and *Cosmopolites sordidus* abundance

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Abstract

The control of pests and diseases is one of the main challenges of sustainable agriculture. Plantains, with an annual production of nearly 12 million tons, are a significant staple food crop in West and Central Africa, as well as in Central America. *Cosmopolites sordidus* is the major pests for plantains and is present in all production areas. This study assessed how the traits and associated agricultural practices of 12 crops, usually associated with plantains in Cameroun, affected the arthropods trophic network and *C. sordidus* abundance. The abundance and the diversity of arthropods in experimental plots associating plantains with each of the 12 tested crops were measured. Each associated crop was described by a unique profile of traits and agricultural practices. This 'trait' approach allowed linking the plant characteristics to the abundance of arthropods from different trophic groups. Structural equation modelling was used to analyse the interactions between associated crops traits, their associated agricultural practices and the abundance of main trophic groups. The highest abundance of *C. sordidus* was observed in plots with *Ananas comosus* and *Xanthosoma sagittifolium* as associated crops. These plots also had the lowest abundance of omnivores and predators. In contrast, plots with the lowest abundance of *C. sordidus* were those with weeds and *Vigna unguiculata*, where more omnivores and predators were observed. Grouping associated crops by their traits and agricultural practices allowed for drawing conclusions on a wider range than the set of plants tested. For instance, this study showed that plants from the higher strata tend to decrease ground-dwelling predators. The ideal crop traits and agricultural practices to maximize the regulation of *C. sordidus* should not be obtained by a single species of crop but rather by a community of associated crops.

KEYWORDS
agroecology, arthropod food webs, Cameroon, multitrophic interactions, *Musa* spp, pest control, plantain

1 | INTRODUCTION

The control of pests and diseases is one of the main challenges of sustainable agriculture. Enhancing plants diversity in agrosystems is an important lever to increase pest regulation (Ratnadass et al., 2012), especially by enhancing regulating communities, including pest predators and parasitoids. Intercropping strongly influences the whole arthropods community in terms of composition and of trophic interactions, thus altering their interactions with the pests (Letourneau et al., 2011). The regulation mechanisms at stake are complex, but understanding them is necessary to optimize the plants associations in order to enhance pest control. This is particularly important in the case of tropical agrosystems, where the range of possible plant associations and the diversity and abundance of arthropods are large (Brown et al., 2001).

With almost 12 millions of tons produced annually (Lescot, 2023), the plantain is a major staple food crop in West and Central Africa, as well as in Central America. It is often associated with other food crops, coffee or cocoa trees, leading to highly diverse agrosystems (Temple & Kwa, 2019; Zúniga-Gonzalez & Caballero-Hernández, 2024). Among the food crops associated with plantains, some have a short cycle and are planted during several periods of the year (*Arachis hypogaea*, *Zea mays*, *Vigna unguiculata*, etc.), others have a cycle of about 6 months and can only be associated during the rainy seasons (*Ipomoea batatas*, *Solanum nigrum*, *Xanthosoma sagittifolium*, etc.) Some food or cash crops persist more than a year (*Manihot esculenta*, *Theobroma cacao*, *Carica papaya*, etc.) To date, there is limited knowledge on the effect of these different associated crops on the arthropods' community in plantain fields, and ultimately on the regulation of its pests. With climate changes, there is a necessity to conceive more resilient cropping systems. This involves a better understanding on the regulation services sustained by the crops associated with plantain.

Cosmopolites sordidus is the major pest for plantains and is present in all production areas (Blomme et al., 2020; Dassou et al., 2023). The larva of *C. sordidus* feeds exclusively on the banana or plantain corm, creating galleries. The attacked corms produce fewer roots, which compromise the anchorage of banana in the soil. Damaged plants grow slower and can die in case of severe attacks (Gold et al., 2001). In Cameroon, *C. sordidus*, combined with nematodes, is responsible for up to 40% of yield loss in plantain fields (Dépigny et al., 2019). The adults of *C. sordidus* disperse in banana fields, laying eggs on banana plants. While it is the main biotic constraint of plantain production, the control of *C. sordidus* in these systems remains poorly studied.

A recent review highlighted the dramatic need for studies to better understand the natural control of *C. sordidus* (Tresson et al., 2021). Mollot et al. (2014) have proven, in export banana systems, that the ant *Pheidole* spp. and the earwig *Euborellia caraibea* can predate *C. sordidus*. In diversified plantain systems, Dassou et al. (2016) showed a correlation between plant diversity and abundance of arthropods trophic groups in plantain fields, with a positive correlation between the abundances of omnivores and predators' trophic groups with plant diversity. These authors showed that intercropping influences ants' abundance, which contributed to the control of *C. sordidus*, but the effect of intercropped plant species remained unclear (Dassou et al., 2015). In export banana systems, there was clear evidences that the presence of grasses dramatically increases the predation of *C. sordidus* eggs by ants (Mollot et al., 2012), but understanding the role of the characteristics of the associated plant in the regulation remains difficult to address. Some plant characteristics (e.g. C3 vs. C4 weeds) were shown to alter the trophic level of predators and thus their potential of regulation of *C. sordidus* (Tixier et al., 2013).

This study assessed how the traits and associated agricultural practices of 12 crops, usually associated with plantains in Cameroun, affected the arthropods trophic network and *C. sordidus* abundance. A better knowledge of natural control of *C. sordidus* in diversified cropping systems may help designing agroecological cultivation systems. An original 'trait' approach was developed to decipher the effect of plant characteristics (biophysical traits and associated agricultural practices) on the multi-trophic structure of the arthropod community. This approach is an attempt to go beyond the species identity effect. In the first step of analysis, the 12 crops were described through their respective position on the axes of a multiple correspondence analysis (MCA) that was constituted using plant traits. Then, the characteristics of the associated crops, as defined by their positions on the MCA axes, were correlated with the abundance of arthropod trophic groups, including *C. sordidus*. Finally, it conducted a comprehensive examination of the multi-trophic relationships using a Structural Equation Model, thereby providing an integrative perspective on the complex interplay between plant traits and arthropod communities.

2 | MATERIALS AND METHODS

2.1 | Location and experimental design

The experiment took place in a plot located in the Littoral region of Cameroon, city of Njombé (GPS 4°34′11.9″ N 9°38′46.8″ E). The soil is a rich brown andosol (Combroux, 1957). The climate is Equatorial Guinea type with an average mean temperature of 26–28°C and an average annual rainfall of 2300–3200 mm (mainly distributed from March to October). The field was irrigated from November to February, with 35 mm weekly.

The experiment was set up in July 2015 with the planting of the associated crops, followed the planting of the plantains (*Musa* spp., AAB plantain subgroup, "Mbouroukou n°3" variety) in August 2015. The data were collected 13 months after planting (during the month of September). The associated crops chosen for the experiment are listed in Table 1. These associated crops were chosen for their importance as food crop in Cameroun, their aptitude to grow in the area, and their diversity in terms of cycle length and capacity to fix nitrogen for some of them.

The field was divided into elementary plots of 12 × 10 m, each consisting of six plantains and one of the 12 associated food crops or

TABLE 1 Values of the traits and associated agricultural practices of the 12 intercrop species tested in this study.

Intercrop species	Woody [a]	Nfix+ [b]	Creeping [a]	Hairy [a]	Flowery [a]	Annual [b]	Tall [a]	C/N [c]	Cycle length (month)[a]	Weedings (n.)[a]	Litter+ [a]
Ananas comosus					✓			51	18	5	
Arachis hypogaea		✓				✓		16	3	8	✓
Cajanus cajan	✓	✓			✓		✓	32	18	1	✓
Colocasia esculenta								34	7	4	✓
Cucumeropsis manii			✓	✓	✓	✓		10	5	7	✓
Glycine max		✓		✓	✓	✓		13	4	7	
Ipomoea batatas			✓					38	6	7	✓
Manihot esculenta	✓						✓	24	18	3	
Solanum nigrum					✓	✓		12	6	11	
Vigna unguiculata		✓	✓		✓	✓		44	5	3	✓
Xanthosoma sagittifolium								16	5	5	
Zea mays					✓	✓	✓	36	3	9	✓

[a]Measured during the experiment.

[b]Determined from literature.

[c]Measured for all species except for *Cucumeropsis manii* and *Vigna unguiculata* that were determined based on literature.

the two additional treatments considered as controls: bare soil and spontaneous weeds. The bare soil in the corresponding treatment was maintained with herbicides applied every 2 months, to simulate the situation in some farms. The 14 treatments were repeated four times, leading to 56 elementary plots, completely randomized. There were 1.5 m alleys of bare soil between elementary plots. The bare soil of the alleys was maintained with herbicide applications every 2 months. Herbicide application were only done in the plots with the bare soil treatment and on alleys between plots. This may have affected the mobility of ground-dwelling arthropods between elementary plots and few days afterwards. To ensure all elementary plots were in the same conditions, herbicide was also applied on the border of the experimental plot.

2.2 | Arthropod trapping methodology

Arthropods were trapped in September 2016, after the harvest of the first cycle of plantain. The associated crops had been in place for 13 months. The crops with short cycles were replanted to ensure the same crop association during the 13 months. Between two replantations, the soil was prepared by hand tillage.

Flying arthropods were captured with a hand-powered vacuum, sucking an entire associated crop for 2 min. This technique allowed for the capture of arthropods walking on the leaves and stems of associated crops. For each of the 56 elementary plots, one sampling was carried out at dusk and another at dawn.

Crawling arthropods captured pitfall traps composed of circular plastic containers of 15 cm of diameter and 15 cm depth (yellow colour). These pitfalls were filled with 2 cm of soapy water and located in the middle of each elementary plot (56 pitfalls in total), and the edge of the container was placed at the soil level. To ensure a good conservation of arthropods, traps were collected twice, once at dusk and once at dawn (with a maximum time in the trap of 12 h).

Arthropods from vacuum sampling and from pitfalls were analysed together by Thibault Ramage, he is a specialist of tropical arthropods. The taxonomy of each captured arthropod was determined up to the species level for ants, up to the family for other adult arthropods, and up to the order for the juveniles. Five groups were identified only to the class (Acari, Chilopoda, Collembola, Diplopoda and Isopoda). The trophic groups of the captured arthropods were determined by literature.

Cosmopolites sordidus were trapped using pseudostem traps. Each trap was made from two half pieces of a 40-cm-long pseudostem of plantain, located next to a flowering plantain. The pseudostem traps were more suitable for the experimental setup than pheromone traps, which could have attracted *C. sordidus* from a larger radius, potentially even from other elementary plots.

2.3 | Determination of the crops' traits and agricultural practices

Associated crops were described using nine plant traits and two agricultural practices associated with the plant. Agricultural practices were included because they influence the presence and abundance of arthropods (e.g., the presence of crop residues after harvest). All plant traits and agricultural practices values used in the analysis were those observed or measured on each associated crop during the experiment.

Plant traits included:

- *Type of plant tissues* constituted the associated crop. An associated crop was considered "Woody" when it included lignified tissues or

"Herbaceous" when it was only constituted by non-lignified tissues (categorical variable: Woody or Herbaceous). This trait was determined by direct observation of plants.

- *N-fixation capacity*. The capacity of the associated crop to fix atmospheric nitrogen. An associated crop was classified as either leguminous or non-leguminous (categorical variable: Nfix− or Nfix+).
- *Plant architecture*. An associated crop was classified as creeping if it could not stand upright, and as erected if it was standing upright (categorical variable: Creeping or Erected).
- *Plant hairiness*. The characteristics of the surface of the stem of the associated crop. Associated crops were classified either hairy or hairless (categorical variable: Hairy or Hairless).
- *Presence of flowers*. An associated crop was classified as 'flowery' when it reached the flowering stage during the experiment, and as 'non-flowery' when it did not reach the flowering stage (categorical variable: Flowery or Non-flowery).
- *Plant perennity*. An associated crop was classified as annual when it needed to be re-planted after harvest, else it classified as perennials (categorical variable: Annual or Perennial).
- *Plant height*. An associated crops was classified as 'tall' when the maximal height was above 1.5 m or as 'small' when the maximal height was below 1.5 m (categorical variable: Tall or Small).
- *C:N ratio*. The ratio between the carbon and the nitrogen content in the dry biomass of the associated crop (continuous numerical variable). It was obtained by C-N analysis performed in the lab "Unité de service Analyses" (Cirad) (C and N total by Dumas dry combustion).
- *Plant cycle length*. The length of the associated crop cycle from planting to harvest. The hypothesis was that arthropods communities could develop and be more complex when the associated crops have a longer cycle (continuous numerical variable expressed in month: Cycle length).

Agricultural practices associated with the plants included:

- *Number of manual weeding* needed during the 18 months of the experiment (numerical variable). On the elementary plots with associated crops, weeding was done manually. The weeds were removed, but left on the plot, leading to an increase of plants residuals (continuous numerical variable: Weedings).
- *Litter return*. The associated crops were classified as 'litter+' when they had litter that returned to soil during the growth period or after harvest, and as 'litter−' when there was none. Plant residues can constitute habitats and resources for arthropods (categorical variable: 'Litter+' or 'Litter−').

2.4 | Statistical analysis

The first objective of this analysis was to classify the associated crops based on their traits and agricultural practices. A multiple correspondence analysis (MCA) was conducted on the qualitative and quantitative traits and agricultural practices of the associated crops using FactoMineR package of the R software (Lê et al., 2008). The MCA included 12 treatments with associated crops, excluding the bare soil and the spontaneous weed treatments, as they had no trait values by definition. The MCA axes that explained at least 10% of the variance of the associated crop traits and associated agricultural practices were kept for the subsequent analysis.

The effect of the treatments on the arthropod community was analysed using all 14 treatments. The 'lsmeans' (Lenth, 2016) and 'multcomp' (Bretz et al., 2016) packages were used to perform a 'sidak' post-hoc test on a 'poisson' generalized linear models, which was used to compare the effect of the treatments on the abundance of each trophic group.

The second objective of this analysis was to test the response of the abundance of trophic groups and of *C. sordidus* to the associated crops, described by their values on MCA axes as established in the previous step. To conduct a holistic analysis, a structural equation model (SEM) was built (Grace, 2006). The structure of the network analysed was established based on literature and expected effects of plant traits and associated agricultural practices on the abundance of arthropods from different trophic groups, then cascading to *C. sordidus* abundance. Given that all response variables included in this SEM were counting data, the sub-models were exclusively Poisson General Linear Mixed Models (GLMMs). The effect of the treatment repetition was addressed through a random effect on the intercept for all sub-models. The SEM was implemented using the piecewise SEM (version 2.3.0) R-package (Lefcheck, 2016). The piecewiseSEM package allows testing the significance of links within a causal network, solving the network as a whole, thus estimating the direct and indirect effects of predictors on response variables. The equations constituting the SEM are shown in Table 2. This set of equations hypothesizes a bottom-up effect of plant traits on the multi-trophic community of arthropods and a top-down control of *C. sordidus*.

All statistical analyses were performed with R 4.2.2 (R Core Team, 2022) and with a significant threshold of 0.05.

3 | RESULTS

3.1 | Determination of associated crops' traits and agricultural practice axes

Each associated crop was described by a unique profile of traits and agricultural practices (Table 1). There were two woody crops, *Cajanus cajan* and *Manihot esculenta*, all other crops were non-woody. Among the 12 associated crops, four were leguminous plants. Three associated crops were creeping plants while the others were erected. Among the associated crops, *Ananas comosus*, *M. esculenta* and *Glycine max* did not return any litter to the soil. *Ananas comosus* and *M. esculenta* were harvested at the very end of the experiment and the entire crops of *G. max* were harvested. As *Xanthosoma sagittifolium* had slow growth (only few leaves), it

TABLE 2 Set of generalized linear mixed models (GLMMs) constituting the global model based on a priori hypotheses regarding the relationships between trophic group abundances, associated crops traits and agricultural practices and weevil abundance.

Response variable	Explanatory variable	Hypothesized mechanisms
D	PC1 + PC2 + PC3	Effects of crops traits and agricultural practices on detritivores abundance
H	PC1 + PC2 + PC3 + D	Effects of crops traits and agricultural practices and detritivores abundance on herbivore abundance
O	PC1 + PC2 + PC3 + H + D	Effects of crops traits and agricultural practices, detritivores and herbivores abundance on omnivores abundance
P	PC1 + PC2 + PC3 + O + H + D	Effects of crops traits and agricultural practices, omnivores, herbivores and detritivores abundance on predators' abundance
W	PC1 + PC2 + PC3 + P + O + H + D	Effects of crops traits and agricultural practices, omnivores herbivoroues, detritivores and predators' abundance on *Cosmopolites sordidus* abundance

Note: D: detritivores abundance; H: herbivores abundance; O: omnivores abundance; P: predators abundance; PC: crops traits and agricultural practices defined by the three axes of the Mixed Component Analysis; W: *Cosmopolites sordidus* abundance.

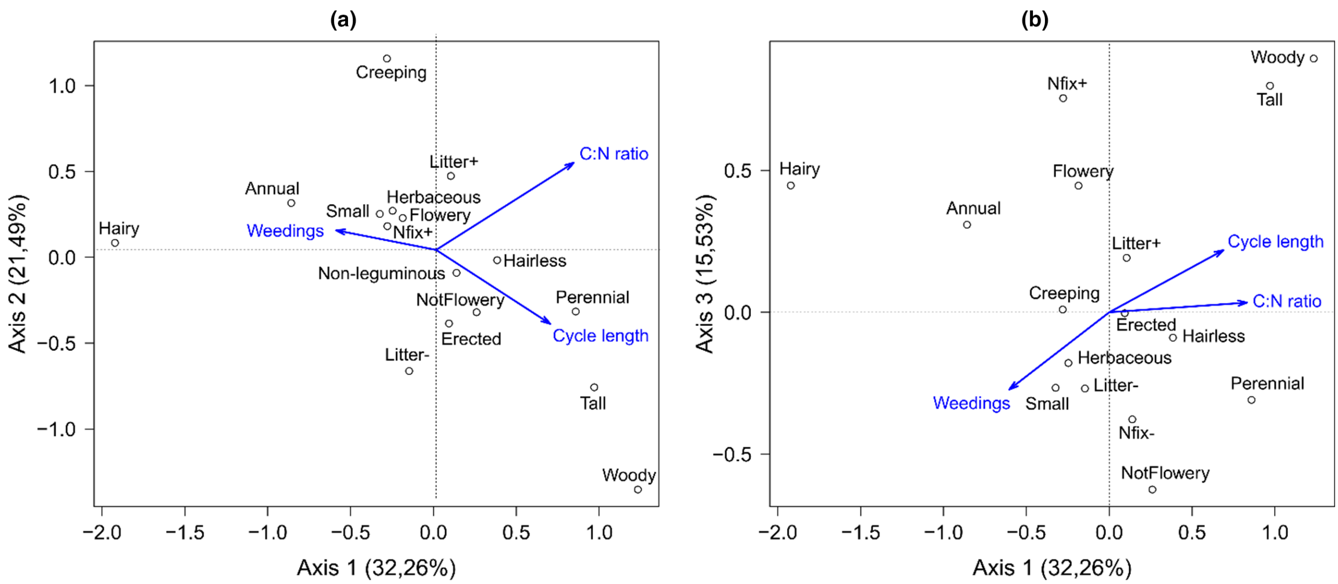

FIGURE 1 The Multiple Correspondence Analysis (MCA) results on the constitution of 3 axes defined by the crops traits and associated agricultural practices (a for axis 1 and 2 and b for axis 1 and 3).

did not produce crop residues during the experiment. All the other associated crops produced significant residues. Three associated crops were significantly higher than the others (above 1.5 m): *C. cajan*, *M. esculenta*, and *Zea mays*. The presence of hairs on the crop was observed for *Cucumeropsis manii* and *G. max*. The C:N varied between 10 and 51. The associated crops were weeded between 1 and 11 times during the experiment. The crops cycle lasted between 3 and 18 months.

Three axes of the MCA were selected, explaining a total of 69.19% of the variability (Figure 1). The first axis explained 32.26% of the variability, the second 21.40% and the third 15.53%. The first axis was positively correlated with the cycle length, the C:N ratio of associated crops, and the presence of lignin in the crops. Conversely, it was negatively correlated with the presence of hairs, the number of weed control, and the fact that it was annual crops (vs. perennial). The second axis was positively correlated with the creeping associated crops, the presence of crop residues, and with higher C:N ratio. It was negatively correlated with the woody characteristic and the cycle length. The third axis was positively correlated with the fact that the crop is leguminous, tall and woody. It was negatively correlated with the number of weed controls and the fact that the associated crop did not produce flowers.

3.2 | Trophic network characterization

In total, 3592 arthropods belonging to 128 taxa were identified. The trophic groups of 154 juveniles could not be identified and were thus excluded from the analysis. The identified groups included 550 detritivores, 1051 herbivores, 1002 omnivores and 835 predators. The Formicidae family included 1112 individuals.

The detritivores were more abundant in bare soil treatment (Figure 2). Very few detritivores were observed in *C. esculenta* (taro crops) and in *A. comosus* (pineapple) treatments. Few herbivores were observed on *A. comosus*, *G. max* (soy bean), *S. nigrum* (black nightshade), and bare soil treatments. The highest abundances of herbivores were observed in *V. unguiculata* (cowpea) treatment. The abundances of arthropods from omnivores and predator trophic groups were usually observed in the same treatments, except for *Z. mays* (corn) that showed a high abundance of omnivores but a low abundance of predators. *Cosmopolites sordidus* were observed in all treatments with more than 20 individuals on average in *A. comosus*, *M. esculenta*, *X. sagitifolium* and on some plots of *C. manii* treatments. Fewer *C. sordidus* were trapped in *V. unguiculata* and *S. nigrum* treatments (creeping crops).

3.3 | The effects of the associated crops on the trophic network

The SEM was built assuming bottom-up relationships from lower to higher trophic groups, except for *C. sordidus*. For all trophic groups as *C. sordidus*, all possible interactions with plant traits and agricultural practices and the abundance of all other arthropod groups were tested. This approach resulted in a global model composed of five linear sub-models linking the three axes representing the plant traits and agricultural practices, the four trophic groups, and the weevil abundance (Table 2 and Figure 3).

The characteristic of associated crops described by the first axis of the MCA (PC1) was significantly correlated with the abundance of all trophic groups (Table 3). PC1 was negatively correlated with the abundance of arthropods from predator and omnivore trophic groups. Conversely, PC1 was positively correlated with the abundance of herbivores and *C. sordidus*. The characteristic of associated crops described by the second axis of the MCA (PC2) was strongly positively correlated with the omnivore trophic group and more lightly correlated with the predator and herbivore trophic groups. PC2 was negatively correlated with the abundance of *C. sordidus*. The characteristic of associated crops described by the third axis of the MCA (PC3) was positively correlated with the detritivore trophic group and slightly positively correlated with the herbivore trophic group. The abundance of *C. sordidus* was strongly and negatively correlated with PC3, while it was moderately positively correlated with PC1.

Within the trophic network, the abundance of predators increased with the abundance of herbivores and omnivores. Finally, the abundance of *C. sordidus* was only slightly positively correlated with the abundance of omnivores, while it was not significantly correlated with any other trophic groups.

4 | DISCUSSION

4.1 | Effects of the associated crops traits and agricultural practices on the trophic network

There was a positive relationship between PC1 and *C. sordidus* abundance, through a direct positive effect on *C. sordidus* and an indirect negative effect on omnivore's abundance. A positive value of

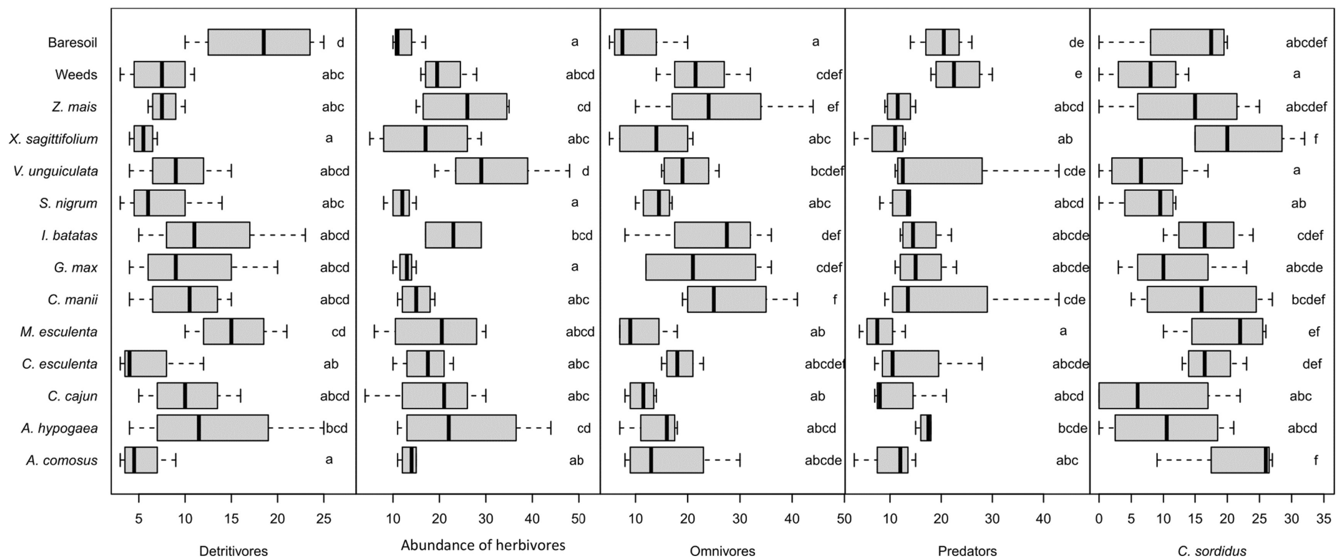

FIGURE 2 Abundance of arthropods captured for each trophic group and for each associated crop in the 56 elementary plots of the experiment. Letters on the right of each boxplots show the result of the 'sidak' post-hoc test achieved on 'poisson' generalized linear models used to compare the effect of the associated crop on the abundance of each trophic group.

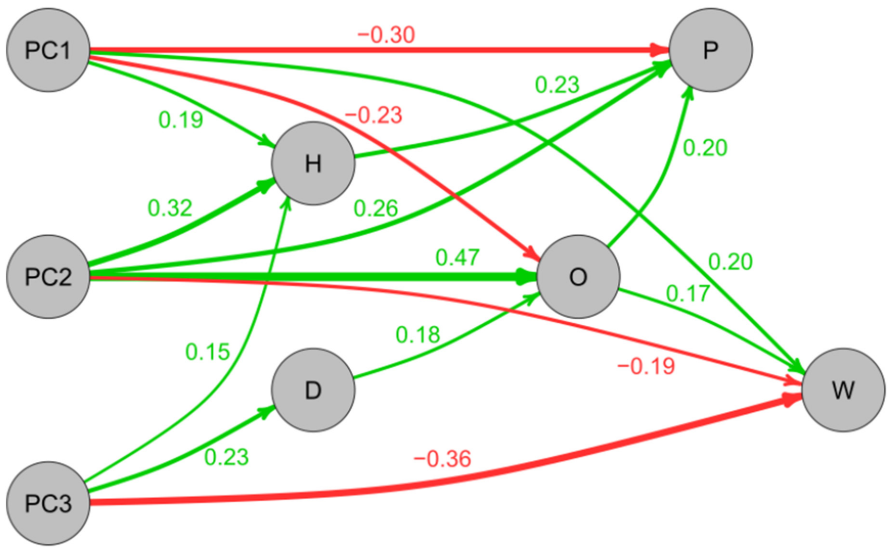

FIGURE 3 Significant ($p > 0.05$) links among the cascading effects of the associated crop traits and agricultural practices on the abundance of arthropods and weevil in plantain plots as tested in the piecewise SEM (non-significant links are not presented). With D: detritivores abundance; H: herbivores abundance; O: omnivores abundance; P: predators abundance; PC: crops traits and agricultural practices defined by the three axes of the Mixed Component Analysis; W: *Cosmopolites sordidus* abundance. Green arrows: positively correlated effect; red arrows: negatively correlated effect. The thicker an arrow, the bigger the effect. Numbers next to each arrow indicates its standardized coefficient as estimated in the SEM (all coefficients are presented in Table 3).

TABLE 3 Pathway coefficient estimates from the structural equation modelling (p-value of the Fisher's $C = 0.304$).

Response	Predictor	Estimate	Std.Error	*p* Value	Std.Estimate
P	PC1	−0.1274	0.0354	3.00E-04	−0.3011***
P	PC2	0.1336	0.0497	0.0072	0.2571**
P	PC3	0.0151	0.0518	0.7701	0.0248
P	D	0.0059	0.0077	0.4444	0.0681
P	H	0.0125	0.0045	0.0053	0.2294**
P	O	0.0111	0.0048	0.0217	0.2032*
O	PC1	−0.0949	0.0298	0.0015	−0.2272**
O	PC2	0.2385	0.0399	0	0.4652***
O	PC3	−0.0286	0.0451	0.5259	−0.0475
O	D	0.0153	0.0066	0.0214	0.1793*
O	H	−0.0026	0.0043	0.5501	−0.0475
H	PC1	0.0745	0.0287	0.0094	0.1919**
H	PC2	0.1503	0.0336	0	0.3152***
H	PC3	0.0852	0.0399	0.0329	0.1521*
D	PC1	−0.0208	0.0393	0.5958	−0.0544
D	PC2	−0.0736	0.0491	0.1342	−0.1564
D	PC3	0.1285	0.0571	0.0244	0.2326*
W	PC1	0.1048	0.0358	0.0034	0.2019**
W	PC2	−0.1222	0.0463	0.0083	−0.1918**
W	PC3	−0.2728	0.0475	0	−0.3649***
W	O	0.0116	0.0047	0.0132	0.1736*
W	P	−0.0053	0.0062	0.3887	−0.0691

Note: D: detritivore; H: herbivore; O: omnivores; P: predator; PC1, PC2 and PC3: crops traits and agricultural practices defined by the three axes of the Mixed Component Analysis; W: *Cosmopolites sordidus*.

*p-value <0.05, **p-value <0.001, ***p-value <0.0001.

PC1 corresponds to tall perennial crops with long cycle. It is consistent with the results obtained in a previous study (Poeydebat et al., 2017) that showed that plants from the higher strata tend to decrease ground-dwelling predators. Furthermore, *C. sordidus*, a nocturnal species, could be favoured by shade from higher plant species. Similar behaviour was showed in coffee plantations for *Exophthalmus jekelianus*, another weevil from the Curculionidae family (Henderson & Roitberg, 2006).

There was a strong positive relationship between PC2 and the abundance of the omnivore trophic group, which was mainly composed by species from the Formicidae family. A positive value of PC2 corresponds to creeping associated crops with a high C:N ratio and with litter returns to soil. There was also a negative relationship between PC2 and *C. sordidus* abundance. This is consistent with previous studies that showed that ants can be direct predators of *C. sordidus* (Abera-Kalibata et al., 2007, 2008). There was also a positive relationship between PC2 and the abundance of predators. In our case, a higher C:N ratio (meaning lower N content) did not reduce predators as often suggested (Fallahpour et al., 2020). Our result shows that an associated crop characteristic cannot be considered separately in our study and that the interactions between the different traits and agricultural practices are complex. The effects of the nitrogen rate in the associated crops on arthropods could be balanced by other plant traits or cultivation techniques.

There was a strong negative relationship between PC3 and the abundance of *C. sordidus*. A positive PC3 corresponds to woody, tall, leguminous crops that flowered during the experiment and that produced crop residues. One possible explanation for the observed negative effect of PC3 on *C. sordidus* is that taller plants may impede the insect's semiochemical perception, potentially by altering air flow within the plot and reducing its ability to locate plantains. While PC3 had little explanatory power for the abundance of most trophic groups, a positive relationship was observed for detritivores and herbivores. This may be attributed to the fact that plants with positive PC3 values produce litter and are woody, providing favourable resources for detritivores, which is consistent with the study of Poeydebat et al. (2017). To assess stability of the interaction between plant traits and arthropod's community over the year, it would be interesting in future studies to do more sampling, especially during the dry season.

4.2 | Interest in characterizing plants by combination of traits and agricultural practices to unravel their effect on trophic networks

Our study by plant traits and agricultural practices, rather than by plant identity, aimed at establishing some generic rules that link plant effects on arthropod community and on pest regulation. Functional traits of plants are now commonly used to understand the performance of a given plant community in terms of growth, reproduction and survival (Violle et al., 2007). It was successfully used in banana agroecosystems to assess the services provided by cover plants in banana cropping systems (Damour et al., 2015).

The highest abundance of *C. sordidus* was observed for treatments with *A. comosus* and *X. sagittifolium*. These plots also had the lowest abundance of omnivores and predators, suggesting that these crops may dampen trophic control of *C. sordidus*. In contrast, plots with the lowest abundance of *C. sordidus* were those with weeds and *V. unguiculata*, where more omnivores and predators were observed. These plants are characterized by their high soil coverage, which is consistent with previous studies showing that cover crops increase omnivores and predators abundance by providing prey (Duyck et al., 2011) and suitable habitats (Dassou et al., 2016).

Omnivores, primarily represented by the family Formicidae, were less abundant on bare soil, *X. sagittifolium*, *M. esculenta* and *C. cajun* treatments. *Xanthosoma sagittifolium* was replanted several times due to poor growth, and previous studies have shown that planting perturbations can reduce ant abundance (Diaz, 1991; Folgarait, 1998). *Manihot esculenta* and *C. cajun* were the two tallest perennial associated crops studied, and their shade probably inhibited weed growth, resulting in low plant diversity on these plots. This is consistent with findings that low plant diversity is correlated with low ant diversity (Perfecto & Snelling, 1995). In our study, the trophic group of omnivores played a pivotal role in the food web, with significant connections to plant levels (PC1 and PC2), to detritivores and predators, respectively, at the bottom and the top of the food web, and finally to *C. sordidus*.

The highest abundance of herbivores was observed in *V. unguiculata* plots, potentially due to its robust growth, its high herbaceous biomass production, and the presence of flowers. This is consistent with previous findings that high biomass production in vine crops attracts more herbivores (Hough-Goldstein & LaCoss, 2012). In line with the results of Singh and Singh (2014), there was a positive correlation between the presence of herbivores and predators in *V. unguiculata*. Plots covered with weeds had the highest abundance of predators, confirming Dassou et al. (2016) finding that predator abundance is positively correlated with plant diversity on a plot.

Detritivores were more abundant on bare soil than on any other associated crop, potentially due to the presence of weed residues from herbicide application. This also shows the effect of herbicide application on the arthropod's community. *Ananas comosus* attracted few detritivores and herbivores, possibly due to compounds that affect arthropods, similarly to the bromelain that is known to participate to the regulating of pathogens (Lopez-Garcia et al., 2012; Salampessy et al., 2010). The low abundance of detritivores on *X. sagittifolium* may be attributed to its poor growth and low biomass production during the experiment.

4.3 | Consequences on the associated crops choice in plantain-based cropping systems

As shown in our study, regulating *C. sordidus* using associated crops is complex, as many antagonistic relationships are possibly at play. For instance, PC1 directly disfavours predators but indirectly favours them by favouring herbivores. Further research could focus on species identity, as the top-down effect of a trophic group is not the only determinant of community structure (Romero & Srivastava, 2010).

To facilitate field application of our results, it would be interesting to focus on the direct effects of associated crop traits and agricultural practices on *C. sordidus* abundance to identify a combination of associated crops corresponding to PC3. The ideal crop traits and agricultural practices to maximize the regulation of *C. sordidus* should not be obtained by a single species of crop but rather by a community of associated crops. Further experimentations with a mix of associated crops are still needed. Been a bit speculative, our results suggest that a better community of plant should have low PC1 and high PC2 and PC3. A first suggestion would be to optimize PC3 with tall, woody, leguminous plants (e.g. *C. cajun*), while PC2 and PC1 will be maximal and minimal, respectively, with creeping, herbaceous, hairy plants that produce litter (e.g. *C. manii*). Given the importance of plant diversity, it may be beneficial to include natural weeds in sustainable cropping systems, potentially in mechanically controlled strips to limit competition with other cultivated crops. One limitation of our study lies in the fact that plots were relatively small (12 × 10 m). In the future, it would be interesting to test the most promising assemblages of plants intercropped with plantains on a larger scale.

Grouping associated crops by their traits and agricultural practices allowed drawing conclusions on a wider range of plants than the one tested. This method could help in selecting beneficial crop mixes to associate with plantain for agroecological production from a large panel of options. This trait-based approach, already recognized through the work of Garcia et al. (2019), has been expanded here to include agricultural practices. It also provides a simplified method for studying interactions between a plant or group of mixed plants and the trophic network.

5 | CONCLUSION

This study has demonstrated that the 12 crops typically associated with plantain in Cameroon significantly influence both the arthropod trophic network and the abundance of *C. sordidus*. To extrapolate conclusions applicable to a broader range of associated crops, this study strategically employed the traits and associated agricultural practices as descriptors of their impact on the arthropod community. It was discovered that a specific combination of plant traits and agricultural practices could contribute to the regulation of *C. sordidus*. Based on these findings, it is recommended to maintain a diversity of plants in plantain fields. For instance, a mix that favours the regulation of *C. sordidus* could include tall, woody, leguminous plants (e.g., *C. cajun*) in combination with creeping, herbaceous, hairy plants that produce litter (e.g., *C. manii*). Overall, our study underscores the importance of adopting a holistic approach to decipher the role of the plant community on the multi-trophic community of arthropods and on pest regulation.

AUTHOR CONTRIBUTIONS

Pauline Pugeaux: Conceptualization; investigation; data curation; formal analysis; writing – original draft; writing – review and editing. **Sylvain Dépigny:** Conceptualization; writing – review and editing. **Dominique Carval:** Conceptualization; writing – review and editing. **Gabriel Fansi:** Investigation; data curation. **Philippe Tixier:** Conceptualization; writing – original draft; formal analysis; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that supported the findings of this study are available at https://dataverse.cirad.fr/dataset.xhtml?persistentId=doi:10.18167/DVN1/VFV9O5.

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